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Ontogenetic niche partitioning in a facultatively anadromous salmonid: Implications for population dynamics☆

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ABSTRACT

Species management and conservation efforts are often based on range-wide trends, assuming dynamic equilibrium across space and time, even though fine-scale variability may be driving local dynamics. *Oncorhynchus mykiss* is a globally introduced, facultatively anadromous salmonid that is experiencing demographic shifts characterized by greater proportions of population remaining in freshwater. The degree of niche overlap between age classes of *O. mykiss* in freshwater environments may dictate how resources are partitioned within populations. We conducted a meta-analysis of age-specific *O. mykiss* habitat use to evaluate the degree of niche-partitioning between age classes and how age-specific habitat use relates to global in-stream and landscape level habitat variation. *O. mykiss* used deeper habitats as they grew towards maturity but did not partition habitat based on water velocity or substrate composition. As annual precipitation increased, *O. mykiss* used deeper and shallower habitats, and as summer air temperature increased, *O. mykiss* used shallower habitats. *O. mykiss* of native origin used deeper habitats than nonnative *O. mykiss*. However, a large proportion (42–99%) of variation in habitat use was associated with study or ecoregion, making climactic predictors unreliable for predictive species distribution or population dynamics models. Although the exact mechanisms driving geographic variability in *O. mykiss* habitat use are not fully understood, our results boost our understanding of how demographic shifts affect population resilience under climate change. Further research incorporating individual competitive behavior in predictive population models may elucidate the links between resource availability, demographic rates, and long-term *O. mykiss* population stability.

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1. Introduction

Niche breadth refers to the range of a species', population's, or individual's niche, including habitat use, diet, and environmental tolerance (Sexton et al., 2017). It is widely hypothesized that there is a positive relationship between a species' niche breadth and its geographic range (Pyron, 1999, Slatyer et al., 2013). Although a species' designation as a generalist or specialist varies by spatial scale, generalist species are more likely to have broader geographic ranges (Slatyer et al., 2013). However, within those broad geographic ranges, a species may occupy different niches or exhibit varying life-histories given a variety of factors such environmental conditions, resource availability, biotic interactions, and population dynamics (Ingram et al., 2018, Martin et al., 2020). Species with broad geographic ranges may therefore vary in their management and conservation needs depending on how niche breadth is influenced by localized environmental factors, population dynamics, and species interactions (Martin et al., 2020).

Intraspecific competition is one way population dynamics may be affected by variation in niche breadth (de Roos et al., 2002, Svanbäck and Bolnick, 2007, Parent et al., 2014). Organisms with size structured populations that do not undergo drastic changes in habitat use due to, for example, metamorphosis, may still exhibit ontogenetic niche shifts associated with size (Ebenman, 1987; de Roos et al., 2002). Niche shifts associated with size in these species may include shifts in diet (ex. ability to ingest larger prey), accessible or preferred cover, behavior (ex. schooling vs. territoriality in fish), or mobility and activity levels (Werner and Gilliam, 1984). The degree of niche overlap or separation between size or age classes may determine the type and severity of intraspecific competition that arises and the degree to which intraspecific competition regulates population dynamics where resources are limiting (Ebenman, 1987; de Roos et al., 2002). Most of the literature on density-dependent competition in size structured populations has focused on competition within age or size classes, which typically leads to reduced juvenile survival or reduced reproductive rates (Ebenman, 1987; Cushing and Li, 1992). Less emphasis has been placed on competition across age or size classes, which often leads to a reduction in juvenile growth rates and smaller size at maturity (Cushing and Li, 1992; Cantin and Post, 2018). For example, when resource requirements are shared across size classes and larger individuals have a competitive advantage, shifts in population dynamics that lead to more larger individuals may reduce the resources available for smaller individuals and create cycles or bottlenecks in population dynamics (Ebenman, 1987; Cantin and Post, 2018).

Oncorhynchus mykiss, commonly known as rainbow trout (freshwater resident) or steelhead trout (anadromous), has a complex life history and populations vary greatly regarding size structure, migratory strategy, and phenotypic diversity (Quinn, 2005; Kendall et al., 2015). *O. mykiss* has the widest native range of any Pacific salmonid species, which extends from northern Mexico up through Alaska and across the Bering Strait to northeastern Russia (Thompson et al., 2012; McPhee et al., 2014). *O. mykiss*, being a popular food and game fish, has also been introduced globally and have established many successful populations in regions such as eastern North America, western Europe, east Asia, and Patagonia (Crimmon 1971, Scott et al., 1978, Pascual et al., 2001). This broad range encompasses a vast gradient of climate conditions and habitat types including desert, grassland, forest, and alpine environments (Thompson et al., 2012; McPhee et al., 2014). Within these broad ecoregions, *O. mykiss* experience finer scale environmental heterogeneity within and among individual watersheds (McPhee et al., 2014). Although a generalist at broad scales relative to other salmonids, *O. mykiss* are thermally limited and require cold, highly oxygenated water, restricting their ability to exploit available habitat within watersheds (Ebersole et al., 2001; Boughton et al., 2009). Within thermally tolerable environments, *O. mykiss* also require the presence of coarse substrate for spawning, refugia from predators and competitors, and nutrient rich invertebrate prey (Ebersole, 2001; Boughton et al., 2009). These habitat features may be limiting for specific age or size classes, leading to intraspecific competition and negative density dependence.

O. mykiss exhibit a high degree of phenotypic plasticity throughout their life cycle in response to environmental variation (Quinn, 2005; Kendall et al., 2015). This phenotypic plasticity manifests as anadromy or residency (rearing and maturation in freshwater) at the extremes, with up to 35 unique life-history variants in between (Thorpe, 2007; Moore et al., 2014; Hodge et al., 2016). *O. mykiss* typically emerge as fry in the spring and select a migratory pathway after 0–4 years of freshwater rearing (Kendall et al., 2015). Fish who migrate to the ocean then spend 1–3 years rearing before returning to spawn in freshwater, typically homing to the same tributary of origin but occasionally straying (Quinn, 2005; Kendall et al., 2015). Fish who mature in freshwater are able to spawn the following winter and are more likely to be iteroparous (Kendall et al., 2015). Anadromous and resident adults frequently interbreed, and anadromous parents can produce resident offspring, and vice versa (Kendall et al., 2015). Other variations in life history include age at maturity, time spent rearing in freshwater/marine, and run timing (winter and summer runs). It is suspected that O. mykiss adopt these different life-history pathways to maximize their fitness under the varying conditions provided by freshwater and marine environments. (Satterthwaite et al., 2010; Kendall et al., 2015; Dobos et al., 2020). Life-history trajectory is likely a genetically coded threshold trait, where size, growth rate, and body condition interact with phenological cues in the environment to trigger either smolting or maturation (Kendall et al., 2015).

Historically, most native *O. mykiss* populations expressed both life-history forms where there was access to the ocean, meaning a portion of adults would leave the system prior to the summer months, which often present the most limiting growth conditions for rearing juveniles (Danehy et al., 2017; Myrvold and Kennedy, 2018; Kelson and Carlson, 2019). However, the creation of man-made barriers to migration as well as global introductions have led to the prevalence of landlocked rainbow trout populations where all adults remain in the freshwater system year-round (Lindley et al., 2006; Winans et al., 2018). It is also speculated that climate change and watershed alteration have created conditions that reduce the fitness benefits of anadromy relative to residency and lead to more *O. mykiss* maturing in freshwater, a trend that is suspected to intensify over time (Satterthwaite et al., 2010; Benjamin et al., 2013; Savvaitova et al., 2020). *O. mykiss* are aggressively competitive relative to other Pacific salmonids—the frequency and intensity of intraspecific agonistic behavior is positively associated with fish density, and larger fish generally have a competitive advantage when it comes to securing higher quality territories and food resources (Hartman, 1965; Abbott and Dill, 1985; Gross, 1985, Keeley, 2001).

Table 1
Summary of predictor variables hypothesized to influence *O. mykiss* habitat selection.

