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Phenological mismatch, carryover effects, and marine survival in a wild steelhead trout *Oncorhynchus mykiss* population

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ABSTRACT

Climate-driven changes in the oceans, such as shifts in prey timing and abundance, could influence variability in population productivity of marine fishes. For example, according to the match/mismatch hypothesis, the temporal matching of the young salmon outmigration from freshwater to the ocean relative to the timing of availability of their prey could influence their marine survival. Indeed, understanding patterns and processes of marine survival is particularly pressing in many salmon and steelhead trout populations due to recent declines. To determine whether phenological mismatches between juvenile salmonids and their prey could contribute to low ocean survival, we analyzed the migration timing and ocean survival of 22,116 tagged juvenile steelhead trout *Oncorhynchus mykiss* over 12 years from the Wind River, Washington State, USA. We used a Bayesian multilevel modelling approach with variable selection to assess how survival was associated with body size, river exit date, the biological spring transition date (the day when northern zooplankton first appeared in the coastal region near the Columbia River estuary), and the degree of mismatch (the effect of the interaction between individual outmigration timing and biological spring transition date). The variables with the highest probability of contributing to individual survival were fish size (100%), river exit date (99%), the interaction between year and river exit date (91%), and the biological spring transition date (64%). Fish that were larger than average at outmigration had higher ocean survival, providing further evidence that freshwater growing conditions have carryover effects on marine survival. Years with greater annual phenological mismatches such as those years with late biological spring transition dates (i.e., occurring after June 1st), or warm sea surface temperatures, had sufficiently low marine survival to compromise recovery goals. Substantial intra-annual variation in outmigration timing buffered the population from inter-annual variation in optimal outmigration timing. Collectively these findings indicate that freshwater growing conditions, migration timing, and the timing of high-quality food availability in the nearshore coastal environment work in concert to influence individual survival and annual smolt-to-adult returns.

1. Introduction

There is a need to understand how shifting ocean conditions influence variability in the productivity of commercially, recreationally, and ecologically important fishes. Marine fish population productivity is linked with size-dependent survival in early life history stages, which may depend on the timing and abundance of suitable prey for somatic growth (Anderson, 1988; Hjort, 1914). Therefore, timing and abundance of prey during early life stages likely elicits bottom-up control of population productivity (Platt et al., 2003; Ware and Thomson, 2005). Understanding the effects of variable timing and abundance of prey on individual survival could increase predictability of population productivity, especially in the face of a changing climate (Cushing, 1990). Specifically, the match/mismatch hypothesis has been used to explain variability in marine fisheries productivity through examining the timing and abundance of prey relative to the predator phenology. It

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postulates that when prey are abundant during a sensitive life-history stage of the predator, predator survival will be higher than average, but if predator and prey phenology become out of sync, predator survival will decrease (Cushing, 1990, 1969). For example, Durant et al. (2005) found that a phenological mismatch between food and food requirements decreased survival in Atlantic cod *Gadus morhua*. However, not all individuals/species are equally sensitive to phenological mismatches. Sensitivity to mismatches may be influenced by intrinsic traits such as body condition, which are affected by experiences in other life stages (i.e., carryover effects) (Anderson et al., 2013; Thackeray et al., 2016). For example, larger individuals could withstand greater phenological mismatches than smaller individuals with presumably poorer body condition (Ohlberger et al., 2014). Thus, the match/mismatch hypothesis is an important framework in this era of increasing climate change-driven variability, and is likely one of several key components for understanding how ocean conditions control productivity of marine fish populations.

Variability in ocean survival has resulted in extreme population swings in migratory Pacific salmon *Oncorhynchus* spp., likely shaped in part by climate-driven changes in prey abundance during the first few months at sea. For example, Mantua et al. (1997) found that during positive phases of the Pacific Decadal Oscillation (PDO) Alaskan salmon populations had a 200% increase in adult returns, likely caused by warmer ocean temperatures resulting in higher zooplankton (food) abundance for young salmon. However, the relationship between PDO and salmon recruitment was much weaker in more southern populations such as those of the Columbia River since zooplankton dynamics for the Washington and Oregon coast are influenced by different environmental conditions than in Alaska (Gargett, 1997). Other oceanic correlates representing processes occurring on varying temporal and spatial scales, including El Niño Southern Oscillation (ENSO), North Pacific Gyre Oscillation (NPGO), sea surface temperature, salinity, and upwelling, have been associated with salmon population dynamics, contingent on the scale at which they were tested (Francis and Hare, 1994; Kilduff et al., 2015; Malick et al., 2015b; Mueter et al., 2005; Nickelson, 1986; Pearcy, 1992; Scarnecchia, 1981). Environmental conditions (e.g., sea surface temperature, salinity, upwelling strength) occurring within 1000 km from the river mouth are often more strongly correlated with salmon survival and productivity than environmental conditions that persist at larger temporal and spatial scales (Malick and Cox, 2016; Mueter et al., 2007, 2002b, 2002a), supporting the hypothesis that ocean conditions experienced during the first few months at sea can strongly influence salmon productivity. The strength of the correlation between local food abundance and survival suggests that bottom-up control during the early marine period is a strong driver of survival. However, it is less clear what role, if any, the timing of food availability and/or phenological synchrony with juvenile salmon outmigration may play in restricting survival through this period.

There is some evidence that match/mismatch dynamics may contribute to ocean survival of salmon. Salmon that enter the marine environment during peak food (zooplankton) availability grow faster (Fiechter et al., 2015; MacFarlane, 2010) and because growth during early marine residence is highly correlated with survival to adulthood (Beamish and Mahnken, 2001; Friedland et al., 2014), it is likely that the matching of smolt ocean entry and peak prey abundance influences salmon survival and productivity (Chittenden et al., 2010; Ryding and Skalski, 1999; Satterthwaite et al., 2014). However, the few studies that have looked at survival as a function of salmon migration timing relative to prey abundance have had mixed results. Scheuerell et al. (2009) found that for both Snake River Chinook salmon *O. tshawytscha* and steelhead trout *O. mykiss,* migration timing was important for survival, however the timing of the spring upwelling transition date (the date that Ekman transport switches from primarily downwelling to primarily upwelling in the spring, and a proxy for the timing of the spring phytoplankton bloom) was not an important driver of survival. Salmon migrating in early—to mid-May had 4 – 50 times higher survival than fish migrating in mid-June, regardless of changes in the spring upwelling transition date. However, timing of the spring upwelling transition date was an important predictor of survival for hatchery coho salmon *O. kisutch* (Ryding and Skalski, 1999), though this relationship may have changed over time (Rupp et al., 2012). Further, ocean survival was highest when hatchery Chinook salmon from California's Central Valley were released within 70 – 115 days of the upwelling transition date; evidence that a phenological match increased survival (Satterthwaite et al., 2014). Using phytoplankton as a more direct proxy of zooplankton prey availability, Chittenden et al. (2010) found that hatchery coho salmon from British Columbia, Canada had 1.5 – 3 times higher survival when smolts were released coinciding with peak marine phytoplankton productivity. Similarly, changes in the timing and abundance of local phytoplankton blooms were related to the number of adult pink salmon that return to freshwater (Malick et al., 2015a). Thus, there is evidence that a phenological mismatch affects survival of Pacific salmon in some systems. However, most of these studies were on hatchery fish, which are genetically, morphologically, physiologically, and behaviourally different than wild fish (Naish et al., 2007; Swain et al., 1991). Hatchery fish often have lower marine survival than wild salmon (Jonsson et al., 2003) and may respond differently to match/mismatch with prey, possibly as a result of their lack of life history and phenological diversity (Sturrock et al., 2019). Therefore, there is an important knowledge gap with regards to potential impacts of match/mismatch dynamics, especially for wild salmon survival.

Somatic growth rates and subsequent survival in the early marine environment may be influenced by preceding freshwater conditions that carry over to the ocean environment. Freshwater conditions (e.g., habitat quality, temperature, density dependence) control body size and condition of smolts (Bailey et al., 2018; Rich et al., 2009; Schindler et al., 2005), with larger smolts generally having higher ocean survival than smaller smolts (Duffy and Beauchamp, 2011; Healey, 1982; Henderson and Cass, 1991; Ward et al., 1989). Thus, changes to the freshwater environment that alter fish growth and body size can subsequently impact ocean survival. For example, climate change-driven warming has altered growth and life-history patterns of Bristol Bay sockeye salmon *O. nerka* smolts from Alaskan Lakes; smolts now are younger and substantially smaller than those from even 20 years ago (Rich et al., 2009; Schindler et al., 2005). This shift was accompanied by a decrease in overall ocean survival rates and population productivity (Tillotson and Quinn, 2016). Freshwater growing conditions could also influence trade-offs associated with the timing of smolt outmigration. For slower-growing fish, migrating later in the season allows for more freshwater growth which increases size at outmigration in order to reach a smolt size that is viable in the ocean. However, this freshwater growth comes at a cost of lost ocean growth opportunities and a delay in outmigration timing, which may decrease survival (Mortensen et al., 2000). Thus, freshwater growing conditions may influence both size as well as timing at outmigration. Furthermore, the effect of phenological mismatch could be size-dependent (Ohlberger et al., 2014), such that matching with food availability in the early marine environment is more important for smaller fish which may be more sensitive to mismatches than larger fish. Freshwater growing conditions can influence size at outmigration which impacts marine survival of migratory salmonids, and the strength of this effect may depend on ocean feeding conditions during the first few months at sea.

Understanding the underlying processes and temporal patterns of marine survival is of timely importance for many salmon and steelhead trout populations given recent population declines and subsequent imperiled conservation status. For example, declines in ocean survival rates of steelhead trout have contributed to declining population trends that have sparked conservation concerns (Kendall et al., 2017). In 2017, a record low return of adult Chilcotin and Thompson River steelhead trout (58 and 177, respectively) in British Columbia, Canada, representing an 80% decline in population size over the last three generations, led the Committee on the Status of Endangered Wildlife in Canada

(COSEWIC) to conduct an emergency assessment which found the populations to be at imminent risk of extinction ('Endangered' designation; COSEWIC, 2018), and stakeholders are now urging the Canadian Government to list these populations under the Canadian Species At Risk Act (SARA; Whitemore and Sandborn, 2018). Indeed, 80% of steelhead trout populations in the Pacific Northwest have declined in the past 40 years, and decreases in marine survival are likely a strong contributor to these spatially coherent population declines (Kendall et al., 2017; Ward, 2000). For example, smolt-to-adult survival rates decreased from 15% on average before 1990 to just 3.5% for the Keogh River steelhead trout population in British Columbia, Canada (Ward, 2000). Such dramatic decreases in marine survival have led to closures of freshwater recreational fisheries and challenged other fisheries management and recovery efforts. In the Columbia River Basin alone, >$500 M USD per year is invested into a fish and wildlife program largely devoted to the recovery of salmon and steelhead trout affected by dams (NPCC, 2017). However, current recovery scenarios depend upon smolt-to-adult return rates (SAR) for steelhead trout and spring Chinook salmon averaging a minimum of 4% (2 – 6% inter-annual range; NPCC, 2014), targets which are not regularly being met for the majority of populations (McCann et al., 2016). If marine survival decreases below the levels included in recovery scenarios, steelhead trout populations will likely continue to decline unless other sources of mortality are further decreased (McCann et al., 2016). Thus, studies that examine how potential factors, such as phenological mismatch with ocean prey and/or freshwater carryover effects, influence marine survival of steelhead trout populations are relevant to informing management and recovery efforts and targets.

