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# Influence of ocean ecosystem variation on trophic interactions and survival of juvenile coho and Chinook salmon

James P. Losee, Jessica A. Miller, William T. Peterson, David J. Teel, and Kym C. Jacobson

**Abstract:** The community of trophically transmitted marine parasites of juvenile coho (*Oncorhynchus kisutch*) and Chinook (*Oncorhynchus tshawytscha*) salmon across 8 years (2002–2009) was related to indices of physical and biological ocean conditions and adult returns. When the biomass of lipid-poor, southern origin copepods in the coastal ocean was high during juvenile salmon outmigration from fresh water (April–June), yearling coho and Chinook salmon harbored a different trophically transmitted parasite fauna and exhibited lower survival compared with years when the southern copepod biomass was low. As copepods are key intermediate hosts in many marine parasite life cycles, these results support a trophic linkage between the copepod community and salmon prey. Interannual variation in the parasite community was correlated with survival of coho salmon ( $r = -0.67$ ) measured 1 year later and adult returns of Upper Columbia River summer and fall Chinook salmon ( $r = -0.94$ ) 3 years from the time of ocean entry.

**Résumé :** La communauté de parasites marins à transmission trophique des saumons cohos (*Oncorhynchus kisutch*) et quinnats (*Oncorhynchus tshawytscha*) juvéniles observée sur une période de 8 ans (2002–2009) a été reliée à des indices des conditions physiques et biologiques du milieu océanique et aux retours d'adultes. Quand la biomasse de copépodes du sud pauvres en lipides dans l'océan côtier était élevée durant la descente des saumons juvéniles à partir de leur milieu d'eau douce (d'avril à juin), les saumons cohos et quinnats de l'année présentaient une faune de parasites à transmission trophique différente et des taux de survie plus faibles que durant les années où la biomasse de copépodes du sud était faible. Comme les copépodes sont des hôtes intermédiaires clés dans le cycle biologique de nombreux parasites marins, ces résultats appuient l'existence d'un lien trophique entre la communauté de copépodes et les proies des saumons. Les variations interannuelles dans la communauté de parasites ont été corrélées avec la survie des saumons cohos ( $r = -0,67$ ) mesurée 1 an plus tard et avec les retours de saumons quinnats adultes estivaux et automnaux du cours supérieur du fleuve Columbia ( $r = -0,94$ ) 3 ans après leur entrée en mer. [Traduit par la Rédaction]

## Introduction

Large fluctuations in the abundance of Pacific salmon (*Oncorhynchus* spp.) were documented soon after the arrival of Euro-American settlers in the Columbia River region in the early 1800s (Lichatowich 1999). However, retrospective studies in the Northern California Current (NCC) indicate that salmon abundance fluctuated with shifts in ocean conditions centuries prior to modern-day fishing (Mantua et al. 1997; Beamish et al. 1999). While correlative studies suggest that interannual variation in salmon abundance is linked to local and basin-scale variation in ocean conditions (Mackas et al. 2007), the processes driving that variation are not completely understood. Conventional wisdom holds that variable ocean conditions during the first few weeks at sea determine the level of recruitment of adult salmon populations (Percy 1992). Studies have demonstrated associations between juvenile salmon survival during their first ocean summer and the Pacific Decadal Oscillation (PDO) (Mantua et al. 1997; Rupp et al. 2012), the date of physical spring transition (Logerwell et al. 2003), the strength and timing of coastal upwelling (Scheuerell and Williams 2005; Williams

et al. 2014), sea-surface temperature (SST) (Mueter et al. 2002), and alongshore transport (Bi et al. 2011).