Parameter	Type	Definition/unit	Reference
Age	Categorical	Young of year, fry, age 0, subyearling Juvenile, age 1-3, yearling Adult, age 4 +	
Ecoregion	Categorical	EPA level 1 ecoregion, World Wildlife Fund ecoregion	Olson et al. (2001), Omernik et al. 2014
Region	Categorical	Geographic location	
Stream name	Categorical	Name of sampled stream	
Basin size	Continuous	km^2	
Basin forest cover	Continuous	%	
Basin slope	Continuous	%	
Minimum watershed elevation	Continuous	m	
Mean annual precipitation	Continuous	cm	
Mean summer maximum temperature	Continuous	C	
Nativeness	Logical	Are *O. mykiss* native to the study site? (1 = Yes, 0 = No)	
Ocean access	Logical	Do *O.mykiss* in the study site have access to the ocean? (i.e. not landlocked by natural or artificial barrier; 1 = Yes, 0 = No)	
Congeners	Logical	Are other *Oncorhynchus* native to the study site? (1 = Yes, 0 = No)	
Summer	Logical	Was this study conducted during the summer months? (1 = Yes, 0 = No)	
Habitat variable	Categorical	Total depth (cm) Focal water velocity (cm/s) Mid-column water velocity (cm/s) Focal elevation (cm) Substrate (Modified Wentworth classification) 1 = plant detritus, 2 = silt, 3 = sand, 4 = gravel (2-15 mm), 5 = pebble (16-63 mm), 6 = cobble (64-256 mm), 7 = boulder (>256 mm), 8 = bedrock Distance to cover (cm)	Wentworth (1922) Cummins (1962)
Habitat variable value + SD/SE	Continuous	Mean value	
Available habitat value + SD/SE	Continuous	Mean value	
Sample size	Continuous	*n*	

More resident adults remaining in the system year-round than typical under historic conditions may negatively affect rearing habitat availability if quality habitat is limiting by reducing the per capita resources available torearing juveniles, thus influencing the growth rates and life-history trajectories of individuals in younger cohorts (Keeley, 2001, Satterthwaite et al., 2010). If a higher proportion of larger *O. mykiss* defend limited space during the summer months, it is possible that a resulting increase in densities of smaller fish in relatively lower quality habitat may lead to slower growth rates and higher mortality associated with starvation, predation, and disease (Keeley, 2001, Cantin and Post, 2018). Reductions in growth rate or body condition may subsequently reduce opportunities for juvenile *O. mykiss* to reach developmental thresholds required for smolting, causing difficult to predict feedback loops in the population size structure (Satterthwaite et al., 2010; Cantin and Post, 2018). Although density dependent interactions among juvenile *O. mykiss* have been heavily studied (Keeley, 2001; Myrvold and Kennedy, 2018; Dobos et al., 2020), there is a dearth of information regarding density dependent interactions among *O. mykiss* of different ages and no investigation into how these interactions influence habitat use, population stability, or life-history trajectories. It is critical to understand the nuances governing how changes in habitat availability will be partitioned amongst river-dwelling age/size classes to predict population-level responses to habitat management (Keeley, 2001, Robinson et al., 2017).

Species distribution models (SDM) are widely used to predict demographic responses to environmental change and make habitat restoration decisions (Elith and Leathwick, 2009, Lee-Yaw et al., 2022). A key assumption of SDMs and habitat restoration is the habitat matching rule, which states that an individual's use of a habitat patch is directly associated with its quality (Van Horn 1983, Cassini 2011). SDMs, however, largely fail to incorporate various forms of competition or other biotic interactions that influence the habitat use decisions of individuals (Cassini 2011, Lee-Yaw et al., 2022). The first step in understanding whether a species or life-history type will benefit from increasing or manipulating habitat is to understand how that habitat is partitioned between individuals, and how habitat partitioning varies across environmental gradients (Tregenza, 1995, Cassini 2011). The objective of this study is to assess how ontogenetic shifts in the niche breadth of *O. mykiss* vary along environmental and geographic gradients. To do this, we synthesized available literature on age-specific habitat use of *O. mykiss* across the species' native and introduced (nonnative) range to understand sources of variation in niche partitioning across young of year (YOY), juvenile, and adult age classes.

2. Methods

2.1. Data compilation

We conducted a meta-analysis following the suggestions of Thorson et al. (2015). We searched Google Scholar and Web of Science for peer-reviewed research articles that pertained to age-specific habitat use in *O. mykiss*. We did not limit our search by publication year. We used the following character string to search the published literature:

(Oncorhynchus mykiss OR Salmo gairdneri OR steelhead trout OR rainbow trout OR redband trout) AND (habitat OR habitat requirements OR habitat suitability OR resource selection OR velocity OR depth OR temperature) AND (age OR fry OR subyearling OR age 0 OR young of year OR juvenile OR yearling OR age 1 OR adult OR age 3).

We initially selected articles that 1) presented original research results (i.e., not a review, editorial, or book chapter), 2) specifically targeted *O. mykiss* (i.e., not other salmonids), 3) were spatially and temporally explicit, 4) were field studies (i.e., not a laboratory experiment or hatchery study), and 5) addressed age-specific habitat use. We limited our search to the first 15 pages of results. If a study was suspected to be relevant based on the title, it was downloaded for further scrutiny. We then inspected the abstracts of all downloaded papers to verify they addressed habitat use quantitatively for one of the following six habitat use variables: total depth (cm), mean column water velocity (cm/s), focal water velocity (cm/s), distance to cover (cm), focal elevation (cm), and substrate (modified Wentworth classification; Cummins, 1962; Table 1). If the quantitative requirement was met, a study was classified as a 'suitable paper'. For each suitable paper, we searched for and extracted the following for each habitat feature where use was reported: season (spring, summer, fall, and/or winter), geographic region, ecoregion, watershed, stream name, drainage area (km^2), mean basin slope (%), mean annual precipitation (cm), basin forest cover (%), mean summer high temperature (C°), minimum basin elevation (m), whether *O. mykiss* were native to the study area, whether *O. mykiss* had access to the ocean or were landlocked, whether there were other *Oncorhynchus* sp. in the study site, fish age, mean used value + standard deviation (SD)/standard error (SE) of the habitat feature, mean available value + SD or SE of the habitat feature, and sample size (n; Table 1). As size-at-age is highly variable across the *O. mykiss* range and dependent on local growth conditions, we only recorded the age class defined in each study and did not attempt to classify fish by size; furthermore, we only included studies that explicitly stated an age class. If substrate was not reported using the modified Wentworth classification, which assigns a single value to a range of substrate sizes, we assigned it to the closest substrate class (Wentworth, 1922; Cummins, 1962; Table 1). We categorized regions in North America based on the Environmental Protection Agency (EPA) level 1 ecoregions (Omernik et al., 2014). For data from outside North America, we used the World Wildlife Fund world ecoregions and categorized them with the most similar EPA ecoregion (i.e., studies in Hokkaido, Japan were classified as "Marine west coast forest"; Olson et al., 2001). To retain papers that pooled age classes in their analyses due to non-significant differences, the reported values were assigned to each age independently. For spatial variables not listed in the article, we derived those variables from publicly available data (Gray 2022, Okada, 2017, U.S. Geological Survey, 2016, Zanaga et al., 2022). Importantly, the parameters reported in the literature are highly variable and there is a significant amount of missing data regarding sample size, precision, and accuracy. We used SD as our primary measure of variance. If SE and n were provided, we converted SE to SD. To retain studies that did not report sample sizes, the coefficient of variation (CV) was calculated for studies that report mean and SD (or mean and SE + n), and averaged across studies (Conroy and Peterson, 2013). The average CV was then used to estimate the SD for studies where either SD, SE, or sample size were not reported.

2.2. Analysis

2.2.1. Niche overlap

To evaluate the degree of niche overlap across age classes, we computed standardized mean differences (SMD; Harrison, 2011) in habitat use between age groups (YOY vs juvenile, juvenile vs. adult, YOY vs. adult) using the 'escalc' function in the R package 'metafor' (Viechtbauer, 2010). Specifically, the SMD is calculated as:

$$SMD = (m_1 - m_2)/sdpi$$

$$sdpi = \sqrt{\frac{(n_1 - 1)sd_1{}^2 + (n_2 - 1)sd_2{}^2}{n_1 + n_2 - 2}}$$

Where m_1 and m_2 refer to the mean of each group, n_1 and n_2 refer to the size of each group, sd_1 and sd_2 refer to the standard deviation of each group, and *sdpi* refers to the pooled standard deviation of the two groups. We considered the SMD statistically significant if the absolute value of the estimate was ≥ 0.5 (Andrade, 2020) and the 95% confidence intervals did not overlap zero. A large SMD meant there was little overlap in habitat use between ages. We conducted all analyses in program R version 4.1.0 (R Development Core Team, 2021).