Here we investigated how ocean survival of wild salmon is influenced by the potential match or mismatch of their outmigration timing with ocean prey availability as well as other potential factors. We addressed this question using an extensive dataset spanning 12 years and including over 22,000 individually-marked wild steelhead trout smolts from the Wind River, a tributary of the Columbia River (Washington State, USA). We used a multi-level model that included both annual variables and within-year variables thought to possibly affect individual smolt ocean survival. Each variable had an associated *a priori* hypothesis (Table 1). For example, we predicted that larger individual fish would have higher survival than smaller fish. Further, based on the match/mismatch hypothesis, we predicted that timing of outmigration and prey availability would influence the individual and annual patterns of survival. Using annual data on the biological spring transition date (the first day northern and energy-dense zooplankton were found off the Oregon coast; Miller et al., 2017), we predicted that there would be an optimal biological spring transition date, which would result in the highest annual survival probability (annual mismatch hypothesis). We also hypothesized that there would be an optimal outmigration date within each year that would result in the highest individual survival probability and that this optimum would differ based on the biological spring transition date (individual mismatch hypothesis). We discovered that in years where the biological spring transition date was earlier, cohort survival was higher (annual mismatch hypothesis), but within a year, fish that emigrated closer to the biological spring transition date did not always have higher survival (individual mismatch hypothesis).

For the second phase of model selection, the Annual Covariate Inclusion Model, we compared eleven correlated annual variables (e.g., biological spring transition date, PDO) and demonstrated that multiple annual variables impacted survival including sea surface temperature, spring upwelling transition date, PDO and the ecosystem indicator. Thus, in addition to individual-level variables, growing conditions in the ocean were important predictors of steelhead smolt survival.

2. Materials and methods

We combined data from two existing long-term datasets to determine if individual and annually-averaged ocean survival of steelhead trout smolts were related to size (fork length), outmigration timing, cold-water affiliated (northern) copepod biomass, and individual and/or annual phenological mismatch. We used individual size, outmigration date, and survival data of greater than 22,000 individually-marked Wind River steelhead trout, collected by the Washington Department of Fish and Wildlife, as well as the biomass of northern copepod taxa and the biological spring transition date, collected by NOAA Northwest Fisheries Science Center. We combined these two datasets and ran an integrated multilevel model with variable selection terms to determine parameter inclusion probabilities. Multilevel models incorporate fixed and random effects that are nested within multiple groups. In our case, we had two groups: an individual-level model that estimated individual survival probabilities, nested within a group-level model that estimated annual survival probability. This accounted for the non-random probability of survival due to shared conditions (explained/fixed and unexplained/random) throughout the steelhead trout life cycle, while also enabling examination of factors that operate at the within year/

Table 1
Variable definitions and associated hypotheses.

Variable	Abbrev.	Hypothesis	Reference
River Exit Date	RE	Outmigration timing matters, regardless of the timing of the biological spring transition date.	(Ryding and Skalski, 1999; Scheuerell et al., 2009)
River Exit Date Squared	RE^2	There is an optimal outmigration date, where probability of survival starts low, increases to an optima, and decreases across river exit dates.	Scheuerell et al., 2009)
Individual Mismatch	RE*Year	The optimal timing of outmigration varies across year in correspondence with the phenology of ocean prey.	(Chittenden et al., 2010; Satterthwaite et al., 2014; Scheuerell et al., 2009)
Annual Mismatch	BIO	Annual survival probability is highest in years where the biological spring transition date occurs before average river exit date for that year.	(Cushing, 1990, 1969)
Annual Mismatch Squared	BIO^2	There is an optimal biological spring transition date, where annual survival probability decreases if peak zooplankton abundance is too early, rises to an optimum coincident with annual average river exit date, and decreases where the biological transition date occurs after average river exit date.	(Cushing, 1990, 1969)
Northern Zooplankton Biomass	Z	Increased biomass of lipid-rich, northern copepods increases survival probability.	(Peterson and Schwing, 2003)
Size	FL	Larger individual fish have higher survival probability than smaller fish.	(Beamish and Mahnken, 2001; Ward et al., 1989)
Size by River Exit Date	FL*RE	The effect of river exit date on survival probability is dependent on size, where the effect of river exit date is stronger in smaller fish.	(Weitkamp et al., 2015)
Size by Year	FL*Year	The effect of the timing of the biological spring transition date depends on fish size, where annual variation such as changes in the biological spring transition date is less important for larger fish.	(Anderson et al., 2013; Litz et al., 2017)

individual-level scale. For the first phase of model selection, hereafter, the Biological Spring Transition Date Model, the group-level fixed effects included a yearly effect of biological spring transition date and the individual-level of the model included size, outmigration timing, northern copepod biomass, the degree of mismatch (strength of interaction between outmigration date and annual biological spring transition date), and other associated interactions. For the second modelling phase, hereafter the Annual Covariate Inclusion Model, the group-level fixed effects included a yearly effect of one of eleven correlated annual variables (i.e., biological spring transition date, spring upwelling transition date, upwelling strength, air temperature (as a proxy for sea surface temperature), PDO, Aleutian Low Pressure Index (ALPI), ENSO, northern copepod biomass anomaly, southern copepod biomass anomaly, Columbia River discharge and an ecosystem indicator). These are not all the variables that could effect marine survival, as the aim of this study was not to elucidate all factors related to marine survival, but instead to determine if phenological mismatch could be a factor influencing marine survival. The variable selection approach separated the variable selection process from the parameter estimation process of that covariate's effect size to determine which covariates were useful predictors of steelhead trout survival (Royle and Dorazio 2008).

2.1. Wind River steelhead trout

The Wind River steelhead trout population is a wild population in the Lower Columbia River. These fish have a relatively short migration compared to other Columbia River steelhead trout populations, and pass only one hydropower dam. Thus, this population may provide a conservative indicator of smolt-to-adult return rates, with presumably higher survival than more upstream Columbia River populations that have a more perilous downstream migration. Understanding the factors that influence survival of Wind River steelhead trout could help elucidate the factors that affect ocean survival of Columbia River salmon and steelhead trout more broadly. The Wind River is a 582 km^2 watershed located 245 km from the Pacific Ocean on the border of Washington and Oregon, USA (Fig. 1). It is composed of three sub-basins, Trout Creek, Panther Creek and the upper mainstem Wind River, and exits to the Columbia River 15 km upstream from the Bonneville Dam. Shipherd Falls at river kilometer three on the Wind River is a natural barrier to all upstream migrating salmonids, with the exception of summer steelhead trout, which can pass over it. However, some wild steelhead trout, and all hatchery Spring Chinook salmon returning to the Carson National Fish Hatchery, pass upstream of the falls via a fish ladder and trap. Consequently, the only anadromous species in the watershed are wild summer and winter steelhead trout (~200 – 1500 adults and ~8000 – 40,000 smolts) and hatchery spring Chinook salmon. Wind River steelhead trout smolts are mostly summer run, as fewer than ten spawning winter steelhead trout are passed above the falls. The watershed has been managed as a wild steelhead trout gene bank with no hatchery steelhead trout planted in the watershed for the past 20 years. Wind River steelhead smolts are predominantly age-2 (range 1 – 4 years old), with sizes ranging from 78 to 280 mm (Figs. S1, S2) and migrate to the ocean between early April and late June with an average migration duration of ~11 days (range 2 – 59 days) (Figs. S1, S3). They spend between ~1 – 3 years in the ocean before returning as adults to spawn (Fig. S4). A small percentage of spawning steelhead trout return to the ocean as kelts and may return to freshwater to spawn again in subsequent years. This system has been comprehensively monitored since the 1990s. Beginning in 2003, individual Passive Integrated Transponder (PIT) tagging of juvenile steelhead trout and close to 100% detection at Bonneville Dam fish ladders of adults that survive the ocean stage has enabled analyses linking individual traits (size and outmigration timing) to ocean survival.

Starting in 2003, juvenile steelhead trout were tagged with PIT tags

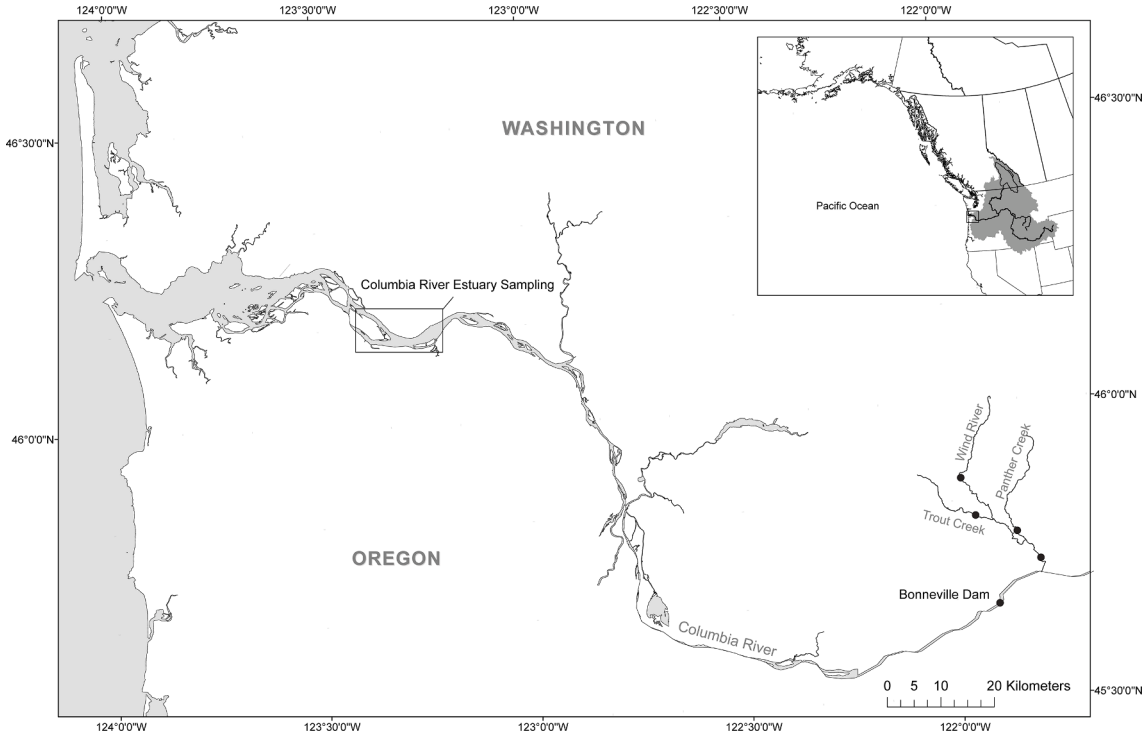

Fig. 1. Lower Columbia River and the Wind River Basin. There are four rotary screw traps in the Wind River Basin (Upper Wind River, Lower Wind River, Trout River, and Panther Creek), and one set of PIT tag detection arrays at the Bonneville Dam, indicated by black dots. A mobile PIT tag detection array is towed in transects in the Columbia River estuary and the sampled area is indicated by the black box. Zooplankton observation site (NH 05) is located off the map, approximately 200 km south of the Columbia River estuary.