These observations have led researchers to hypothesize that ocean conditions and salmon abundance are linked through bottom-up processes that regulate the quality (lipid content) and species composition of their food supply (Hooff and Peterson 2006). In addition, relationships between ocean conditions and Pacific salmon abundance have proven useful in efforts to forecast adult returns of some Pacific salmon populations (Scheuerell and Williams 2005; Rupp et al. 2012; Burke et al. 2013; Williams et al. 2014). However, fish recruitment models that include only physical oceanographic indices often perform well for periods of time but may become unreliable following a shift in ocean conditions (Beamish et al. 1999; Rupp et al. 2012). This phenomenon highlights the need for a better understanding of the mechanisms that link variation in ocean conditions and adult Pacific salmon abundance.

Fluctuations in the abundance and species composition of the copepod community in the NCC coincide with variation in the PDO, SST, and ocean circulation (Peterson and Schwing 2003; Hooff and Peterson 2006; Keister et al. 2011). In years with consis-

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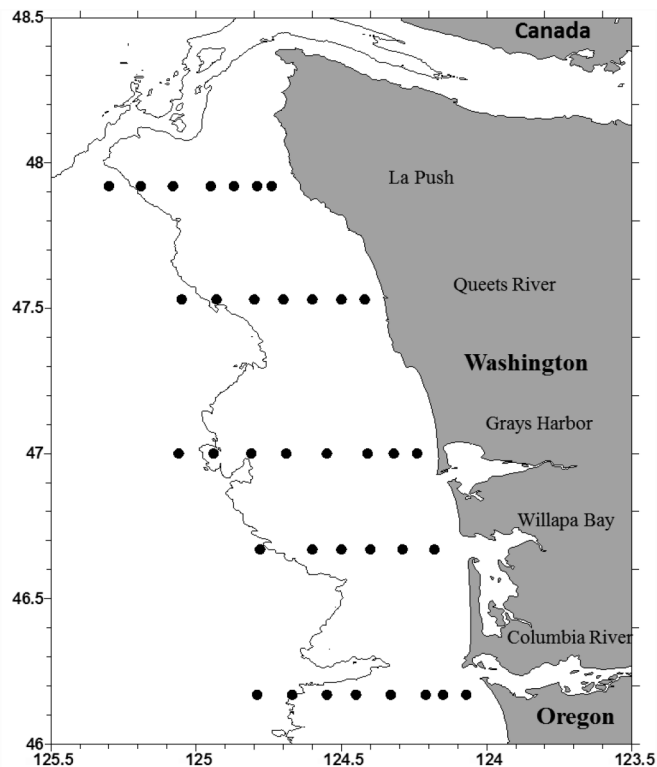
tently negative values of the PDO, the summer copepod community is dominated by large-bodied, lipid-rich, subarctic boreal species (Hooff and Peterson 2006), which are likely transported to coastal waters of Washington and Oregon from the north (Keister et al. 2011). In contrast, in years of positive PDO, the copepod community is characterized by smaller, subtropical species, which tend to be relatively lipid-poor (Hooff and Peterson 2006; Lee et al. 2006; Mackas et al. 2007) and are likely transported from the south or offshore. Mackas et al. (2007) reported a positive relationship between the growth and survival of juvenile salmon during late spring – early summer and the biomass of lipid-rich copepod species on the Vancouver Island continental shelf during the same period. However, because copepods do not make up a large proportion of the diet of juvenile salmon (<1% by mass), the mechanistic link among ocean conditions, juvenile salmon diets, and salmon survival has remained unclear (Brodeur et al. 1992). This relationship could reflect covariation among several ocean indicators or potentially represent variation in the copepod community that cascades up the food web through the large zooplankton (euphausiids, crab larvae, amphipods) and small forage fish (smelts, herring, anchovy) upon which young salmon feed.

Although there is increasing evidence that bottom-up processes regulate salmon abundance (Mackas et al. 2007; Daly et al. 2013), the amount or composition of prey found in the stomach of juvenile salmon does not appear to relate to year class strength (Daly et al. 2009). This lack of correlation is likely due to the fact that stomach content analysis reflects only what the juvenile salmon have consumed during its most recent meal, a few hours before capture. To better understand the link among variation in copepod communities, salmon diet and survival, an alternate measure of diet is needed, one that integrates over time periods longer than a fraction of a day. Such a measure is provided through analysis of trophically transmitted parasites (those that rely on predator-prey interactions to complete complex life cycles), which represent “markers” of food items consumed within the past days to months (Baldwin et al. 2008).