2.2.2. Mixed effect models

Prior to model fitting, we visually inspected the data and screened continuous predictor variables for collinearity. We assumed a correlation between pairs of predictor variables was potentially problematic when the Pearson's correlation coefficient ($|r|$) was ≥ 0.7 and we did not include those parameters in the same model (Akaike, 1973; Moore and McCabe, 1989). To improve model convergence and facilitate comparison of parameter estimates, we centered and scaled all continuous predictor variables to a mean of zero and

Table 2
Means, standard deviations (SD), and number of data points for each habitat variable and age class included in the final analysis.

Habitatvariable	Ageclass																			
	Young of year					Juvenile					Adult					Pooled				
	Mean	SD	Min	Max	N	Mean	SD	Min	Max	N	Mean	SD	Min	Max	N	Mean	SD	Min	Max	N
Focal point velocity (cm/s)	11.15	9.38	0.00	31.80	35	13.78	12.82	0.30	50.00	38	14.79	12.46	0.40	55.00	23	13.06	11.56	0.00	55.00	96
Total column depth (cm)	28.06	14.23	5.75	59.70	20	48.74	24.85	5.75	123.50	33	67.89	33.86	30.10	171.00	38	44.31	28.05	5.75	171.00	91
Substrate size class (modified Wentworth)	5.78	0.80	3.90	7.00	7	5.24	1.43	2.30	7.20	15	5.37	2.24	0.16	7.30	9	5.49	1.43	0.16	7.30	41
Distance to cover (cm)	35.33	30.95	9.00	1.60	9	29.07	27.27	10.00	0.74	10	21.85	24.79	8.00	0.74	8	29.02	27.33	0.74	104.00	27
Focal elevation (cm)	35.33	30.95	1.80	23.00	7	29.07	27.27	3.00	30.00	15	21.85	24.79	6.10	47.50	12	14.77	9.65	1.80	47.50	34

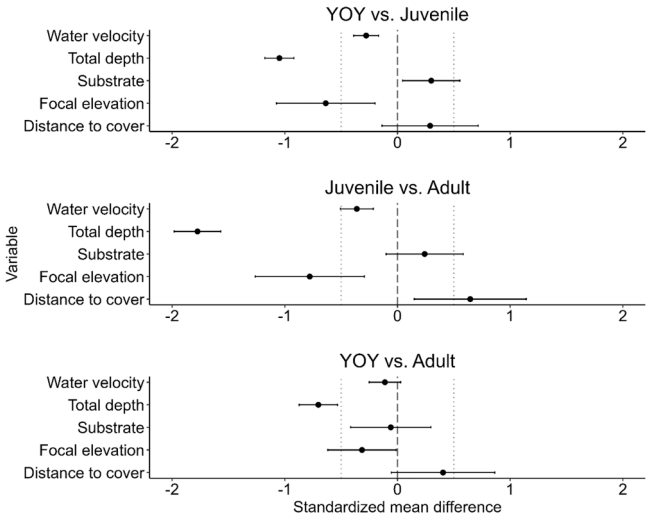

Fig. 1. Pairwise comparisons of habitat use overlap between *O. mykiss* age classes (Young of year (YOY), juveniles, and adults) using standardized mean difference (SMD) or Hedge's g. The SMD is significant if the estimated effect size is $\geq |0.5|$ and the 95% confidence interval does not include zero. The dashed line represents zero and the dotted lines represent the significance threshold ($\pm$ 0.5).

standard deviation of one.

The mean used habitat values presented in each study served as the response variable in all models. The meta-data were weighted based on the inverse of the variance of the used habitat value reported or calculated for each study to incorporate the precision of each value into our final estimates (Lajeunesse, 2010). For each habitat variable (total depth, water velocity, substrate, distance to cover, and focal elevation), we defined separate sets of a priori models composed of subsets of covariates (Table 1; Appendix A). Each model represented alternative hypotheses regarding drivers of variation in age-specific habitat use, such as but not limited to thermal tolerance, primary productivity, or the evolutionary history of the population (Appendix A). We also compared the a priori models to global models of all non-correlated variables and null (intercept only) models (Arnold, 2010; Appendix A). Age was included in all models as it was the primary relationship of interest relative to all other parameters, with juveniles as the reference category. For each continuous predictor variable, we determined whether it should be included in the model set as a linear or quadratic relationship by selecting the parameterization with the lowest Akaike's Information Criterion adjusted for small sample sizes (AICc; Hurvich and Tsai, 1989).

We used the R package 'lme4' to run all mixed-effect models (Bates et al., 2015). We first ran a random effects analysis of variance on global models for each habitat variable comprised of all uncorrelated covariates to partition variation within and among ecoregions and studies and quantified their relative contribution to the total meta-data variation using intraclass correlation coefficients (ICC; Nakagawa et al., 2017). We then included the best-supported random effect structure in the candidate models for each habitat variable.

We used AICc to rank the candidate models and calculated Akaike weights (following Burnham and Anderson, 2002) to evaluate the relative strength of support for the models in the candidate set using the R package 'MuMIn' (Barton, 2013). We considered any model with an Akaike weight that fell within 1/8 of the top model weight to be within the supported set (Royall, 1997). Where there was model selection uncertainty (i.e., multiple models in the supported set), we inspected the individual parameters of the models in the supported set. Following Arnold (2010), we considered a parameter uninformative if the effect size was biologically insignificant and if the 85% confidence interval widely overlapped zero. We interpreted the biological significance of an effect based on the magnitude and precision of the effect relative to the distribution of values of the predictor variable. If multiple models in the supported set contained informative parameters, we report the results of each model (Arnold, 2010). We then used the R package 'merTools' to obtain age-specific habitat use predictions and associated 85% confidence intervals across the range of informative parameters (Knowles et al., 2023). Using this package, we were able to include all uncertainty in the model in our predictions by drawing fitted values from sampling distributions of the fixed and random parameter estimates.

2.2.3. *Relative probability of use*

We also generated probability distribution functions (PDF) based on predicted values at mean covariate values for each age class of *O. mykiss* to estimate the relative probability an individual would use a habitat patch given depth, velocity, and substrate values. We normalized the PDFs so the habitat features with the highest relative probability of use would receive a probability of use = 1. We considered a habitat likely to be used if the probability of use was $\geq$ 0.5 and highly likely to be used if the probability of use was $\geq$ 0.75.

Table 3
Parameter estimates of top-ranked model or averaged model set for each habitat variable (depth, water velocity, substrate).

Habitat variable	Model	Parameter	Mean	Std. Error	Lower 85% CI	Upper 85% CI
Depth (cm)	Age + Precipitation^2	Intercept: Juvenile	52.00	7.26	41.54	62.45
		Age: YOY	-11.02	2.26	-14.27	-7.76
		Age: Adult	6.75	2.75	2.79	10.71
		Precipitation	7.34	4.64	0.66	14.03
		Precipitation^2	-2.88	1.25	-4.68	-1.08
	Age + Native	Intercept: Juvenile, Nonnative	38.95	8.54	26.65	51.25
		Age: YOY	-11.16	2.27	-14.42	-7.89
		Age: Adult	6.9	2.75	2.94	10.87
		Native: Yes	13.99	9.78	-0.09	28.06
Velocity (cm/s)	Age + Precipitation + Summer temp	Intercept: Juvenile	15.42	2.00	12.54	18.31
		Age: YOY	-1.86	1.10	-3.45	-0.27
		Age: Adult	1.44	1.35	-0.50	3.39
		Precipitation	-3.15	1.94	-5.93	-0.36
		Summer temp	-5.56	1.83	-8.20	-2.92
Substrate (Wentworth)	Age	Intercept: Juvenile	5.67	0.31	5.22	6.12
		Age: YOY	-0.23	0.12	-0.41	-0.05
		Age: Adult	0.14	0.14	-0.06	0.33

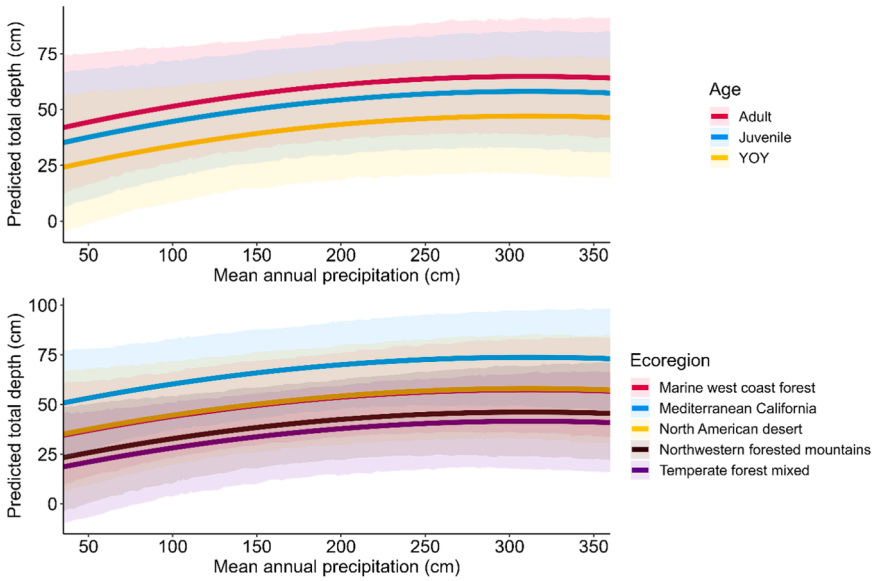

Fig. 2. Change in depth of used habitat by *O. mykiss* predicted by mean annual precipitation by age class (top) and ecoregion (bottom). Shaded areas correspond to the 95% confidence interval of the fitted line. YOY = Young of year.