Table 2
Mean annual values for mismatch variables and smolt-to-adult return rates.

Year	Biological Spring Transition Date	River Exit Date (range)	Mean FL (range)	Smolt-to-Adult Returns (survivors/total)
2003	21-May	May 7 (Apr 11 – Jun 13)	164 (122, 256)	0.029 (39, 1343)
2004	10-May	May 2 (Mar 31 – Jun 7)	164 (114, 258)	0.022 (47, 2105)
2005	02-Aug	May 3 (Apr 4 – Jun 6)	163 (122, 255)	0.018 (38, 2097)
2006	10-May	May 11 (Mar 30 – Jun 12)	162 (120, 226)	0.037 (48, 1298)
2007	22-Mar	May 6 (Apr 3 – Jun 8)	162 (102, 280)	0.058 (158, 2741)
2008	04-Mar	May 10 (Apr 4 – Jun 29)	160 (125, 238)	0.070 (81, 1155)
2009	24-Mar	May 10 (Apr 5 – Jun 11)	163 (125, 215)	0.076 (102, 1346)
2010	18-Jun	May 7 (Apr 5 – Jun 2)	161 (120, 237)	0.044 (89, 2006)
2011	08-Apr	May 14 (Apr 9 – Jun 27)	159 (120, 215)	0.018 (25, 1404)
2012	04-May	May 15 (Apr 14 – Jun 26)	158 (130, 239)	0.035 (41, 1159)
2013	06-May	May 9 (Apr 2 – Jun 21)	161 (90, 227)	0.039 (103, 2613)
2014	06-May	May 4 (Apr 5 – Jun 8)	159 (78, 234)	0.028 (79, 2849)

Biological transition date is the first day of the year that cold water zooplankton are detected at NH 05. Remaining columns are mean river exit date, fork length (FL, in mm), and smolt-to-adult returns as a proportion of survivors over total number tagged.

at one of four locations on the Wind River (the upper Wind River, Trout Creek, Panther Creek, and the outlet of the Wind River to the Columbia River; Fig. 1) to determine smolt-to-adult return rates as part of a monitoring project led by the Washington Department of Fish and Wildlife. Rotary screw traps were installed annually on or near April 1st and operated until the end of June in order to capture the end of the juvenile steelhead trout outmigration. Juvenile steelhead trout were captured using a rotary screw trap, anesthetized with MS-222, measured for fork length (FL, in mm), PIT tagged (12 mm tag) and released upstream (1.5 – 6 km) of the trap in which they were captured in order to estimate screw trap capture efficiency. Tag retention and mortality trials were conducted and found minimal tag loss (0.1 – 1%) and short-term tag-related mortality (~1%) (T. Buehrens, unpublished data). Juvenile steelhead trout could be recaptured at several rotary screw traps in the Wind River (the upper Wind River, Trout Creek, Panther Creek, and the outlet of the Wind River to the Columbia River) and detected at downstream static arrays at the Bonneville Dam and at a towed array in the Columbia River estuary. As juveniles, the recapture rate at screw traps and detection efficiency at downstream arrays is low (T. Buehrens, unpublished data), therefore river exit date was the last date that each of the juvenile steelhead trout were detected or the day they were captured as they out-migrated from the Wind River (typically the day they were tagged). We expected that there might be an optimum day of outmigration (either due to phenological synchrony or other environmental factors) and therefore included a river exit date squared term in our model to account for this possibility (see Statistical Analyses section). Data from PIT tags were obtained from the Pacific States Marine Fisheries Commission (www.ptagis.org).

Survival to adulthood was determined by subsequent detection at the Bonneville Dam as adults. Steelhead trout from the Wind River are protected under the U.S. Endangered Species Act (ESA) and therefore are not targeted for harvest by fisheries below Bonneville Dam. Incidental catch in commercial fisheries is estimated to be less than 2%, based on neighbouring wild steelhead trout populations from the Columbia River (WDFW and ODFW, 2018a, 2018b). Thus, survival was determined by detection at Bonneville Dam, which has a near 100% detection efficiency for PIT tagged adult salmon (Burke et al., 2006). To-date no tagged Wind River adults have been detected upstream without first being detected at Bonneville Dam (T. Buehrens, unpublished data). All returning steelhead trout that were tagged in the Wind River as juveniles returned on their maiden spawning migration (first time spawning) on or before three years in the ocean (Fig. S4), therefore we included only juvenile salmon tagged between 2003 and 2014 to allow for up to three years growth in the ocean. We considered a fish to have 'survived' if the fish was detected at Bonneville Dam adult fish ladders more than 330 days after it was tagged and released as a smolt. Fish were considered 'dead' if they were not detected at Bonneville dam by December 31, 2017. Based on this criterion, 22,116 juvenile fish were PIT tagged between 2003 and 2014, and 850 survived and returned as adults (Table 2). We used fork length at tagging for size measurement in our analyses and acknowledge that fork length at tagging is only a proxy of fork length at ocean entry as it is likely that fish grew during their 245 km migration downstream.

2.2. Zooplankton biomass estimates and biological spring transition date

The coastal shelf of Oregon experiences vernal changes in zooplankton abundance and community composition, resulting in seasonal increases in abundance and quality of salmon prey in coastal environments. In the spring, alongshore wind stress changes from predominantly poleward (downwelling favorable) to predominantly equatorward (upwelling favorable) which reverses coastal currents and results in a shift in the zooplankton community. During the winter, the copepod community is dominated by warm water southern species (e.g., *Mesocalanus tenuicornis*, *Paracalanus parvus*, *Ctenocalanus vanus*, *Clausocalanus pergens*, *C. arcuicornis, and C. parapergens*, *Calocalanus styliremis*, and *Corycaeus anglicus*), while during the summer, the copepod community is dominated by cold water-affiliated, lipid-rich boreal/northern species (e.g., *Pseudocalanus mimus*, *Acartia longiremis*, and *Calanus marshallae*) (Peterson and Miller, 1977). The timing of this seasonal shift from southern/winter to a boreal/summer copepod community is defined as the biological spring transition date (Peterson and Keister, 2003). The fall transition is signalled by a reversal from predominantly upwelling to downwelling wind stress resulting in the

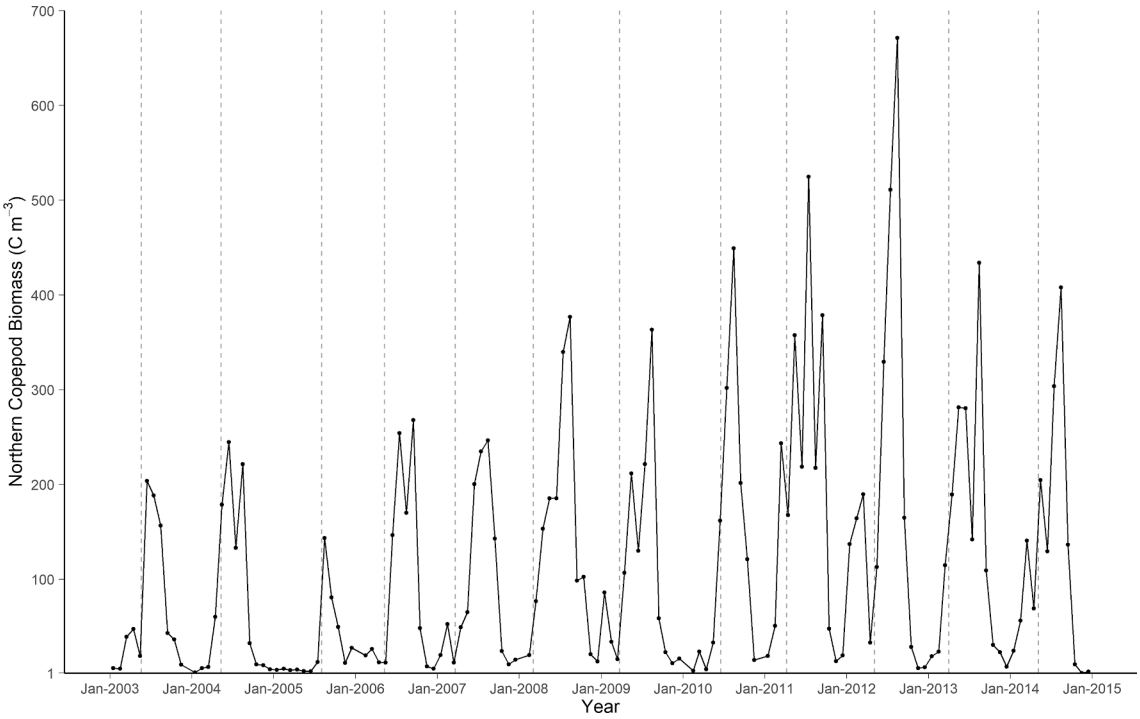

Fig. 2. Northern copepod biomass between 2003 and 2015 from biweekly to monthly collections off Newport, Oregon (46.5°N). Grey dashed line indicates the biological spring transition date for each year (Peterson and Keister, 2003). Northern/boreal copepod communities are dominated by *Pseudocalanus mimus*, *Acartia longiremis*, and *Calanus marshallae* (Hooff and Peterson, 2006; Peterson and Miller, 1977).

return of the predominantly poleward flowing currents and a return of the southern/winter copepod community. The largest differences in total copepod biomass occur seasonally with copepod biomass peaking during the summer months and decreasing in the winter months (Hooff and Peterson, 2006; Fig. 2). However, large scale oceanographic patterns such as El Niño Southern Oscillation (ENSO) or shifts in Pacific Decadal Oscillation (PDO) can also affect the biomass and species composition of zooplankton on interannual time scales (Fisher et al., 2015; Keister et al., 2011).