Differences in species composition and abundance of trophically transmitted parasites in salmon can signal variation in the presence or abundance of specific zooplankton taxa that serve as intermediate hosts (Marcogliese 1995; Zander et al. 2000). As copepods serve as a first intermediate host in the life cycle of many trophically transmitted marine parasites, it may be possible to identify linkages among ocean conditions, copepod communities, and planktivorous prey of salmon that have not been documented through stomach content analyses or analysis of stable isotopes.

The objectives of this study were to determine if the species composition and abundance of the marine trophically transmitted parasites of juvenile coho (*Oncorhynchus kisutch*) and Chinook (*Oncorhynchus tshawytscha*) salmon are related to (i) the physical and biological ocean indices during early juvenile marine residency, (ii) the size and condition of juvenile salmon during early marine residency, and (iii) their subsequent survival. We quantified inter-annual variation in the trophically transmitted parasites of yearling coho and Chinook salmon during a period of variable ocean conditions (2002–2009) and related that variation to basin- and local-scale oceanographic variables. From this information, we suggest that there is climate-driven variation in lower trophic levels that support juvenile salmon, which can be reflected in their trophically transmitted parasite community. In addition, parasite communities of juvenile salmon were compared with variation in the marine zooplankton community. If interannual variation in the species composition of the copepod community is indicative of a change in the diet of salmon or their prey (i.e., mesoplankton or smaller planktivorous fish that feed on copepods), we expect a corresponding shift in salmon parasites that use copepods as intermediate hosts. Finally, parasite assemblages of juvenile salmon across years were compared with fluctuations in size, condition,

Fig. 1. Station locations (circles) along five transects in the northern Pacific Ocean where juvenile coho and Chinook salmon were collected.



and adult returns to provide support for direct mechanistic linkages between ocean conditions and salmon survival.

## Materials and methods

### Fish collection

Samples were collected during 10 days in late June in 2002–2009. Sampling stations were located on five transects (3 to 50 km offshore) ranging from La Push, Washington (47°55'N), to the Columbia River (46°53'N) (Fig. 1). Juvenile salmon were collected during daylight hours using a Nordic 264-rope trawl towed in the upper ~20 m of the water column. Tows lasted for 15–30 min at an approximate speed of 6.5 km·h<sup>-1</sup>. Yearling coho and Chinook salmon were distinguished from subyearling, subadult, or adult based on fork length (Fisher et al. 2007) and then immediately frozen.

### Genetic stock identification

Microsatellite DNA baseline data for individual assignment to genetic stock were available for Columbia River coho (Van Doornik et al. 2007) and Chinook salmon (Seeb et al. 2007). The genetic stock origin was estimated for each fish using the likelihood model of Rannala and Mountain (1997), as implemented in the genetic stock identification software ONCOR (Kalinowski et al. 2007). Coho salmon were genotyped at 11 microsatellite DNA loci (Van Doornik et al. 2007), and Chinook salmon were genotyped at 13 loci (Teel et al. 2009). Only coho from the Columbia River stock group and Chinook salmon from the Upper Columbia River summer and fall (UCR Su–Fa) genetic stock groups (mean ± SD probability of assignment: coho = 93.8% ± 0.122%, Chinook salmon = 91.6% ± 0.130%) were included in this study because they are the predominate juvenile salmon stocks off Oregon–Washington in June (Teel 2004; Fisher and Percy 2005; Van Doornik et al. 2007).