3. Results

3.1. Summary

We initially obtained 177 peer-reviewed articles that met our search criteria and of those, used 32 papers that contained suitable quantitative habitat use information. The year of completion for each study ranged from 1967–2019. Of those 32 studies, 20 represented native populations and 12 represented nonnative populations. We extracted 346 data points that included all six original habitat variables (depth, column water velocity, focal water velocity, substrate, distance to cover, and focal elevation), all three age classes (YOY, juvenile, adult), and nine distinct ecoregions regions across four countries (USA, Canada, Japan, and Liechtenstein; Appendix B). The used values for focal water velocity and mean column water velocity were not significantly different (p-value $>$ 0.05). Therefore, we pooled the results into one water velocity measure representing focal point velocity for studies that reported only one metric. When a study reported both focal and column velocity, we used focal velocity in our final analysis. We further verified that this did not alter our interpretation of results by running separate mixed-effect models for each velocity metric separately (Appendix A). We then removed extreme visible outliers leaving us with 289 data points for focal water velocity (n = 96), total depth (n = 91), substrate (n = 41), distance to cover (n = 27), and focal elevation (n = 34, Table 2). The small number of data points for focal elevation and distance to cover precluded our ability to successfully fit models relating use of those habitat variables to our

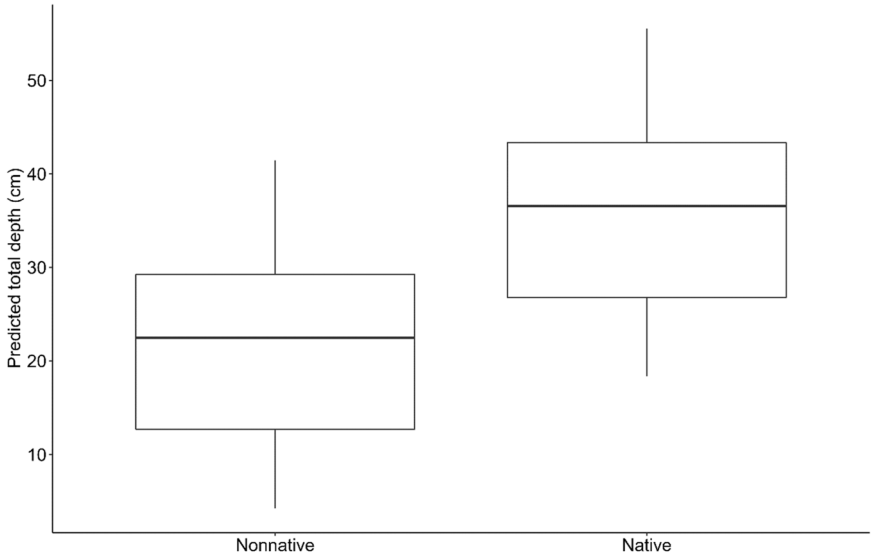

Fig. 3. Differences in depth of used habitat between native and nonnative juvenile *O. mykiss*.

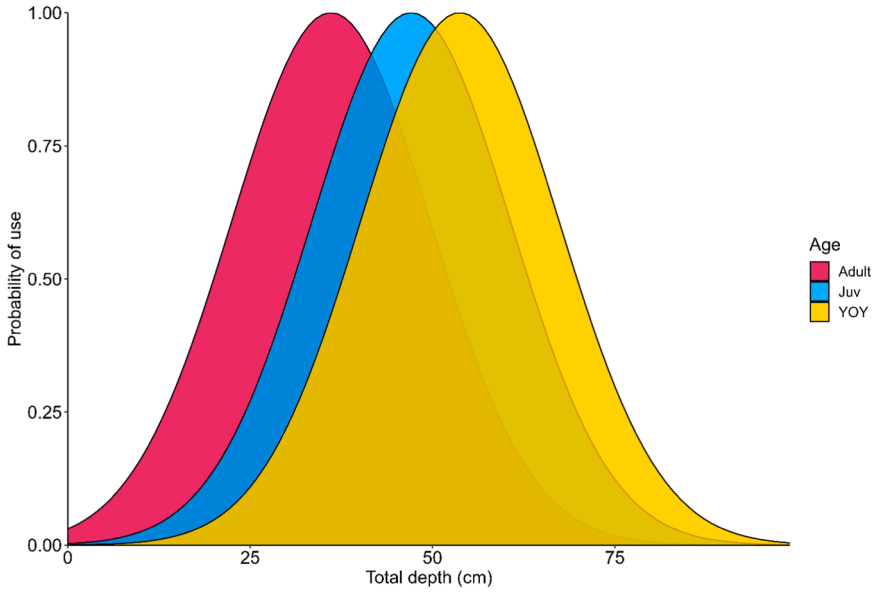

Fig. 4. Probability of habitat use associated with total column depth by *O. mykiss* age class. YOY = Young of year, Juv = Juvenile.

covariates. Across studies and age classes, mean focal point water velocity for *O. mykiss* was 13.06 cm/s (SD = 11.56), mean total depth was 44.31 cm (SD = 28.05), mean substrate size used was pebble (Wentworth class 5, range = gravel to cobble), mean distance to cover was 29.02 cm (SD = 27.33), and mean focal elevation was 14.77 cm (SD = 9.65; Table 2).

3.2. Niche overlap

When the meta-data were standardized by their reported variances, there were significant pairwise differences in depth, focal elevation, and distance to cover between some age classes (YOY vs. Juvenile, Juvenile vs. Adult, and YOY vs. Adult). All three pairs used significantly different depths from one another (SMD > 0.5, Fig. 1), with the largest degree of differentiation being between YOY and adults (SMD = −1.77, CI = −1.57 to −1.98), YOY being found in shallower depths than both juvenile and adult *O. mykiss*. YOY were observed at significantly lower focal elevations (i.e., were observed closer to the streambed) than both juvenile and adult *O. mykiss* (Fig. 1), which may be due to YOY using shallower habitats than other age classes. Finally, YOY were observed significantly closer to cover than adults (SMD = 0.65, CI = 0.15 to 1.14, Fig. 1). There were no significant differences among age class pairs for water

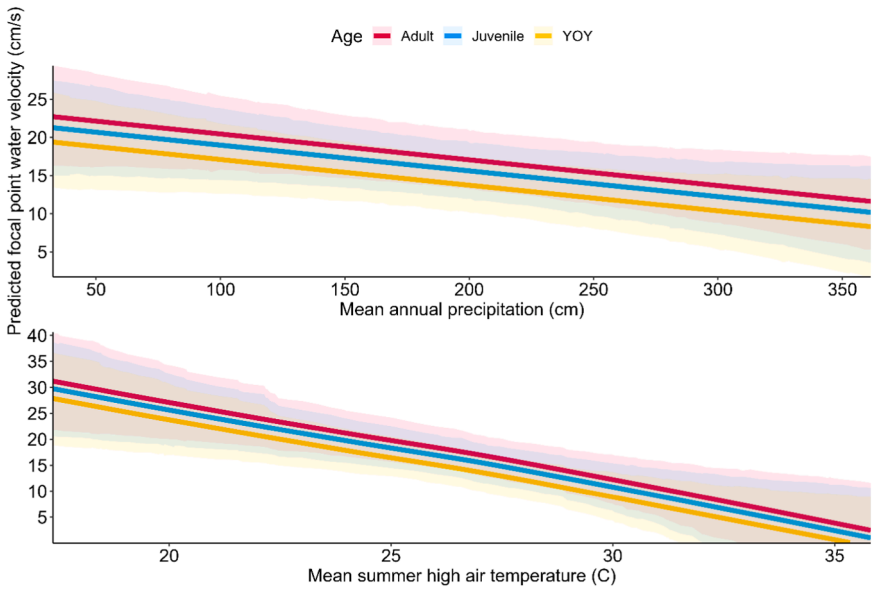

Fig. 5. Age specific change in focal point water velocities used by *O. mykiss* predicted by mean annual precipitation (top) and mean summer high air temperature (bottom). Shaded areas correspond to the 95% confidence interval of the fitted line.

velocity or substrate use (Fig. 1).