Copepod biomass and the date of the annual biological spring transition were determined from plankton samples collected twice monthly to monthly from a station (NH 05) located on the Newport Hydrographic Line, 9 km off the coast of Newport, Oregon in 60 m water depth (44.65°N, 124.18°W) approximately 200 km south of the Columbia River estuary (for detailed methods see Peterson and Keister, 2003). Briefly, zooplankton were collected using a 202 μm mesh size, 0.5 m diameter plankton net towed vertically from near the sea floor to the surface at a rate of 30 m/min. Zooplankton samples were preserved in a 5% buffered formalin/seawater solution and were subsampled with a 1.1 ml Stempel pipette for copepod species identification and enumeration. Density was determined as the number of individuals per m^3 of water sampled and the northern copepod biomass was estimated using length to mass regressions standardized to units of mg C m^{-3} for the cold water taxa (Hooff and Peterson, 2006; Fisher et al., 2015).

The biological spring transition date represents the first day of the year that the northern copepod (zooplankton) community was first reported at NH 05 as defined by cluster analysis (Peterson and Keister, 2003), and obtained by NOAA Northwest Fisheries Science Center (www.nwfsc.noaa.gov/). The match/mismatch hypothesis proposes that there should be an optimum biological spring transition date, which would result in a parabolic relationship between biological spring transition date and survival. We therefore calculated a quadratic term (biological spring transition date squared) to account for nonlinearity between the biological spring transition date and survival in our models (see Statistical Analyses section).

Zooplankton are not a main prey item of juvenile steelhead trout, making up only a small fraction their diet (Daly et al., 2014), yet certain zooplankton species can be used as an index of ocean conditions. Appearance of the northern copepod community in the spring signals a transition to shorter, more energy-dense food chains and an ocean ecosystem that is more favourable to the growth and survival of salmonids (Daly et al., 2013; Peterson et al., 2014). In reality, juvenile steelhead trout are likely preying upon euphausiids and icthyoplankton, however conditions favourable to these juvenile steelhead trout prey are similar to those favourable to northern copepods (Daly et al., 2014). Therefore, rather than a direct prey resource, we consider northern copepod biomass and the timing of the biological spring transition to be proxies of abundance and timing of ocean conditions favourable to salmon.

In our analyses, biweekly northern copepod species biomass was linked with salmon outmigration date, such that the zooplankton biomass estimate closest to the tagging date of the juvenile steelhead trout was used as the northern zooplankton biomass experienced by that fish. Therefore, each biomass estimate approximates the conditions experienced by individual fish across outmigration dates.

2.3. Oceanographic and annual variables

Other oceanic processes that operate at large spatial and temporal scales can also influence ocean survival of steelhead trout. These processes are thought to influence marine productivity through affecting nutrient availability and growing conditions of phytoplankton as well as plankton community composition and energy density (Gargett 1997). These oceanic processes are correlated with the biological spring

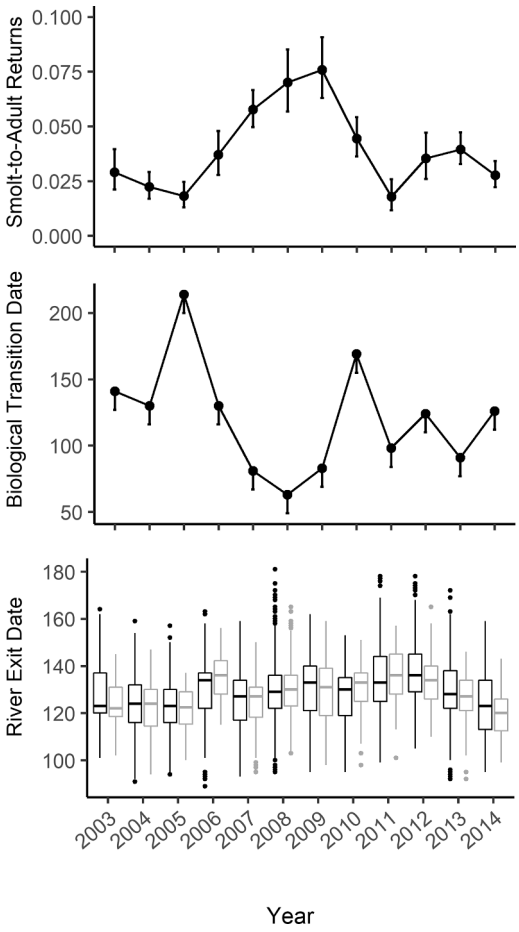

Fig. 3. Yearly smolt-to-adult return (SAR) rates (top), biological spring transition date, which is the first day cold water zooplankton were found off the coast of Newport, OR (middle) and year-day of river exit (boxplots with the 25th, median, and 75th percentiles) and fate (survivors (light grey) and deaths (black); bottom) for smolt ocean entry years 2003 – 2014.

transition date and thus are not independent from match/mismatch but could also be important. For example, when the PDO is negative, the peak in abundance of northern (lipid rich) zooplankton is larger and earlier, and growing season for fish is longer (Keister et al., 2011; Mantua et al., 1997). While it is difficult to untangle these potentially linked processes, it is worth comparing the importance of the mismatch variable (biological spring transition date) in the context of these large-scale oceanic processes. We therefore completed a separate analysis on annual survival data (Annual Covariate Inclusion Model) comparing models including each of these processes, with a degree of mismatch model to determine whether mismatch or these other large-scale correlated variables were most strongly related to ocean survival.

Potential climate variables that are known to influence zooplankton dynamics were collated from existing databases for the years 2003 – 2014. We used mean March to June Coastal Upwelling Index as an indicator of upwelling strength at 45^{o}N 125^{o}W (National Marine Fisheries Science's Pacific Fisheries Environmental Laboratory, (www.cbr.washington.edu/dart/, Bakun, 1973) and see Scheuerell et al. 2009)). The physical spring transition date was calculated as the date when the cumulative sum of the Coastal Upwelling Index (beginning January 1) switched from decreasing to increasing, indicating a change from downwelling to upwelling (see Satterthwaite et al. 2014). Mean March to June air temperature was used as a proxy of sea surface temperature (SST), as a continuous dataset of SST was not available near the Columbia River estuary for the time period of interest (see Mueter et al., 2002b; Nickelson, 1986). We used air temperature data from two NOAA buoy stations; 46029 (46.14^{o}N 124.49^{o}W) and 46,041 (47.35^{o}N, 124.74^{o}W, National Data Buoy Center; www.ndbc.noaa.gov/)). We included mean April to June Columbia River discharge (gage height, ft) measured at the Bonneville Dam (USGS site 14128870), as discharge/flow rate could affect survival as well as the size of the Columbia River plume and thus feeding opportunities (Burla et al. 2010, Phillips et al. 2017). We also used the mean March to June Pacific Decadal Oscillation estimates (PDO; Nathan Mantua, http://research.jisao.washington.edu/pdo/), mean April to June El Niño Southern Oscillation estimates (ENSO; National Weather Service, www.cpc.ncep.noaa.gov/), and Aleutian Low Pressure Index (ALPI; https://open.canada.ca/). We also used three measures of the marine ecosystem: northern copepod biomass anomalies, southern copepod biomass anomalies, and a composite metric of 15 ecosystem indicators derived from principal component analysis (PC1 scores of physical and biological indicators such as sea surface temperature/salinity, upwelling, deep sea temperature/salinity, southern and northern copepod anomalies, biological spring transition date, PDO, ENSO, etc.; see Peterson et al., 2014)) used to forecast adult spring and fall Chinook and coho salmon returns to the Columbia River (Table S1; Peterson et al., 2014).

2.4. Statistical analyses

2.4.1. Modelling approach

We used Bayesian multilevel regression models to account for the hierarchical nature of our study system with individual-level covariates (e.g., body size) nested within group- and annual-level covariates (e.g., biological spring transition date; Gelman and Hill, 2007; Hox et al., 2018). Our multilevel models predicted steelhead trout survival as a function of scaled and centered individual- and annual-level covariates. Specifically, we assumed individual steelhead trout survival $\phi_{i,y,s}$ followed a Bernoulli distribution with survival probabilities $\mu_{i,y,s}$ estimated from a multilevel regression using a logit-link function such that:

$$\phi_{i,y,s} \sim Bernoulli(\mu_{i,y,s})$$

where $\phi_{i,y,s}$ was a zero or one indicating whether an individual fish i survived or not. The probability of survival was calculated using the inverse logit transformation of $\mu_{i,y,s}$,

where $\mu_{i,y,s}$ was a linear function of individual- i, year- y, and site- s level predictors and interactions.

2.4.1.1. Biological spring transition date model. For the first phase of model selection, the individual level of the model took the form:

$$logit(\mu_{i,y,s}) = \beta_0 + \beta_{FL}FL_i + \beta_{RE}RE_i + \beta_{RE^2}RE_i^2 + \beta_Z Z_i + \beta_{FL.RE}FL_iRE_i + \beta_{FL.Y_y}FL_i + \beta_{RE.Y_y}RE_i + w_{y,s} \quad (1)$$

where β_{FL}, β_{RE}, β_{RE^2}, β_Z, and $\beta_{FL.RE}$ were individual level predictors of size FL (fork length), river exit date RE (the year-day the smolt left the Wind River), river exit date squared RE^2(representing optimal river exit date), northern zooplankton biomass Z (matched with outmigration date for individuals), and the interaction between size and river exit date, respectively. The model also included cross-level interactions $\beta_{FL.Y_y}$ and $\beta_{RE.Y_y}$ which described annual adjustments to the effect of size and river exit date on survival. The annual adjustment to the effect of size on survival was modeled as follows:

$$\beta_{FL.Y_y} = \beta_{FL.BIO}BIO_y + \varepsilon_y^{year.FL.BIO} \quad (2)$$

where the annual adjustment to the effect of size was a fixed effect $\beta_{FL.BIO}$ of the biological spring transition date BIO each year, and a year-specific random effect $\varepsilon^{year.FL.BIO}$:

$$\varepsilon_y^{year.FL.BIO} \sim normal(0, \tau^{year.FL.BIO}) \quad (3)$$

The annual adjustment to the effect of river exit date on survival was modeled as follows:

$$\beta_{RE.Y\,y} = \beta_{RE.BIO} BIO_y + \varepsilon_y^{year.RE.BIO} \quad (4)$$

where the annual adjustment to the effect of size was a fixed effect $\beta_{RE.BIO}$ of the biological spring transition date *BIO* each year, and a year-specific random effect $\varepsilon^{year.RE.BIO}$:

$$\varepsilon_y^{year.RE.BIO} \sim normal(0, \tau^{year.RE.BIO}) \quad (5)$$

Finally, the model also included a group-level (year and site) effect $w_{y,s}$, where the group-level model acted as a prior for individual-level year-site specific intercept (Gelman and Hill, 2007):

$$w_{y,s} = \beta_{BIO} BIO_y + \beta_{BIO^2} BIO_y^2 + \varepsilon_{y,s}^{year.s} \quad (6)$$

modeled as fixed effects β_{BIO} of the biological spring transition date *BIO* and β_{BIO^2} of the biological spring transition date squared BIO^2 (representing optimal timing of spring productivity) for each year, and a nested random effect of site within year:

$$\varepsilon_{y,s}^{year.s} \sim normal(\varepsilon_y^{year}, \tau_{site}) \quad (7)$$

based on a global (across sites) random effect of year:

$$\varepsilon_y^{year} \sim normal(0, \tau_{year}) \quad (8)$$

We used Bayesian variable selection to determine the probability that a parameter occurred in the best model, which consequently provided an intrinsic estimate of parameter importance. In Bayesian variable selection each variable $X_{i,j}$ is multiplied by a Bernoulli distributed inclusion probability ω with prior probabilities of 0.5 (Hooten and Hobbs, 2015; Royle and Dorazio, 2008) such that:

$$logit(\mu_{i,y,s}) = \beta_0 + \omega\beta_1 X_{i,y} + \epsilon_{y,s} \quad (9)$$