### Analysis of parasites

A total of 373 Columbia River yearling coho salmon and 234 UCR Su–Fa yearling Chinook salmon were examined for trophically transmitted parasites. Parasite recovery from stomachs, intestines, body cavities, and swim bladders was completed according to standard necropsy procedures (Arthur and Albert 1994). The majority of parasites were identified to species. To confirm the identity of certain species, individual parasites were compared with specimens from the reference collection of R. Olson at the Hatfield Marine Science Center (Newport, Oregon, USA) and type specimens from the US National Parasite Collection (Beltsville, Maryland, USA).

### Physical and biological environmental indices

To determine if variation in the trophically transmitted parasite community of juvenile salmon is related to ocean conditions, we examined associations between the parasite community and the following indices of ocean conditions. While many of these environmental variables show strong covariation, each represents different processes hypothesized to be important drivers of food-web variation functioning at a variety of spatial scales.

#### Pacific Decadal Oscillation (PDO) index

The PDO index is the leading principal component (PC) of North Pacific monthly SST variation northward of 20°N (Mantua et al. 1997). Negative values of the PDO are typically associated with a cold and strong California Current and lipid-rich copepod communities in the shelf waters of the NCC, whereas positive values of the PDO have been associated with poleward transport of warm surface water and copepod species that are smaller and lipid-poor (Mackas et al. 2007; Keister et al. 2011). We calculated the mean value for January to June as well as 3-month running means for the 6 months prior to capture of juvenile salmon for each year of the study. Calculations were based on data from the University of Washington (<http://jisao.washington.edu/pdo/>).

#### North Pacific Gyre Oscillation (NPGO)

The NPGO index represents the second PC analysis of sea surface height anomalies (SSHa) of the North Pacific. Variation in the NPGO has been positively correlated with various measures of productivity (nutrients and chlorophyll) in the North Pacific Ocean (Di Lorenzo et al. 2008). If fluctuations in the NPGO are related to variation in prey composition for salmon, we expect interannual variation of the NPGO to relate to variation in the species composition or abundance of trophically transmitted parasites. Similar to the PDO, we calculated 3-month running means as well as the 6-month mean for the period prior to our sampling (January–June).

#### Sea-surface temperature (SST)

SST has been used as a proxy for water mass (i.e., warm offshore water versus cold upwelled waters) and an indicator of the copepod community present on the shelf (Morgan et al. 2003). The mean daily SST was calculated during the period of juvenile emigration (April–June) to determine if variation in SST was related to variation in parasite assemblage during early marine residency. Calculations were based on data from the NOAA buoy 46050 (44.6°N, 124.5°W) (<http://www.ndbc.noaa.gov>).

#### Cumulative upwelling

Cumulative cross-shelf transport in the NCC influences productivity in the nearshore marine environment (Pierce et al. 2006) and is related to the distribution of zooplankton on the shelf (Keister et al. 2009). We hypothesized that cumulative upwelling would be related to the abundance and composition of trophically transmitted parasites (that rely on zooplankton) in juvenile salmon. We summed daily values of Bakun's coastal upwelling index for months prior to our ocean sampling (January–June) for each year in this study (Bakun 1973).

### Columbia River plume volume

Several factors such as wind stress, river discharge, and tidal dynamics can alter the size and shape of the Columbia River plume. If interannual variation in the plume volume or associated fronts alters the composition of salmon prey (De Robertis et al. 2005), we expect the abundance or species composition of the parasite community of juvenile salmon to covary with variation in plume volume across years. Plume volume data were obtained from the Center for Coastal Margin Observation and Prediction (Center for Coastal Margin Observation & Prediction 2012; <http://www.stccmop.org>, version DB14). We used the output from daily simulations of the plume (defined as coastal waters <28 PSU) (Zhang et al. 2004; Zhang and Baptista 2008) and calculated plume volume for the months of peak salmon outmigration (April–June) prior to our cruises as described by Burla et al. (2010).