3.3. Depth

When running a global model with all uncorrelated variables, the most parsimonious random effect structure, which included separate random effects of study and ecoregion, indicated that 42% of the variation in depth use was between studies and 46% of the variation was between ecoregions. The remaining 12% was residual variation. We therefore ran all mixed models with both ecoregion and study level random effects. There was high model selection uncertainty as 12 models were included in the supported set (Appendix A). Only two models in the supported set contained unique informative parameters, which were age, mean annual precipitation and its quadratic effect, and nativeness, therefore we used both models for predictive purposes (Table 3).

As fish grow towards sexual maturity, they use deeper water (Fig. 2). This is consistent with our analysis of niche overlap using SMD, which indicated significant partitioning between age pairs (Fig. 1). As mean annual precipitation increased, *O. mykiss* of all ages and ecoregions used deeper habitats (Fig. 2). Among ecoregions, *O. mykiss* used the deepest habitats in Mediterranean California and shallowest in temperate mixed forest (Fig. 2, Appendix C). Across age classes, *O. mykiss* of nonnative origin used shallower habitats than *O. mykiss* of native origin (Fig. 3).

The normalized probability distribution function computed from values predicted by the top model indicate that habitats that are highly likely to be used ($p \geq 0.7$) by *O. mykiss* occurs at depths between 49–59 cm for YOY, depths between 60–70 cm for juveniles, and depths between 67–77 cm for adults (Fig. 4). 31% of habitat likely to be used based on depth ($p \geq 0.5$) by YOY is shared with juveniles (Fig. 4). 56% of habitat likely to be used based on depth by juveniles is shared with adults (Fig. 4). There is no overlap in the range of depth values likely to be used by YOY and adults (Fig. 4). It is unclear whether this degree of partitioning is due to the fitness benefit of different depths for each age class or whether it is due to competitive exclusion or avoidance.

3.4. Water velocity

When running a global model with uncorrelated variables, the most parsimonious random effect structure, which included the random effect of study, indicated that $>$ 99% of the variation in depth use was among studies. The remaining $<$ 1% was composed of residual variation. We therefore ran further mixed models with only study as a random effect. Four models were included in the supported set of models predicting age-specific water velocity use (Appendix A). The top model contained age, mean high summer air temperature, and mean annual precipitation, and the other three models contained subsets of parameters in the top model with similar parameter estimates. We therefore used our top model for predictive purposes (Table 3).

As fish age and grow, they can exploit faster water, with YOY using the slowest water velocities and adults using the fastest water velocities (Fig. 5). However, the age effects have wide confidence intervals and are not highly informative (Table 3). This is consistent with our analysis of niche overlap using SMD, as there were no significant partitioning of water velocities between age pairs (Fig. 1). As mean annual precipitation increased, *O. mykiss* were found in slower water (Fig. 5).

The normalized probability distribution function computed from values predicted by the top model indicate that habitats that are highly likely to be used ($p \geq 0.75$) by *O. mykiss* occurs at water velocities between 8–16 cm/s for YOY, velocities between 10–18 cm/s

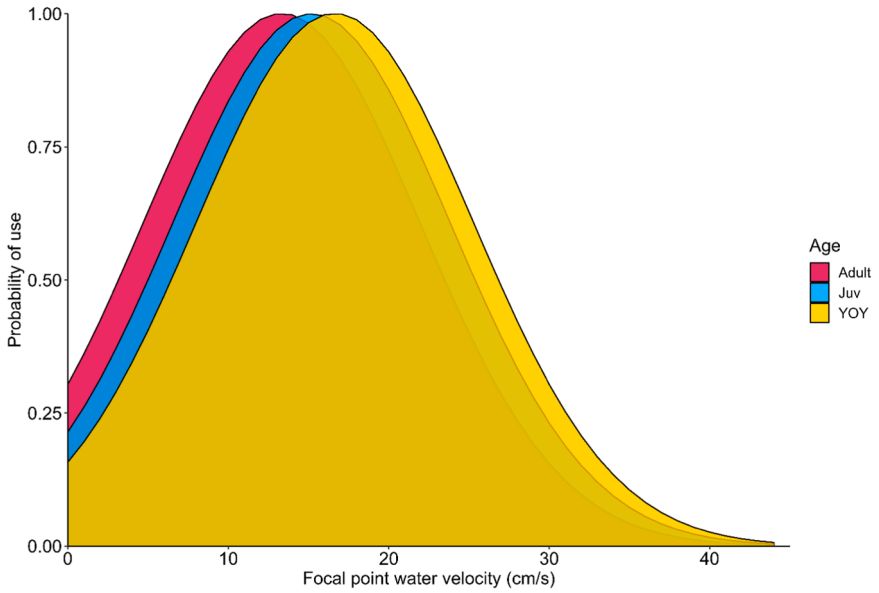

Fig. 6. Probability of habitat use associated with water velocity (cm/s) by *O. mykiss* age class. YOY = Young of year, Juv = Juvenile.

for juveniles, and velocities between 11–19 cm/s for adults (Fig. 6). 92% of habitat likely to be used based on water velocity ($p \geq 0.5$) by YOY is shared with juveniles (Fig. 6). 93% of habitat likely to be used based on water velocity by juveniles is shared with adults (Fig. 6). 85% of habitat likely to be used based on water velocity by YOY is shared with adults (Fig. 6). It is unclear whether this lack of habitat partitioning between age classes is due to overall preferences for slower habitat or the relative availability of different flows in sampled systems.

3.5. Substrate

When running a global model with uncorrelated variables, the most parsimonious random effect structure indicated that > 99% of the variation in substrate use was between studies nested within ecoregions (Appendix C). The remaining < 1% was composed of ecoregion alone and residual variation (Appendix C). We therefore ran further mixed models with study nested within ecoregion as a random effect. There was high model selection uncertainty as nine models were included in the supported set (Appendix A). The top model included only the effect of age, which was uninformative (Table 3). The second model was the null model and subsequent models in the supported set had low Akaike weights as well as uninformative or weakly informative parameters (Appendix A). We therefore failed to detect any relationships between substrate use, age, and our suite of covariates.

4. Discussion

This meta-analysis is the first attempt of this scale to understand how *O. mykiss* niche breadth varies ontogenetically and across environmental gradients. There is evidence for some ontogenetic shifts in habitat use, specifically when it comes to partitioning habitat based on depth. However, our results show that given current available literature, there are large overlaps in niche breadth between age classes and much of the variation in habitat use is associated with undetermined environmental and survey-level factors rather than age class. Using both meta-regression and meta-analytical effect size comparisons, we were able to quantify spatial heterogeneity in habitat use and identify habitat resources that may contribute to intraspecific competition between age-classes in *O. mykiss* populations. Species management often relies on broad, range-wide trends to restore habitat or define population benchmarks, assuming some sort of dynamic equilibrium across space and time (Hilborn and Liermann, 1998, El-Habbas and Dormann, 2018). Making management and conservation decisions for species of concern is especially problematic due to the high uncertainty and low availability of fine scale data (Beissinger and Westphal, 1998, Tucker et al., 2021). In the case of *O. mykiss*, the varying demographic responses to environmental change being observed indicate that there is fine scale variability driving population dynamics that has not yet been captured in coarse scale management and conservation planning.