Thus, as the posterior probability of the inclusion variable approaches 0 or 1, certainty that the variable is to be excluded or included, respectively, increases. Conversely, a posterior probability of 0.5 (i.e., the effect of a covariate was as likely as a fair coin flip) demonstrates uncertainty as to whether the variable should be included or not. For variables that included interactions, including quadratic terms, probability of inclusion was adjusted from 0.5 based on the probability of higher-level terms occurring. Thus, the probability of the base term(s) (e.g., x, x_1, x_2) occurring depended on the probability of the higher level term (e.g., x^2, x_1x_2) occurring (Hooten and Hobbs, 2015; Kruschke, 2015; Kuo and Mallick, 1998).

$$\omega_1 = Bernoulli(p_1) \quad (10)$$

$$p_1 = \omega_2 + (1 - \omega_2 0.5) \quad (11)$$

$$\omega_2 = Bernoulli(p_2) \quad (12)$$

The probability of inclusion of the base term ω_1 was either a 0 or 1 based on the mean of the Bernoulli distribution p_1, where p_1 is dependent on the probability of the higher-level interaction occurring. The variable inclusion probability of the higher-level interaction occurring ω_2 was either 0 or 1, given by a Bernoulli distribution with a mean of $p_2 = 0.5$. In the case where the interaction involved a categorical variable, p_2 is the average inclusion probability for each interaction parameter, rather than 0.5. For example, for the interaction between year and size there are twelve parameters (one for each year); a parameter inclusion variable was assigned to each of the twelve parameters and the average of all twelve inclusion parameters was used as p_2 (Kuo and Mallick, 1998). Inclusion probabilities were estimated for all individual-level fixed effects (β_{FL}, β_{RE}, β_{RE^2}, β_Z, and $\beta_{FL.RE}$) cross-level interactions ($\beta_{FL.Y_y}$ and $\beta_{RE.Y_y}$) and group-level fixed effects (β_{BIO} and β_{BIO^2}). Parameter estimates in models employing Bayesian variable selection are intrinsically model-averaged (Kuo and Mallick 1998; Royle and Dorazio, 2008, Hooten and Hobbs, 2015). Parameters with inclusion probabilities greater than 0.5 were considered to be included in the best model(s).

2.4.1.2. Annual Covariate inclusion model. For the second phase of our model selection, the Annual Covariate Inclusion Model, we simplified the individual level of the model to include only covariates that had greater than 50% inclusion probability in the Biological Spring Transition Date Model, and instead tested the annual covariates. The individual level of the Annual Covariate Inclusion Model took the form:

$$logit(\mu_{i,y,s}) = \beta_0 + \beta_{FL} FL_i + \beta_{RE} RE_i + \beta_{RE^2} RE_i^2 + \beta_{RE.Y\,y} RE_i + w_{y,s} \quad (13)$$

The annual adjustment to the effect of river exit date on survival was modeled the same as the Biological Spring Transition Date Model (eqs. (4), (5)). Similarly, this model included a group-level (year and site) effect $w_{y,s}$, which functioned as a prior for individual-level year-site specific intercept (Gelman and Hill, 2007).

$$w_{y,s} = \beta_A A_y + \varepsilon_{y,s}^{year.s} \quad (14)$$

where β_A is a fixed effect of the one of the annual covariates A_y for each year and a nested random effect of site within year (eq (7)), based on a global (across sites) random effect of year (eq (8)).

In the Annual Covariate Inclusion Model we used a different Bayesian variable selection approach to determine the probability that an annual parameter should be included in the model. Most annual predictors were highly correlated (Fig. S9) and thus inclusion of multiple annual predictors would violate the underlying assumptions of linear models. Therefore, we used a categorical predictor variable with a Dirichlet probability distribution to select one of 11 annual covariates for inclusion in the model:

$$A_y = \begin{cases} A_{1,y} & \delta_y = 1 \\ A_{2,y} & \delta_y = 2 \\ \cdots & \\ A_{11,y} & \delta_y = 11 \end{cases}$$

$$\delta_y = categorical\left(\frac{\rho_{nt}}{\sum_{n=1}^{11}\rho_{nt}}\right)$$

where δ_y was an indicator variable (see Table S1 for variable assignment). Each annual indicator had a prior of $\rho_t = 1/11$.

2.4.2. Priors

We used vague priors in order to allow the likelihoods to dominate the priors in determining the posterior. Fixed effects (all β's) were given normal priors with a mean of zero (since our data were scaled and centered), and standard deviation of one or three. The precision parameters (all τ's) were given gamma priors with shape and rate parameters of 0.01. We ran our Biological Spring Transition Date Model with fixed effect priors that had a standard deviation of one or three, since inclusion probability can be strongly influenced by prior variance (Kruschke, 2015). Models fit with parameter priors that were assigned standard deviations of one and three produced similar results, demonstrating our variable selection was robust to changes in standard deviation. We report on the model with the normally distributed priors with mean of zero and standard deviation of one. Fixed effect priors for the Annual Covariate Inclusion Model had a mean of zero and a standard deviation of one.

2.4.3. Model fitting and diagnostics

Our models were fitted in the R statistical computing environment (R Core Team, 2018) with GUI RStudio (v1.1.423, 2018) using JAGS and rjags (Plummer, 2018) and runjags packages (Denwood, 2017). Our models used six MCMC chains with 350,000 iterations. A burn in of 100,000 iterations of each chain was used and the chains thinned at a

rate of 1:100, resulting in 2,500 samples retained per chain. JAGS code for both models can be found in supplementary methods (Appendix I). Starting values were jittered for each chain. We verified chain mixing visually using trace plots and a Gelman-Rubin diagnostic test on each parameter to confirm convergence Rhat < 1.1. We then used graphical posterior predictive checks of predicted vs. observed survival probability for each year (Figs. S5, S10). We checked all covariates for evidence of correlation since inclusion probability can be sensitive to correlations among covariates. None of our sub-annual covariates were correlated, with the highest correlation being 6%.

3. Results

Using a dataset of 22,116 juvenile steelhead trout PIT tagged between 2003 and 2014, we investigated patterns of individual and annual ocean survival of steelhead trout (Table 2). Annual smolt-to-adult survival rates varied from 1.8% to 7.6% and averaged 4%. Smolt size, while variable across individuals within a year, was relatively consistent across years and had no pattern throughout the outmigration period (i.e., larger fish did not emigrate first; Fig. S1). Similarly, average river exit date was also relatively consistent from year to year, but there was substantial within-year variation—about 50 days separated the 5% from the 95% migrant. In contrast, the timing of the biological spring transition date was extremely variable from year-to-year during this time series, with a range of 151 days. The earliest biological spring transition dates occurred in early March and corresponded with some of the highest annual smolt-to-adult survival rates observed in the dataset, while late biological spring transition dates in July and August resulted in among the lowest smolt-to-adult survival rates (Table 2, Fig. S7; Fig. 3).

3.1. Biological spring transition date model

We compared Biological Spring Transition Model fit and variable importance of multilevel models fit with individual and annual variables and associated interactions to determine which variables correlated with ocean survival of steelhead trout. The variables most likely to be included in the top model were size (FL; 100%), river exit date (RE; 99%), river exit date squared (RE^2; 96%), river exit date and year interaction (RE*Year; 91%), and biological spring transition date (BIO; 64%) (Table 3). Parameter estimates show that survival was positively associated with individual size, and negatively associated with the annual biological transition date (Fig. 4). We found evidence of an optimal outmigration date (Figs. 4, 5), and this optimum varied among years (Fig. 6). The most probable model included size, river exit date, river exit date squared, the biological spring transition date, and an interaction between river exit date and year (33%; Table 4).

Table 3
Variable inclusion probability of terms predicting ocean survival of steelhead smolts for Biological Spring Transition Date Model.

Variable	Variable Inclusion Probability
FL	**1.000**
RE	0.993
RE^2	**0.963**
RE * Year	0.907
BIO	**0.639**
RE * FL	**0.209**
Z	0.089
BIO^2	0.087
FL * Year	0.078

Variables include river exit date (RE), fork length (FL), total zooplankton biomass (Z), spring biological transition date (BIO). (*) indicates an interaction term. The RE*Year interaction is the intra-annual mismatch term. Terms that have credible intervals that do not cross zero are bolded.

Survival varied throughout the outmigration period, rising to an optimum that varied across years. Three of the four terms that included river exit date (RE, RE^2, RE*Year) had inclusion probabilities greater than 91%. However, 95% credible intervals of the parameter estimate for river exit date were highly uncertain and spanned zero (mean β_{RE} = -0.12, 95% CI = -0.32 -0.07; Fig. 4; Table S2), where reported parameter values are model-averaged estimates. This indicates that river exit date is an important predictor of survival but that the size of the effect was uncertain. There was clear evidence for an optimal outmigration date as average survival probability across all years in the dataset increased from < 2% survival around April 1st, reaching an optima of 3% survival around May 1st, and decreased throughout the remainder of the outmigration period reaching a low of < 0.5% on June 30th (mean β_{RE^2} = -0.13, 95% CI = -0.19 -0.06; Figs. 4, 5; Table S2). Importantly, the relationship between river exit date and survival differed across years—optimal river exit timing varied annually. Inclusion probability of the interaction between river exit date and year was high (91%), and strength of the effect differed by year (Fig. 4). However, there was no clear pattern between river exit date optima and the annual biological spring transition date (R^2 = 0.01, Fig. 6). This suggests that while inter-annual outmigration timing is likely an important predictor of survival, factors other than just annual biological spring transition date seem to control inter-annual variation in optimal river exit.