### Northern and Southern Copepod indices

If changes in the copepod community composition (i.e., lipid-rich versus lipid-poor copepods) are reflected in the composition of the prey of juvenile salmon, we expect variation in the parasite community to be related to fluctuations in the copepod community. The Northern Copepod Index is the  $\log_{10}$ -transformed monthly biomass anomaly (climatology from sampling for 14 years: 1998–2011) of three species of lipid-rich, boreal, cold-water copepods: *Calanus marshallae*, *Pseudocalanus mimus*, and *Acartia longiremis*. The Southern Copepod Index is the  $\log_{10}$ -transformed monthly biomass anomaly (1998–2011) of a suite of subtropical species considered to be relatively lipid-poor: *Acartia tonsa*, *Calanus pacificus*, *Calocalanus styliremis*, *Calocalanus tenuis*, *Clausocalanus* spp., *Corycaeus anglicus*, *Ctenocalanus vanus*, *Mesocalanus tenuicornis*, and *Paracalanus parvus* (Hooff and Peterson 2006). Both indices were averaged from April to June, which is the period of peak outmigration of Columbia River yearling coho and Chinook salmon from fresh water. All data came from a research program whereby zooplankton were sampled biweekly at a hydrographic station 5 nautical miles (~8 km) off Newport, Oregon (Hooff and Peterson 2006; Keister et al. 2011).

### Juvenile salmon size and condition

If variation in the parasite community of juvenile salmon indicates a bottom-up trophic effect, we expect that the size and (or) condition of juvenile salmon will be correlated with the parasite community across years. Residuals from regressions of  $\ln(\text{wet mass})$  on  $\ln(\text{fork length})$  were used as an indicator of condition. We calculated the mean condition and fork length for both coho and Chinook salmon captured in June in each year of the study for comparison with variation in the parasite community.

### Survival estimates

For Columbia River coho, we used the Oregon Production Index as a proxy for survival. The Oregon Production Index is calculated from estimates of smolt production, spawner escapement, and mortality associated with harvest to generate an estimate of smolt-to-adult survival for Washington, Oregon, and California stocks (Pacific Fishery Management Council 2012). The majority of coho migrate to the ocean as yearlings in spring and return to spawn 16 months later (Pearcy 1992); therefore, we used a 1-year lag from the year of ocean capture to estimate survival of coho salmon.

UCR Su–Fa Chinook salmon exhibit substantial life history diversity and emigrate out of fresh water as both yearling and subyearlings. Owing to our limited catch of subyearling Chinook salmon in June, we included only UCR Su–Fa that exhibited a yearling life history strategy. The yearling life history of UCR Su–Fa Chinook salmon is most commonly associated with the summer run, whereas the subyearling life history is more common in the fall run (Utter et al. 1995; Myers et al. 1998; Waples et al. 2004). Age-at-return for Chinook salmon that enter the ocean as yearlings ranges from 2–6 years; however, the majority of Upper Columbia

**Table 1.** Ocean age for summer- and fall-run Chinook salmon as determined from PIT tag adults returning to Priest Rapids Dam in the Upper Columbia River.

Release year	Proportion of run at ocean age:					n
	0	1	2	3	4	
<b>Summer run</b>						
2002	0.00	0.10	0.29	0.44	0.16	147
2003	0.16	0.16	0.30	0.34	0.04	2917
2004	0.09	0.07	0.28	0.49	0.08	1379
2005	0.10	0.10	0.30	0.46	0.05	237
2006	0.07	0.03	0.38	0.48	0.03	29
2007	0.09	0.09	0.30	0.42	0.09	33
2008	0.07	0.07	0.34	0.52	0.00	29
Overall mean	0.08	0.09	0.31	0.45	0.06	
<b>Fall run</b>						
2002	0.00	0.12	0.26	0.36	0.25	860
2003	0.00	0.19	0.46	0.31	0.04	100
2004	NS	NS	NS	NS	NS	NS
2005	NS	NS	NS	NS	NS	NS
2006	0.00	0.24	0.29	0.41	0.06	17
2007	NS	NS	NS	NS	NS	NS
2008	0.00	0.55	0.30	0.11	0.04	71
Mean (excluding 2004, 2005, 2007)	0.00	0.28	0.33	0.30	0.10	

**Note:** Data courtesy of the Pacific States Marine Fisheries Commission (<http://www.cbr.washington.edu/dart>; Columbia River Data Access in Real Time 1995–present). Total number of fish and mean size at release are included when available. “NS” indicates insufficient data to generate mean estimate.