We found that total depth and focal elevation were most likely to be partitioned by age class (Figs. 1, 2). Depth use was associated with age, precipitation, population origin, and ecoregion (Figs. 2, 3). The mechanisms behind these regional and climactic relationships are unclear based on the coarse resolution of this meta-analysis. We hypothesize that the increase in depth use associated with an increase in precipitation is a function of the amount of water available in a system and subsequent availability of deep-water habitat (Torgersen et al., 2006, Burgers et al., 2014). Fish may be using deeper water in Mediterranean California ecoregions relative to regions included in this meta-analysis due to intensive management of California Central Valley (CCV) watersheds for municipal and agricultural water use, flood control, Chinook Salmon restoration goals, and recreation (Lindley et al., 2006). Most major watersheds in

this system contain impassable dams and river conditions below the dam are subject to the 'bathtub effect', which describes heavily incised and armored channel morphology that results from scouring and low sediment transport (Grant, 2012, Allan, 2021). Therefore, river channels below impoundments may be deeper than they would be under natural conditions due to the loss of bed structure (Grant, 2012). Furthermore, summer reservoir releases are used to alleviate poor water quality in the lower sections of a watershed, increase habitat for other cold-water dependent salmonids, and provide recreational opportunities, which may create deeper habitat than would be normal during summer baseflow conditions (Cardwell et al., 1996, Ahearn et al., 2005, Daniels and Danner, 2020). Finally, native *O. mykiss* populations used deeper habitats than nonnative *O. mykiss* populations (Fig. 3). While the associated mechanisms are unknown, we speculate it may be linked to variability in biotic interactions with native fish communities (Korsu et al., 2010). While the effect of native fish communities on the habitat use of nonnative salmonids has not been studied to our knowledge, the effect of nonnative salmonids on native fish habitat use is well known, and those interactions may work both ways (Korsu et al., 2010, Jenney et al., 2023). These relationships are obviously dependent on the range of depths available and how depth interacts with factors such as prey availability or water temperature in different systems, but the evidence does suggest that depth partitioning by age/size is constant across space and time.

We also found that *O. mykiss* of different age classes are often found using the same flows and substrates, as water velocity and substrate were the least partitioned resources between age classes. Used water velocity did vary across temperature and precipitation gradients, with fish using slower water in areas with higher mean annual precipitation and higher summer air temperatures (Fig. 5). While the processes behind this relationship are unclear based on the resolution of our meta-data, we suspect in watersheds with more rainfall and water availability, more seasonally inundated habitats, such as side channels or floodplains which are characterized by slower flows, were available to fish (Raymondi et al., 2013; Wade et al., 2013). We expected fish to use faster water as air temperature increased due to higher dissolved oxygen concentrations in swift water, however, the opposite relationship is true: in locations that had high mean summer air temperatures, fish were found using slower water. This may be due to fish seeking thermal refugia in deep pools, which tend to have slower flows and cooler temperatures than other mesohabitat types (Matthews and Berg 1997, Allan, 2021). However, our depth and velocity data were not correlated. Another potential explanation is that watersheds with the highest summer temperatures are prone to drought and water availability may be lower than average during the summer months, which is also when most *O. mykiss* sampling occurred across studies (Wade et al., 2013). Low water availability may create low flow conditions that limit the availability of faster water, even if preferred.

Steelhead trout are listed under the Endangered Species Act in 11 of the 15 distinct population segments throughout the west coast of North America (NOAA). Where they are listed, there is growing interest in managing habitat to increase life-history diversity within populations (Satterthwaite et al., 2009, Dobos et al., 2020). A key uncertainty associated with making habitat restoration decisions for *O. mykiss* is how the increased expression of residency and resulting skew in size structure in some populations will interact with habitat availability and climate change (Satterthwaite et al., 2010; Cantin and Post, 2018; Myrvold and Kennedy, 2018). Monitoring habitat use along with demographic rates may be a useful proxy for inferring competitive behavior and identifying resource limitations (Knight et al., 2008). Our results suggest that the shifting availability of certain habitat features may exacerbate intraspecific competition and reduce juvenile growth potential, which aligns with previous studies (Benjamin et al., 2013; Myrvold and Kennedy, 2018; Cantin and Post, 2018). In the native range of *O. mykiss* (i.e. western North America), climate change is projected to lead to an up to 5 °C increase in air temperature and an up to 10% decrease in precipitation (IPCC, 2022). This degree of climate change is expected to alter ecosystem structure, species ranges, and phenology in freshwater systems throughout North America (IPCC, 2022). The increased prevalence of drought, especially in the southernmost portion of the native *O. mykiss* range, may become problematic as lower baseflow conditions might limit the availability of seasonally inundated rearing habitat, reduce habitat connectivity, concentrate more fish of different age/size classes in fragmented pools, and limit their ability to stratify themselves according to depth and focal elevation in the water column (Wade et al., 2013; Sawaske, 2014, Larsen and Woelfle-Erskine, 2018). In our study, the three watersheds with the highest summer temperatures, the Mokelumne River, the Pit River, and the South Fork Trinity River, all contain federally threatened steelhead populations and have been under drought conditions for 15 of the last 20 years (California Department of Water Resources, 2023). An increase in water temperature associated with climate change may also increase metabolic demands and may, alongside shifting demographic structures, further impact the growth opportunities available to rearing juveniles and their subsequent ability to reach smolting/maturation thresholds for growth rate and body condition (Benjamin et al., 2013; Myrvold and Kennedy, 2018).

If *O. mykiss* are unable to stratify themselves vertically according to size, our results suggest that overlapping water velocity and substrate requirements that seem to be consistent across ecoregions and climate conditions may increase competitive exclusion and push smaller fish to habitats with reduced growth opportunities (Cassini 2011, Myrvold and Kennedy, 2018, Cantin and Post, 2018). Water velocity is an important component of fish bioenergetics, as macroinvertebrate drift rates and swimming efficiencies interact directly with temperature to determine net energy intake and growth rates (Naman et al., 2019). As baseflow water levels shrink in many systems, water temperatures increase, and population size structures shift towards more larger individuals remaining in the system during summer baseflow conditions, there may be an increase in density and competition associated with habitat characterized by shared optimal water velocities and thermal tolerances (Knight et al., 2008, Cassini 2011, Myrvold and Kennedy, 2018). Smaller and less-dominant individuals are often either displaced to lower quality habitats by larger, dominant individuals or experience a reduction in fitness benefits associated with their preferred habitat when it is being occupied and defended by larger fish (de Roos et al., 2002; Knight et al., 2008; Cantin and Post, 2018). Without a simultaneous increase in prey availability, populations may experience abundance or life-history bottlenecks, where growth in rearing fish has been stunted by increased metabolic demands, increases in larger fish, and subsequent decreases in available resources (Benjamin et al., 2013; Cantin and Post, 2018; Myrvold and Kennedy, 2018). Stunted growth in rearing *O. mykiss* may prevent juveniles from reaching growth thresholds necessary for smolting

Table A1
Candidate models representing drivers of habitat use variability in *O. mykiss* ranked by AICc. A '+ ' denotes an additive effect and a '* ' denotes an interaction effect.

Habitat variable	Structure	AICc	Delta AICc	Akaike weight
Depth (cm)	Age + Precipitation + Precipitation^2	717.08	0	0.18
	Age	717.13	0.05	0.17
	Age + Nativeness	717.98	0.9	0.11
	Age + Forest cover	718.43	1.35	0.09
	Age + Precipitation + Precipitation^2 + Summer temp	719.01	1.93	0.07
	Age + Season	719.07	1.99	0.07
	Age + Precipitation + Precipitation^2 + Forest cover	719.19	2.11	0.06
	Age + Summer temp	719.37	2.29	0.06
	Age + Basin slope	719.49	2.41	0.05
	Age + Min basin elevation + Ocean access	719.98	2.9	0.04
	Age + Nativeness + Ocean access	719.99	2.91	0.04
	Age + Forest cover + Season	720.44	3.36	0.03
	Age + Precipitation * Summer temp	721.89	4.81	0.02
	Age + Basin slope + Forest cover + Season	722.92	5.84	0.01
	Global	731.43	14.35	0
	Null	749.23	32.15	0
Water velocity (cm/s)	Age + Precip + Summer temp	583.38	0.00	0.37
	Age + Summer temp	583.51	0.13	0.35
	Age + Precip * Summer temp	585.47	2.09	0.13
	Age	587.36	3.98	0.05
	Age + Min basin elevation + Ocean access	588.47	5.09	0.03
	Null	589.04	5.66	0.02
	Age + Basin slope + Drainage area	590.84	7.46	0.01
	Age + Forest cover	591.05	7.68	0.01
	Age * Precipitation + Age * Summer temp	591.08	7.70	0.01
	Age + Drainage area	591.13	7.76	0.01
	Age + Nativeness	591.37	7.99	0.01
	Age + Season	591.38	8.00	0.01
	Age + Nativeness + Ocean access	592.98	9.60	0.00
	Age + Forest cover + Season	593.42	10.04	0.00
	Global	601.30	17.92	0.00
Substrate	Age	53.53	0.00	0.23
	Null	54.13	0.60	0.17
	Age + Forest cover	54.29	0.75	0.16
	Age + Season	55.55	2.02	0.08
	Age + Nativeness	55.64	2.10	0.08
	Age + Drainage area	55.75	2.21	0.08
	Age + Basin slope	56.09	2.55	0.06
	Age + Basin slope + Forest cover	56.31	2.78	0.06
	Age + Forest cover + Season	56.59	3.05	0.05
	Age + Nativeness + Ocean access	58.65	5.11	0.02
	Age + Basin slope * Forest cover	59.54	6.01	0.01
	Global	64.58	11.04	0.00

Table A2
Best-supported models representing drivers variability in focal and column water velocity by *O. mykiss* ranked by AICc. A '+ ' denotes an additive effect and a '* ' denotes an interaction effect.