Years with earlier biological spring transition dates had higher marine survival of steelhead trout. Survival was strongly and negatively related to the biological spring transition date (mean β_{BIO} = -0.39, 95% CI = -0.70 – -0.07; Table S2) and this variable had one of the largest effect sizes of all parameters (-0.39 compared to 0.50 for size; Fig. 4). For example, an average-sized fish (160 mm) migrating during peak outmigration in a year where the biological spring transition date occurred ~ March 22nd (1 SD before the mean biological spring transition date) had 1.5 – 2 times higher probability of survival (4.3%) than it would if it migrated in a year when the biological spring transition date occurred on June 12th (2.6%, 1 SD after the mean biological spring transition date, Fig. 5). Thus, there was partial support for the annual mismatch hypothesis. On the one hand, there was little evidence for an optimum biological spring transition date (9% inclusion probability of the quadratic term, Table 3), indicating a linear relationship where earlier biological spring transition dates were related to higher survival. Yet, annual patterns of the timing of energy-rich (northern) zooplankton availability appear related to annual smolt-to-adult survival rates.

Larger than average individuals had a higher probability of survival than smaller individuals. In the Wind River, average marine survival of steelhead trout larger than 177 mm (1 SD larger than the mean) was 2.5 times higher than a fish of 146 mm (1SD below the mean; Fig. 5). The benefit of large body size was consistent regardless of outmigration date as evidence by the low inclusion probability (20%, Table 3) for the interaction between size and river exit date, (mean $\beta_{FL.RE}$ = 0.07, 95% CI = 0.01– 0.14, Fig. 4; Table S2). Body size also did not interact with year, suggesting no year-specific size-dependent relationship (inclusion probability of 8%). The year intercept included the biological spring transition date and a random effect, where biological spring transition date explained 41% of yearly variation in survival. Northern copepod biomass was included in only 9% of models. The effect size was small and overlapped zero (mean β_Z = -0.03, 95% CI = -0.20 – 0.14; Table S2), indicating a lack of association with survival (Table 3). Finally, site was included as a random effect nested with year, to account for the differences in survival between fish tagged in different locations within the watershed, however coefficients for the random effect of site varied little between sites.

3.2. Annual Covariate inclusion model

Of the eleven annual-level variables evaluated for their potential association with survival, we found that four had inclusion probabilities above 9% (the cut off for variable importance is determined by the

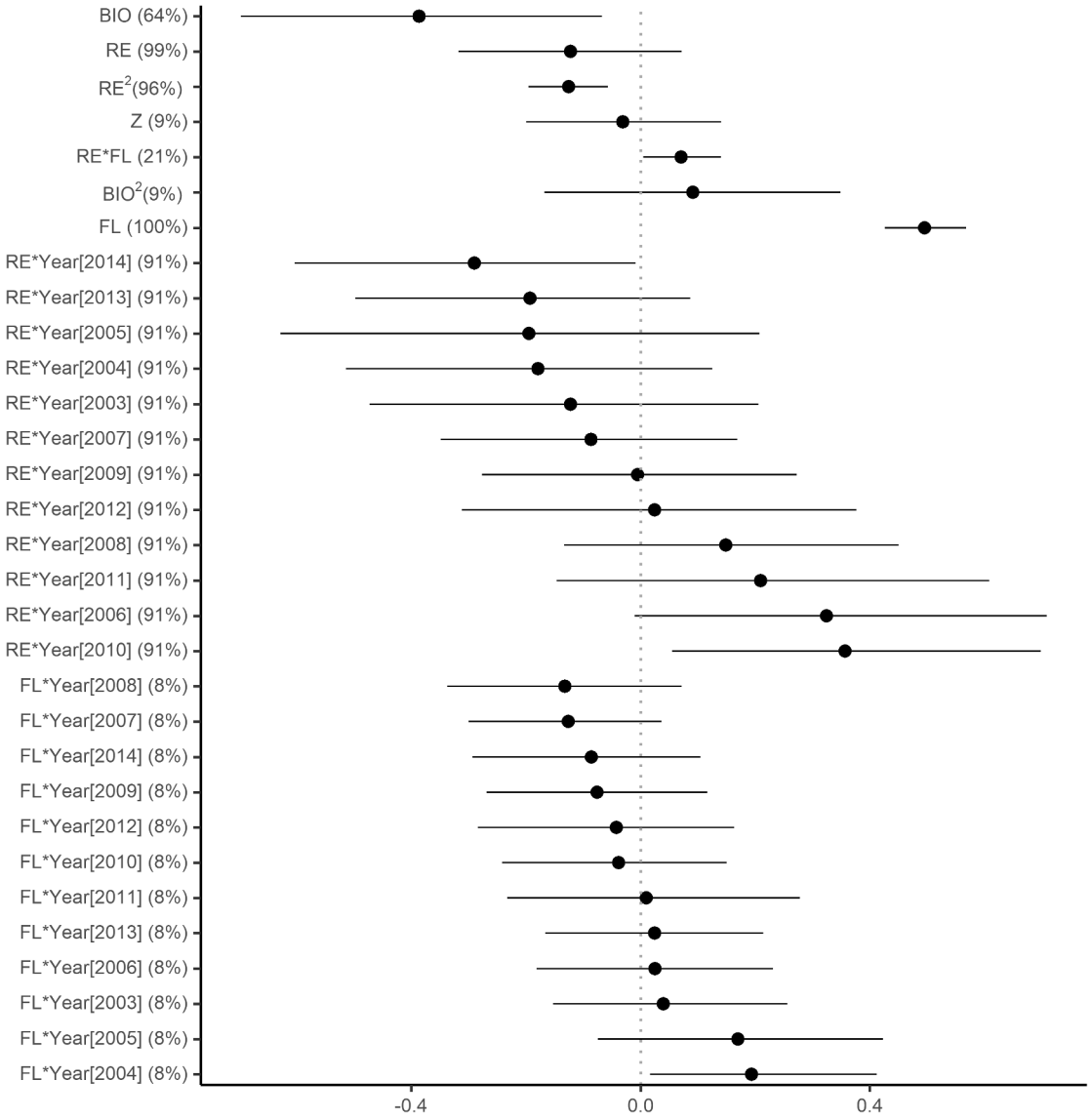

Fig. 4. Coefficients for terms in the Biological Spring Transition Date model. Black point is the mean, and lines are the 95% credible intervals. Variables include river exit date (RE), fork length (FL), northern copepod biomass (Z), spring biological transition date (BIO). (*) indicates and interaction term. Percent in brackets beside each term indicates the variable inclusion probability for that term (Table 3).

number of variables being compared – in this case 11 variables means the cut off is 1/11, or 9%). Air temperature off the coast of Washington, US, was the best predictor with an inclusion probability of 52.7%, followed by the timing of the spring upwelling transition date off the coast of Washington (16.8%), PDO (12.2%) and finally ecosystem indicator (10.4%; Table 5). Biological spring transition date had a lower variable inclusion probability (2.6%) but had credible intervals that did not cross zero (mean β_{A_1} = -0.32, 95% CI = -0.60 – -0.02; Table S3), indicating a large, but uncertain effect size.

4. Discussion

Here we examined individual and annual survival of greater than 22,000 juvenile steelhead trout over a decade of research. Our study had two key findings. First, at the individual level, survival was strongly size- and timing-dependent: larger fish had higher survival and optimal river exit date varied across years. Optimal individual outmigration timing varied within and across years, but this variation was poorly explained by biological spring transition date. Second, across years, survival was higher in years when the biological spring transition date occurred earlier in the year and before Wind River smolt outmigration (Fig. 5). This increased survival also corresponded to earlier spring upwelling transition dates and cooler sea surface temperatures off of coastal Washington. Therefore, we found partial support for both annual and inter-annual mismatch hypothesis (Table 1). Marine survival was dramatically lower in years when the biological spring transition date occurred after smolt outmigration, suggesting that when estuaries and coastal environments have low quality prey/growing conditions when outmigration occurs, marine survival is much lower, compared to years when high quality lipid rich prey is present throughout smolt outmigration. Collectively, our study provides evidence that outmigration year-class strength can be determined by shared conditions experienced during early ocean phase as well as key population traits of size and river exit date governed by freshwater growing conditions.