River summer Chinook salmon that emigrate into the ocean as yearlings return to fresh water 3 years later (~60%, Myers et al. 1998; Williams et al. 2005). In the absence of an estimate of smolt-to-adult return rates for this stock group, adult returns to Priest Rapids Dam have been used previously as a proxy for survival (Miller et al. 2013). Adult PIT tag observations at Priest Rapids Dam indicate that fish returning 3 years after hatchery release made up the highest proportion of returning summer-run Chinook salmon adults during the emigration years examined in this study (2002–2009; Table 1; Columbia River Data Access in Real Time 1995–present). Therefore, to provide an indicator of Chinook salmon survival, we used the number of adult Chinook salmon crossing Priest Rapids Dam from 14 June through 13 August 3 years after juveniles entered marine waters (Columbia River Data Access in Real Time 1995–present). Priest Rapids Dam is located on the mainstem Columbia River above the confluence of the Snake River; therefore, the number of adults counted at this dam includes only adults returning to the upper reaches of the Columbia River. We also lagged adult returns by 2 and 4 years from the time of ocean entry.

### Data structure and statistical analysis

For all analyses, parasite abundance (number of parasites per fish) for juvenile coho and Chinook salmon was averaged by species and year. The data were arranged into two parasite species matrices (one for Chinook salmon and one for coho) and one environmental matrix. In these three matrices, the parasite species or environmental variables formed the columns and years formed the rows. Outlier analysis and summary statistics of matrices were conducted to reveal the need for transformations using PC-ORD (version 6.05; McCune and Mefford 2009). No sample units in either species matrix fell beyond two standard deviations of the mean parasite abundance; therefore, no transformations were used.

Ordinations of sample units in parasite species space were performed using nonmetric multidimensional scaling (NMS) ordination techniques (Mather 1976) to describe variation in the parasite community and relate the parasite communities of coho and

**Table 2.** Sample size, mean ( $\pm$ SE) fork length (FL) and mean ( $\pm$ SE) mass of Upper Columbia River summer and fall Chinook salmon and Columbia River coho collected off Washington, USA.

Year	Chinook salmon			Coho salmon		
	n	FL (mm)	Mass (g)	n	FL (mm)	Mass (g)
2002	32	177 $\pm$ 4	73 $\pm$ 5	68	175 $\pm$ 4	66 $\pm$ 5
2003	29	191 $\pm$ 4	89 $\pm$ 6	40	187 $\pm$ 3	76 $\pm$ 4
2004	37	190 $\pm$ 5	92 $\pm$ 7	44	185 $\pm$ 4	78 $\pm$ 5
2005	13	177 $\pm$ 5	70 $\pm$ 7	19	177 $\pm$ 8	61 $\pm$ 5
2006	35	189 $\pm$ 4	92 $\pm$ 6	47	169 $\pm$ 4	59 $\pm$ 5
2007	34	190 $\pm$ 4	86 $\pm$ 5	58	180 $\pm$ 2	67 $\pm$ 3
2008	23	207 $\pm$ 8	126 $\pm$ 13	48	186 $\pm$ 3	82 $\pm$ 4
2009	31	205 $\pm$ 6	117 $\pm$ 11	49	170 $\pm$ 4	63 $\pm$ 6

Chinook salmon to environmental variation. Sorensen distances were used for all ordinations. Plots and output of instability and stress were examined to identify the number of ordination axes at which the reduction in stress gained by adding another axis was inconsequentially small (Mather 1976). Because of the high frequency of zeros in the community matrix (>40%) and a small number of sample units (only 8 years of data), it was not possible to generate *P* values using Monte Carlo simulations for NMS.