Habitat variable	Structure	AICc	Delta AICc	Akaike weight
Focal water velocity (cm/s)	Age + Summer temp	300.2	0	0.60
	Age + Summer temp + Precipitation	301.7	1.46	0.29
	Age + Summer temp + Precipitation + Precipitation * Nativeness	303.6	3.40	0.11
Mid-column water velocity (cm/s)	Null	365.70	0.00	0.66
	Age + Summer temp	368.70	3.01	0.15
	Age + Forest cover	369.00	3.27	0.13
	Age + Season:Summer	370.30	4.58	0.07

and successful outmigration, leading to more fish maturing in freshwater and a positive feedback loop for anadromy declines (Satterthwaite et al., 2009, 2010; Cantin and Post, 2018). Alternatively, stunted growth in rearing juveniles may increase mortality rates, reduce overall adult recruitment, and lead to population crashes or boom-and-bust cycles (Cantin and Post, 2018).

We are left with more questions than answers when it comes to the competing resource needs between *O. mykiss* age/size classes and how those habitat needs may correlate to growth rates or life-history trajectories. Unexplained differences between studies and ecoregions may be due to biotic interactions that cannot be captured by quantifying habitat alone (Appendix C). The presence of predators and competitors shift habitat selection patterns and species may select completely different habitats depending on

community composition (de Roos et al., 2002, Cassini 2011). An important factor missing from this discussion thus far is the concept of density-dependent habitat selection (Rosenzweig, 1991, Knight et al., 2008). The ideal free distribution assumes that densities of consumers correlate perfectly with densities of resources (Rosenzweig, 1991, Tregenza, 1995). However, we know that habitat selectivity tends to decrease as density increases, as high-quality habitats that are heavily used will have less fitness benefits to individuals than lower quality unexploited habitats (Rosenzweig, 1991, Cassini 2011). Furthermore, there is likely no single "resource" that is being selected for completely on its own (Naman et al., 2019). Fish select habitat based on complex interactions of variables, including assessing how much of that habitat is being actively defended, temperature dependent energetic requirements, avoiding predation, tracking prey communities, etc. (Schlosser, 1987; Knight et al., 2008, Cassini 2011, Naman et al., 2019). Further investigation on how both intraspecific and interspecific competitive behavior affects habitat use of *O. mykiss* and broader population dynamics would be beneficial to better understand the degree to which shifts in habitat availability interact with different forms of competition and to better characterize observed population trends, particularly with the added stressors of climate change (Railsback and Harvey, 2002; Railsback et al., 2003; Knight et al., 2008, Cassini 2011).

The results of this meta-analysis should be interpreted with caution, as there are inherent drawbacks to using meta-analyses to answer ecological questions. Combining results of studies that use different survey techniques and report different metrics is difficult and resulted in several relevant studies of *O. mykiss* habitat use not being included in our analysis. The dominant survey methods for describing habitat use, snorkel surveys and backpack electro-fishing, are seasonally limited and may result in data that is biased towards larger, more visible fish that have not fled the area (Thurow et al., 2006; Banish et al., 2008). The degree of variation associated with study (i.e., our random effect) that is present in all models is notable in this context, as the random intercepts for some studies were as high as 36 cm deeper than the mean for depth and 28.30 cm/s faster than the mean for velocity (Appendix C). Due to the coarseness of our meta-data, it's unknown whether this variation is due to differences in survey implementation or natural variability between sites or populations.

The distinction between habitat use and habitat selection is also important when interpreting our findings (Johnson, 1980; Boyce et al., 2002; Millspaugh et al., 2020). Most studies that presented a mean value of habitat use for a given variable did not present an equivalent value for available habitat. We attempted to explain habitat availability using environmental surrogates such as basin characteristics of climactic patterns to infer what kind of habitat was sampled, but we cannot determine whether fish were using, for example, shallow habitats because they were all that was available, or if shallow habitat was preferred relative to deeper available habitats (Boyce et al., 2002; Millspaugh et al., 2020).

5. Conclusions

Regardless of these limitations, meta-analysis is a powerful tool for the synthesis of evidence (Hilborn and Liermann, 1998, Thompson and Beauchamp, 2016). By summarizing the state of knowledge on ontogenetic shifts in *O. mykiss* habitat use, we identified knowledge gaps that can be the focus of future habitat use studies or inform how variation and uncertainty are included in conservation and management decisions (Hilborn and Liermann, 1998). If empirical data on a population's distribution within a system does not match indices of habitat quantity, quality, or probability of use, increasing or restoring habitat quality according to simplified perceptions of habitat use and population dynamics may not correlate to the desired increase in abundance or recruitment (Cassini 2011, Naman et al., 2019). Decision-support models for *O. mykiss* conservation and management can use our results to form baseline rulesets describing habitat use and, through sensitivity analyses, identify key uncertainties associated with the behavioral mechanisms driving resource partitioning in specific populations (Conroy and Peterson, 2013, Tucker et al., 2021). This knowledge can be used to prioritize *O. mykiss* research and monitoring actions focused on reducing those uncertainties and increasing the predictive power of population and species distribution models. Future investigation into the variability associated with intraspecific competitive interactions and resource limitation may elucidate drivers of decline and instability in certain *O. mykiss* populations and aid future efforts to make effective management decisions and reach conservation goals (Addison et al., 2013).

Although there is still high uncertainty associated with the mechanisms driving age-specific habitat use for *O. mykiss*, the importance of habitat heterogeneity is highlighted in this study. Regardless of whether observed patterns of habitat use and partitioning among age classes of *O. mykiss* are due to preference, avoidance, or competitive exclusion, it is likely that maintaining high habitat quantity and diversity, as well as restoring natural processes that maintain quantity and diversity, maximize the opportunities available for an individual to select habitat patches that generate high fitness potential across the range of environmental conditions and population densities (Hasegawa and Maekawa 2008, Bisson et al., 2009, Beechie et al., 2013, McPhee et al., 2014).

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CRediT authorship contribution statement

Lauren Diaz: Conceptualization, Methodology, Investigation, Formal analysis, Writing- Original Draft, Visualization. **Adam Duarte**: Conceptualization, Validation, Writing- Review & Editing, Supervision, Funding acquisition. **Michael Beakes**: Conceptualization, Writing- Review & Editing, Funding acquisition. **James T. Peterson**: Conceptualization, Validation, Writing- Review & Editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: James Peterson reports financial support was provided by US Bureau of Reclamation Mid-Pacific Region.

Data availability

Data will be made available on request.

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Data statement

The data is available upon request from the corresponding author.

Appendix A

Table A1.

Appendix B. Peer-reviewed studies of *O. mykiss* habitat use included in meta-analysis

Table A1.

Citation	State, Country	Ecoregion	Nativeness	Watershed	Habitat variables reported	Ages reported
Baigún (2003)	Oregon, USA	Northwest forested mountains	Native	North Umpqua River	Total depth, substrate	Adult
Baltz and Moyle (1984)	California, USA	Mediterranean California	Native	Tuolumne River	Total depth,substrate,water velocity,focal elevation	YOY, Juvenile, Adult
Baltz et al. (1991)	California, USA	Northwest forested mountains	Native	Pit River	Total depth,substrate,water velocity,focal elevation	YOY, Juvenile, Adult
Beecher et al. (1993)	Washington, USA	Marine west coast forest	Native	Coastal	Total depth, water velocity	Juvenile
Bustard and Narver (1975)	British Columbia, Canada	Marine west coast forest	Native	Coastal	Total depth, water velocity, focal elevation	YOY, Juvenile
Everest and Chapman (1972)	Idaho, USA	Northwest forested mountains	Native	Clearwater River	Total depth, water velocity	YOY, Juvenile
Fethermen and Avila 2022	Colorado, USA	Northwest forested mountains	Nonnative	Colorado River	Total depth, substrate, water velocity	YOY
Grunbaum (1996)	Oregon, USA	Northwest forested mountains, marine west coast forest	Native	Coastal, North Umpqua River	Total depth,substrate,water velocity,focal elevation, distance to cover	Juvenile, Adult
Hill et al. (2006)	Oregon, USA	Marine west coast forest	Native	Wilamette River	Total depth, substrate, water velocity	Juvenile
Holmes et al. 2014	California, USA	Mediterranean California	Native	Coastal	Total depth, water velocity, distance to cover	YOY, Juvenile
Inoue et al. (2009)	Hokkaido, Japan	Marine west coast forest	Nonnative	Coastal	Distance to cover	YOY
Johnson (2016)	New York, USA	Temperate mixed forest	Nonnative	Lake Ontario	Total depth, substrate, water velocity	YOY
Johnson and Kucera (1985)	Idaho, USA	Northwestern forested mountains	Native	Clearwater River	Total depth, substrate, water velocity	YOY
Johnson et al. (2016)	New York, USA	Temperate mixed forest	Nonnative	Lake Ontario	Total depth, substrate, water velocity	YOY, Juvenile