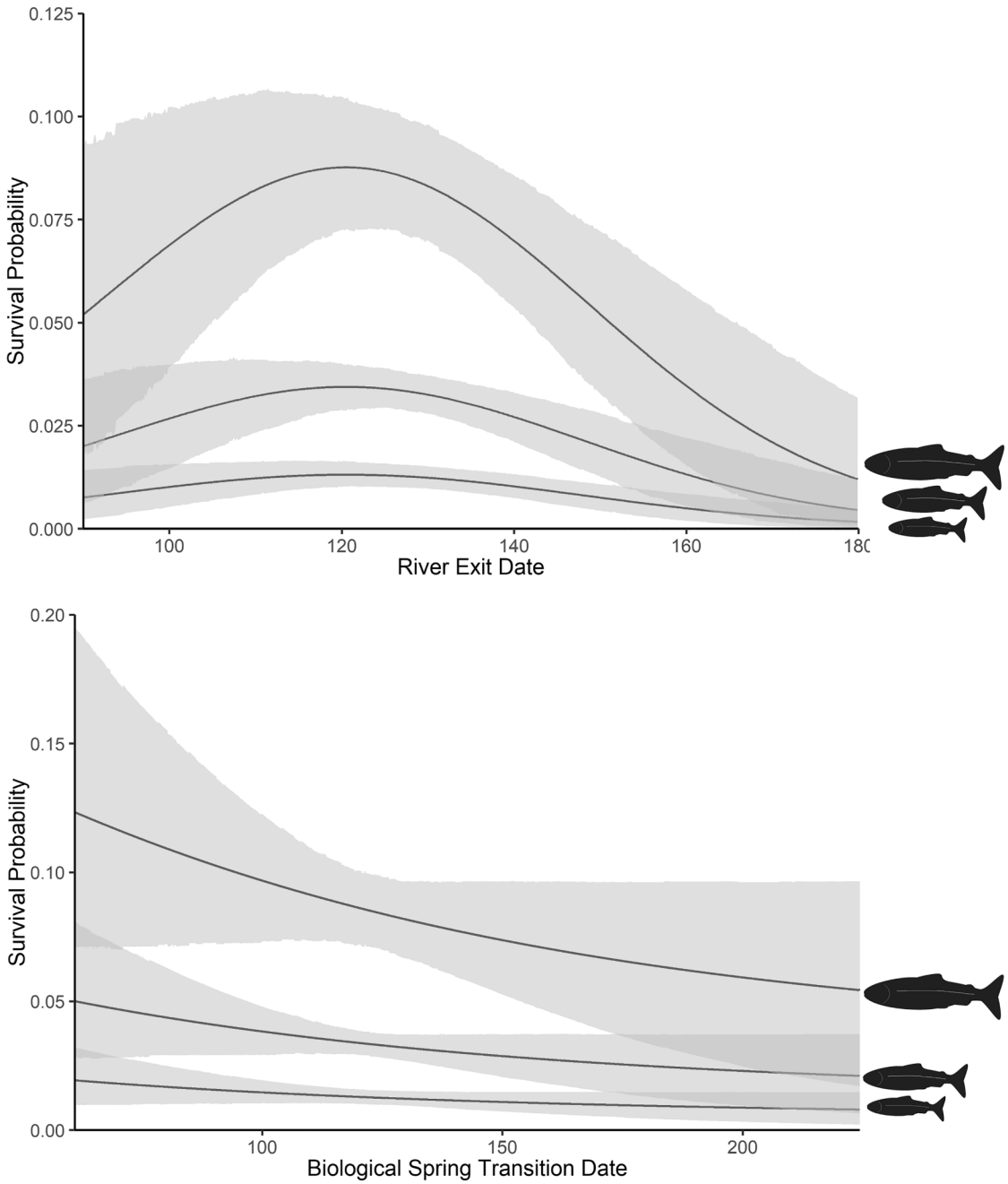

Fig. 5. Posterior predictions of survival probability for Wind River juvenile steelhead trout at the mean and +/- 2 SD of observed sizes (130 mm, 160 mm, 192 mm) across the observed time lags (top) and biological spring transition date (bottom) using model averaged coefficients (Table 3, Fig. 4). Shaded area indicates 95% high probability density interval. Predictions are based on other terms at their mean, and variable weighting based on variable inclusion probability.

Survival was related to outmigration timing, and the optimum outmigration timing varied from year to year. We predicted that outmigration timing would influence the survival of outmigrants (Table 1). Outmigration timing was an important variable for predicting survival, and there was strong evidence for an optimal river exit date. On average, survival probability peaked 7 – 10 days before peak outmigration timing. While we specifically predicted that the optimal river exit date would be related to the annual biological transition date, this was not the case. Instead, annual phenological factors in the estuary or ocean other than annual biological transition date appeared to be associated with optimal river exit date (Fig. 6).

Freshwater growing and migration conditions may also influence inter-annual variation in optimal river exit date. For example, Wind River steelhead smolts migrate for different lengths of time which could represent significant additional unexplained variation in outmigration timing (Figs. S1, S3). Approximately 10% of tagged smolts were subsequently detected downstream 2 – 59 (median 8) days after tagging at either the Bonneville Dam or in the Columbia River estuary. The range in outmigration dates within a year generally spanned 60 days, so differences in migration rates could have modified the window of arrival in the estuary. Therefore, it is possible that any potential relationship between river exit date and biological spring transition date was confounded by differing migration rates.

There was strong evidence that inter-annual timing of prey availability was an important predictor of survival, yet the findings did not conform to the classic match/mismatch hypothesis. Cushing's original

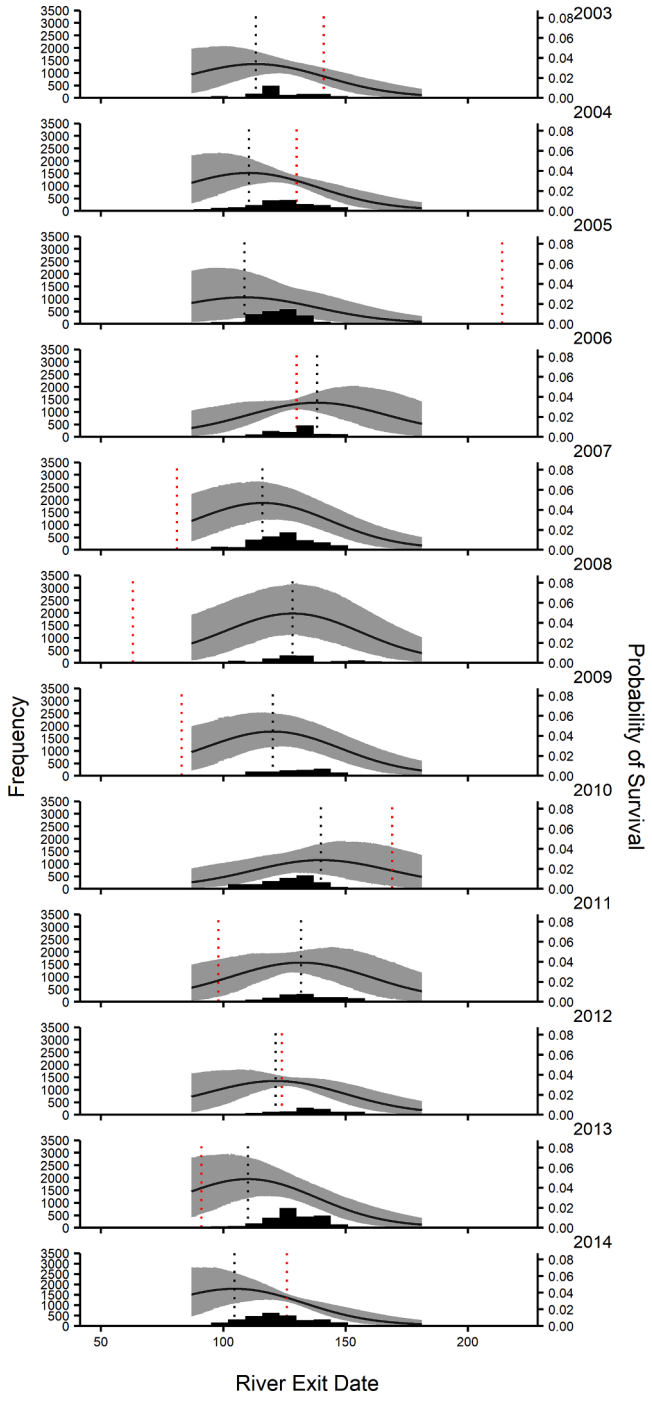

Fig. 6. Effect of the degree of mismatch on model predictions of survival probability for river exit date for each year. The river exit date by year interaction represents the individual-level match/mismatch term. Shaded area indicates 95% high probability density interval. Vertical red line indicates biological spring transition date and dotted black line indicates optimal river exit date for that year. Predictions are based on other terms at their mean, and variable weighting based on variable inclusion probability.

Table 4
Top ten candidate model performance for predicting survival of individual steelhead trout.

Model	Model Probability
FL + RE + RE^2 + RE* Year + BIO	0.325
FL + RE + RE^2 + RE* Year	0.218
FL + RE + RE^2 + RE* Year + BIO + FL*RE	0.086
FL + RE + RE^2 + RE* Year + FL*RE	0.057
FL + RE + RE^2 + RE* Year + BIO + BIO^2	0.049
FL + RE + RE^2 + RE* Year + BIO + zooplankton biomass	0.035
FL + RE + RE^2 + BIO	0.031
FL + RE + RE^2 + RE* Year + BIO + FL*Year	0.022
FL + RE + RE^2 + RE* Year + zooplankton biomass	0.018
FL + RE + RE^2	0.017
FL + RE + RE^2 + RE* Year + FL*Year	0.014
FL + RE + RE^2 + RE* Year + BIO + BIO^2 + FL*RE	0.014

Variables are river exit date (RE), fork length (FL), northern zooplankton biomass (zooplankton biomass), biological spring transition date (BIO). (*) indicates and interaction term. The RE*Year interaction is the intra-annual mismatch term.

Table 5
Variable inclusion probability of terms predicting ocean survival of steelhead smolts for Annual Covariate Inclusion Model.

Variable	Variable Inclusion Probability
Sea Surface Temperature	0.527
Spring Upwelling Transition Date	0.168
PDO	**0.122**
Ecosystem Indicators	**0.104**
Biological Spring Transition Date	**0.026**
Southern Copepod Index	0.019
Upwelling Strength	0.011
ENSO	0.007
Columbia River Discharge	0.007
ALPI	0.006
Northern Copepod Index	0.005

Variables include Aleutian Low Pressure Index (ALPI), Pacific Decadal Oscillation (PDO), El Niño Southern Oscillation (ENSO). Terms that have variable inclusion probabilities higher than 0.09 were included in model averaging. Terms than have credible intervals that do not cross zero are bolded.

match/mismatch hypothesis proposed that both predators and prey are temporally pulsed (i.e., are present in large number for a short period of time within the year), and peak synchrony would result in the highest recruitment (Cushing, 1990, 1969). Based on our annual mismatch hypothesis, we predicted that biological spring transition date would be an important variable in explaining annual patterns in smolt-to-adult survival. Biological spring transition date varied widely across years ranging between March 4th and Aug 2nd (~150 days) whereas average outmigration date did not appear to vary substantially throughout the monitored period (2003 – 2014; Fig. 3). Thus, annual changes in biological transition date represent annual changes in phenological mismatch. However, we found limited evidence for a biological spring transition date that optimized survival, and instead discovered that steelhead trout survival was higher if the biological spring transition date occurred earlier in the year. The transition from a winter to a summer copepod community occurs rapidly and is marked by a drastic increase in zooplankton biomass. Although steelhead trout migration occurs over approximately two months in this system, the window of optimal prey can easily be missed, if outmigration occurs prior to the onset of the lipid rich copepod community following the biological transition (Fig. 2). Thus, rather than a small window of optimal outmigration timing as predicted by the match/mismatch hypothesis, it appeared that survival increases as biological spring transition date gets earlier in this system, at least within the range of observed transition

dates in our short time series. The timing of the biological spring transition date is an index of when energy-rich northern copepods become available to higher trophic levels including larval fish and mesozooplankton. Though copepods are not the dominant prey of juvenile steelhead trout, they are a proxy of good or poor ocean conditions for salmon (Miller et al. 2017). While biological spring transition date was important in our model, it explains only 41% of the yearly variation, and it is likely that other shared freshwater or marine conditions impacted survival. Indeed, results from our Annual Covariate Inclusion Model show that sea surface temperature and spring upwelling transition date were important predictors of steelhead marine survival. Interestingly, both of these variables could be related to growing/feeding conditions in regions north of the Columbia River, where steelhead trout are thought to migrate to quickly and feed (Daly et al., 2014; McMichael et al., 2013; Rechisky et al., 2012, 2009; Van Doornik et al., 2019). This evidence supports the annual mismatch hypothesis but suggests that marine regions to the north are likely more important for steelhead survival, than the Columbia River estuary.

Another possible reason survival is not optimal at a phenological match is that Wind River steelhead trout smolts are larger than other anadromous salmon species and are partly piscivorous by the time they leave their natal rivers (Daly et al., 2014; Myers, 2018). Indeed, steelhead trout are unlikely to eat copepods, but rather we used copepods as an indicator of food web quality, such that in years where the biological spring transition date is earlier, there could be more larval fish in the late spring (Daly et al., 2014). Additionally, the species composition and abundance of larval fish during the winter (Jan to Mar) are good indicators of the future prey available to outmigrating salmon (Daly et al. 2013). Larval fish abundance has been related to juvenile salmon survival and might also be a good indicators of future prey available to outmigrating Wind River steelhead trout smolts. Further analysis into the timing and abundance of larval fish could be an interesting avenue of future salmon mismatch studies. Regardless, our findings add important biological realities to the classic match-mismatch hypothesis, and reveal that when high quality prey are available during ocean entrance, survival of Wind River steelhead trout is higher.

Other studies have found that timing of prey availability matters for salmon. Scheuerell et al. (2009) found similar results to our study using individually tagged Snake River Chinook salmon and steelhead trout. Individuals leaving earlier in the year had higher survival than those leaving later in the year. They found a significant interaction between exit date and year that was not related to spring upwelling date. They did not find evidence that upwelling date affected survival, but noted a small sample of only four years was not enough to examine inter-annual variability. On the other hand, a time lag of 70 – 115 days from the spring upwelling transition date produced an optimal survival probability for hatchery-reared Chinook salmon from the California Valley (Ryding and Skalski, 1999; Satterthwaite et al., 2014). Relationships between smolt migration timing and annual timing of spring productivity have been found in some populations of pink salmon *O. gorbuscha*, where an early spring phytoplankton bloom benefited northern populations. However, these trends were reversed for southern pink salmon populations such as those in southern British Columbia, where later phytoplankton blooms were shown to increase productivity in pink salmon (Malick et al., 2015a; Mueter et al., 2002a). Interestingly, in our study, northern copepod biomass was not strongly correlated with survival, despite evidence that food availability can affect ocean survival (Peterson and Schwing, 2003; Ruggerone and Goetz, 2004; Tanasichuk and Routledge, 2011). Availability of food during the first 45 days in the ocean correlated with sockeye salmon survival in British Columbia (Tanasichuk and Routledge, 2011). Increased food availability shifted the onset of piscivory to be earlier, where an earlier shift to piscivory was correlated with increased growth and survival in subyearling Chinook salmon (Litz et al., 2017). Thus, our study adds to the growing body of evidence that the phenology of nearshore marine prey can influence marine survival in salmon, but the strength of this correlation is likely dependent on species and food web structure (Durant et al., 2005).

Intra-annual variability in outmigration timing likely acts as a buffer that stabilizes populations in the face of unpredictable and highly variable ocean conditions. Outmigration periods for Wind River steelhead trout were broad, ranging more than 60 days. Additionally, migration rates appeared to vary highly among the subset of fish tracked to Bonneville Dam and the Columbia River estuary, ranging from 2 to 59 days. Interestingly, few late migrating fish took longer than 30 days to complete their freshwater migration resulting in later fish having less variable and faster migration rates, compared to fish leaving the Wind River at the beginning of their migration (Fig. S1). Together, the window of ocean-entry by Wind River fish likely varies by more than three months. This breadth in phenological expression may function as a bet-hedging strategy that would in effect protect populations from variability in ocean conditions that are difficult or impossible to predict based on local environmental cues (Beamish et al., 2013; Carr-Harris et al., 2018; Freshwater et al., 2019; Schindler, 2019). Indeed, the optimal date of migration varied across years by ~ 35 days. Within large river systems, different salmon populations have different outmigration timing, and this may further stabilise the metapopulation from extreme swings in ocean conditions (Beamish et al., 2016; Carr-Harris et al., 2018; Sturrock et al., 2019). Here we provide critical empirical support for the hypothesis that breadth in migration timing is a key life-history trait that provides resilience to populations faced with variable ocean climates.

Larger steelhead trout had higher marine survival compared to smaller fish, when all other variables were equal. Thus, marine survival is not just related to oceanic conditions, but also characteristics carried over from freshwater. We found that size at river exit was more important than timing of food availability, where larger fish have higher ocean survival, irrespective of timing of the biological transition date. Previous studies have also found that larger than average salmon smolts may have higher ocean survival (Beacham et al., 2014; Beamish and Mahnken, 2001; Ward et al., 1989), but not always (Anderson, 1988; Beamish et al., 2010; Ulaski et al., 2020). Given that hatchery steelhead smolts are larger than wild steelhead smolts, our results could be interpreted as suggesting that hatchery smolts would have higher survival. However, we suggest caution when applying our results to hatchery fish as hatchery fish may respond differently to shared environmental conditions compared to wild fish, and generally have much lower survival probability (Jonsson et al., 2003). Furthermore, size-at-age may be an important factor determining marine survival, however age data were not available (Ulaski et al., 2020). A diversity of freshwater factors may control steelhead trout smolt size, ranging from species interactions with co-occurring salmon to weather and density dependence (Bailey et al., 2018); our results indicate that these factors can have carryover effects on marine survival.

Our results are particularly important given increased variability in ocean conditions and increased prevalence of anomalous warming events. Climate change is warming sea surface temperatures and advancing zooplankton biomass peaks globally, but not all species are advancing at the same rate (Richardson, 2008). Our model results suggest that phenological shifts towards ocean conditions favorable for an earlier onset of a lipid rich zooplankton community could be beneficial for steelhead trout in this region. However, warm ocean conditions favor a delayed, or non-existent, shift to a lipid rich zooplankton community (Peterson et al., 2017). Low frequency warming events associated with the PDO and ENSO have modified the zooplankton community in the northern California Current, resulting in copepod communities dominated by lipid poor subtropical species (Keister et al. 2011; Fisher et al. 2015). A recent anomalous event, coined 'the Blob', first impacted the northern California Current in the fall of 2014 and lasted at least through 2016. This event had far-reaching effects on the northeastern Pacific pelagic ecosystem (Auth et al., 2018; Peterson et al., 2017). This anomalous event resulted in a lack of a biological spring transition in 2015 and 2016, the two years after our study, such that the copepod community remained a lipid-depleted community, which had only been

recorded once before in the 22-year time series during the strong El Niño in 1997/98. Smolt-to-adult returns for smolts migrating in 2015 were 1.0%, the lowest in the history of the Wind River steelhead trout monitoring project (Buehrens and Cochran, 2018). If 2015/16 years are any indication of future ocean conditions under increasing climate pressure, increased biomass of less nutritious zooplankton are unlikely to be beneficial to steelhead trout. More broadly, the outmigration timing of some salmon species appears to be lagging behind advancement of regional phytoplankton blooms and it is unclear what effect, if any, this will have on salmon population dynamics (Kovach et al., 2013; Otero et al., 2014; Taylor, 2007). Based on our findings, climate-induced shifts in phytoplankton blooms could affect salmon survival insofar as they affect zooplankton community composition and timing of peak biomass of lipid-rich zooplankton species. Indeed, other studies have found that shifts in the zooplankton community composition and abundance can affect the survival of salmon (Peterson and Schwing, 2003). Further investigation of the effect of food quality vs. timing on salmon survival would be an interesting and relevant avenue for future research.

There is overwhelming evidence that bottom-up processes influence anadromous salmon and trout survival, but that does not preclude other factors such as competition and predation from being major contributors to early ocean survival (Pearcy, 1992). For example, Caspian terns *Sterna caspia* and double-crested cormorants *Phalacrocorax auritis* occupying dredge spoil islands in the Columbia River estuary consumed between 10 and 20% of steelhead trout smolts leaving the Columbia River from 2008 – 2013 (Hostetter et al., 2015). In another example, increases in harbour seal *Phoca vitulina* populations have been correlated with decreases in wild Fraser River Chinook salmon (Nelson et al., 2018). Top-down pressure from predation can be size-biased, and is a likely contributor of variation in early marine survival, which is not directly accounted for by our model or the match/mismatch hypothesis (Emmett et al., 2006; Osterback et al., 2013; Roby et al., 2003; Tanasichuk and Emmonds, 2016). However, faster somatic growth rates that occur during a phenological match can buffer predation by reducing predation risk (Pope et al., 1994), thus a phenological match could indirectly reduce top down pressure. Predation risk and competitive ability will also covary with smolt size. Finally, sockeye salmon smolts that compete with abundant odd-year pink salmon populations in the early marine environment have significantly lower growth and survival (Ruggerone et al., 2003). Future studies could include predator abundance or evaluate match/mismatches between salmon, their predators and competitors.

Given recent steelhead trout population declines in the northeast Pacific, it is timely to quantify patterns of ocean survival to begin to understand potential contributing factors. The Northwest Power and Conservation Council maintains a goal of a 4% average smolt-to-adult return rate (SAR) to facilitate viable Columbia River steelhead trout populations (NPCC, 2014), yet in eight of the twelve years observed, the Wind River population SAR has been lower than this threshold, with some years dropping below the lower end of the NPCC target range of 2 – 6%. Wind River steelhead trout have comparatively short migrations, passing only one dam, and therefore presumably experience less riverine and hydrosystem-induced mortality than upstream Columbia River populations. Considering its location in the hydrosystem, the fact that Wind River steelhead trout SAR is frequently below the NPCC targets reveals that poor ocean survival, in addition to riverine and hydrosystem survival, may compromise achieving NPCC viability goals. Because larger individuals have higher survival regardless of the degree of mismatch, it is possible that improvements in freshwater habitat quality that increase growth or size-at-age could buffer some wild steelhead and salmon populations from some of the effects of mismatch. However, since the majority of Wind River steelhead spend their final year rearing in canyon reaches with largely intact habitat (Buehrens and Cochran 2018), it is not immediately clear what, if any, habitat improvements could be implemented to improve freshwater growth for our study population. Further, climate-driven decreases in habitat quality in both freshwater and ocean environments could have a compounding effect on steelhead trout ocean survival and population productivity.

Understanding the mechanisms contributing to variation in smolt-to-adult returns for Pacific salmon could facilitate better run-size forecasts. Steelhead trout are an important recreational fishery species, as well as important ceremonial, and subsistence fisheries for tribes and First Nations. Yet, populations have declined dramatically in the last few decades. Incorporating a more detailed understanding of timing of food availability and energy requirements could help manage these important fish populations. We found that steelhead trout that enter an ocean environment with high quality prey at the base of the food web are more likely to survive than steelhead trout migrating in years when the biological spring transition date is late (after June 1st), and that larger fish are more likely to survive than smaller fish irrespective of degree of mismatch. Thus, phenological mismatches may impact marine fisheries population productivity, but it is important to consider the broader context in which these mismatches occur as other factors such as individual size can have an additive or ameliorative effect on the population-level response.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2021.102533.

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