(*continued on next page*)

(*continued*)

Citation	State, Country	Ecoregion	Nativeness	Watershed	Habitat variables reported	Ages reported
Johnson et al. (2018)	New York, USA	Temperate mixed forest	Nonnative	Lake Ontario	Total depth, substrate, water velocity	YOY, Juvenile
Kalb et al. (2018)	New Mexico, USA	North American desert	Nonnative	Rio Ruidoso	Total depth, water velocity, distance to cover	YOY, Juvenile, Adult
Kocik and Taylor (1996)	Michigan, USA	Temperate mixed forest	Nonnative	Lake Huron	Total depth, water velocity	YOY
Magoulick and Wilzbach (1997)	Pennsylvania, USA	Temperate mixed forest	Nonnative	French Creek	Total depth, water velocity, focal elevation, distance to cover	YOY, Adult
Merz et al. 2016	California, USA	Mediterranean California	Native	San Joaquin River	Total depth, water velocity	YOY, Juvenile
Muhlfeld et al. (2001)	Montana, USA	Northwestern forested mountains	Native	Yak River	Total depth, water velocity, focal elevation	Juvenile, Adult
Nakamoto (1994)	California, USA	Mediterranean California	Native	Trinity River	Total depth, water velocity	Adult
Naman et al. (2022)	Washington, USA	Marine west coast forest	Native	Coastal	Total depth	YOY, Juvenile
Pert and Erman (1994)	California, USA	Mediterranean California	Native	San Joaquin River	Total depth, water velocity, focal elevation	Adult
Reeves et al. (2010)	Oregon, USA	Northwestern forested mountains, marine west coast forest	Native	Coastal, North Umpqua River	Water velocity, focal elevation	Juvenile
Riehle and Griffith (1993)	Idaho, USA	North American desert	Native	Little Wood River	Total depth,water velocity, focal elevation, distance to cover	Juvenile
Robinson et al. (2003)	Arizona, USA	North American desert	Nonnative	Little Colorado River	Total depth, substrate, water velocity	Juvenile
Rodger et al. (2021)	Oklahoma, USA	Temperate mixed forest	Nonnative	Grand River	Water velocity	Adult
Simpkins et al. (2000)	Montana, USA	North American desert	Nonnative	Yellowstone River	Total depth, water velocity	Juvenile
Spina (2000)	California, USA	Mediterranean California	Native	San Gabriel River	Total depth, water velocity	YOY, Juvenile, Adult
Vondracek and Longanecker (1993)	California, USA	Mediterranean California	Native	Sacramento River	Water velocity	Adult
Waite and Barnhart (1992)	California, USA	Northwestern forested mountains	Native	Trinity River	Total depth, water velocity	YOY, Juvenile
Zika and Peter (2002)	NA, Liechtenstein	Northwestern forested mountains	Nonnative	Spiersbach River	Total depth, water velocity	Juvenile, Adult

Appendix C. Intercepts associated with random effects of mixed linear models representing *O. mykiss* age-specific habitat use

Table A2.

Habitat variable	Random effect	Group	Intercept	SD
Depth (cm)	Citation	Baltz and Moyle (1984)	5.36	6.42
		Baltz et al. (1991)	-4.52	5.84
		Beecher et al. (1993)	36.21	8.97
		Bustard and Narver (1975)	-28.89	9.10
		Everest and Chapman (1972)	2.86	7.53
		Fethermen and Avila 2022	-5.47	9.17
		Grunbaum (1996)	15.90	5.61
		Hill et al. (2006)	-13.38	8.53
		Holmes et al. 2014	-13.70	6.59
		Johnson (2016)	-6.96	7.82
		Johnson and Kucera (1985)	-16.11	5.75
		Johnson et al. (2016)	-6.34	7.19
		Johnson et al. (2018)	-9.77	7.18
		Kalb et al. (2018)	1.57	7.62
		Kocik and Taylor (1996)	17.32	8.47
		Magoulick and Wilzbach (1997)	-10.01	8.28
		Merz et al. 2016	1.07	7.48

(*continued on next page*)

(*continued*)

Habitat variable	Random effect	Group	Intercept	SD
		Muhlfeld et al. (2001)	-7.35	5.78
		Nakamoto (1994)	39.68	8.74
		Naman et al. 2021	-27.56	6.76
		Pert and Erman (1994)	27.56	9.61
		Riehle and Griffith (1993)	-3.92	9.26
		Robinson et al. (2003)	-10.04	9.08
		Spina (2000)	-6.67	7.10
		Waite and Barnhart (1992)	-6.54	7.53
		Zika and Peter (2002)	29.70	7.53
	Ecoregion	Marine west coast forest	0.66	5.37
		Mediterranean California	11.20	5.96
		North American desert	-0.49	7.42
		Northwestern forested mountains	-8.05	4.82
		Temperate forest mixed	-3.31	6.24
Velocity (cm/s)	Citation	Baltz and Moyle (1984)	-1.60	1.30
		Baltz et al. (1991)	0.92	1.86
		Beecher et al. (1993)	1.65	3.40
		Bustard and Narver (1975)	-4.34	2.50
		Everest and Chapman (1972)	2.56	3.64
		Fethermen and Avila 2022	1.21	6.14
		Grunbaum (1996)	-7.07	1.59
		Hill et al. (2006)	28.30	3.31
		Holmes et al. 2014	0.24	1.49
		Johnson (2016)	11.60	2.41
		Johnson and Kucera (1985)	-4.01	1.53
		Johnson et al. (2016)	-1.72	1.73
		Johnson et al. (2018)	-16.44	1.65
		Kalb et al. (2018)	-9.72	1.32
		Kocik and Taylor (1996)	6.60	3.65
		Magoulick and Wilzbach (1997)	-5.52	3.23
		Merz et al. 2016	13.24	1.56
		Muhlfeld et al. (2001)	-8.03	1.72
		Nakamoto (1994)	-2.17	3.08
		Pert and Erman (1994)	1.99	3.64
		Reeves et al. (2010)	-9.90	2.05
		Riehle and Griffith (1993)	-3.70	3.16
		Robinson et al. (2003)	-10.81	4.34
		Rodger et al. (2021)	15.52	3.33
		Spina (2000)	-0.60	2.15
		Waite and Barnhart (1992)	-0.98	2.68
		Zika and Peter (2002)	2.80	2.23
Substrate (Wentworth)	Ecoregion: Citation	Marine west coast forest:Grunbaum (1996)	-1.34	0.16
		Marine west coast forest:Hill et al. (2006)	0.30	0.28
		Mediterranean California:Baltz and Moyle (1984)	1.28	0.08
		Northwestern forested mountains:Baltz et al. (1991)	0.36	0.14
		Northwestern forested mountains:Grunbaum (1996)	-0.04	0.22
		Northwestern forested mountains:Johnson and Kucera (1985)	0.49	0.09
		Temperate forest mixed:Johnson (2016)	0.58	0.19
		Temperate forest mixed:Johnson et al. (2016)	-1.66	0.14
		Temperate forest mixed:Johnson et al. (2018)	0.03	0.13

Appendix D. Mean and standard deviation (SD) for all continuous covariate values included in mixed-effect models

Table A2.

Predictor variable	Mean	Sd	Min	Max
Drainage area (km2)	226.99	373.89	7.40	2025.37
Mean basin slope (%)	31.03	15.17	0.10	62.30
Min basin elevation (m)	761.94	827.38	0.00	2435.96
Mean annual precipitation (cm)	119.26	57.87	27.69	362.48
Mean summer high temperature (°C)	28.40	5.31	17.22	36.00
Forest cover (%)	58.08	28.85	2.00	100.00

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