To determine if parasite species composition and abundance differed across years, a multiresponse permutation procedure was used. This method calculates the mean multivariate distance within each year and compares whether the mean within-group distance observed is significantly smaller than mean within-group distances generated by random assignment of sample units to groups. A Sorensen distance measure was used for consistency with the NMS ordinations. A Mantel test was used to determine if variation in the parasite community was related to variation in the seven environmental variables described above. This test is a randomization procedure that calculates the probability that variation within two distance matrices (parasites and ocean conditions) is more similar than expected by chance (McCune and Mefford 2009). We were also interested in identifying the relative importance of each environmental variable. For this we used correlation analysis to compare variation in the parasite community, described by Axis 1 of ordinations of juvenile salmon parasites, to each of the seven environmental variables described above.

The parasite community within juvenile salmon can reflect variation in lower trophic levels. Therefore, if juvenile salmon size at capture and survival are related to variation in lower trophic levels, then size and survival should also be related to variation in their parasite community. Therefore, we used correlation analyses to examine the relationship among fork length, condition factor, and adult returns of coho and Chinook salmon and both the abundance of individual parasites and Axis 1 scores from NMS ordinations of the parasite community.

### Results

Size (fork length) at capture ranged from 137 to 236 mm for UCR Su–Fa Chinook salmon and 108 to 304 mm for Columbia River coho (Table 2). A total of 10 trophically transmitted parasite taxa of marine origin were recovered from 373 juvenile coho, and eight marine parasite taxa were recovered from 234 juvenile Chinook salmon (Table 3). The additional two parasite taxa recovered in coho salmon, *Tubulovesicula* sp. and *Lecithophylum* sp., were rare (<5% of fish). *Lecithaster gibbosus* was the most abundant parasite overall (mean abundance = 1.2  $\pm$  7.8 individuals per fish) and was the only parasite that was present in coho and Chinook salmon in every year of the study (Table 3). The parasite taxa recovered in this study represent a wide range of prey items and trophic levels utilized by their salmonid host, including copepods, euphausiids, and forage fish (Table 4).

**Table 3.** Mean abundance (number of individual parasites per fish) of parasite taxa from the stomach, intestine, and body cavity of coho and Chinook salmon collected in June of 2002–2009 off the coast of Washington, USA.

<i>Oncorhynchus</i> spp.	Parasite taxa	2002	2003	2004	2005	2006	2007	2008	2009
Coho	<i>Anisakis simplex</i>	0.07	0.13	0.07	0.00	0.10	0.05	0.10	0.58
	<i>Bothriocephalus</i> sp.	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	<i>Hemiurus levinseni</i>	0.01	0.25	0.36	0.00	0.00	0.00	0.00	0.00
	<i>Hysterothylacium aduncum</i>	0.13	0.05	0.00	0.05	0.27	0.19	0.31	0.06
	<i>Lecithaster gibbosus</i>	0.10	0.10	0.07	0.79	1.98	0.18	0.88	0.94
	<i>Lecithophyllum</i> sp.	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00
	<i>Parahemiurus merus</i>	0.01	0.03	0.02	0.00	0.02	0.02	0.02	0.00
	<i>Rhadinorhynchus trachuri</i>	0.00	0.15	1.49	0.58	0.06	0.19	0.15	0.18
	Tetraphyllid cestode	0.01	0.00	0.38	0.21	0.06	0.02	0.04	0.02
	<i>Tubulovesicula</i> sp.	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Total		68	40	44	19	47	58	48	49
Chinook	<i>Anisakis simplex</i>	0.34	0.14	0.11	0.08	0.37	0.50	0.39	1.03
	<i>Bothriocephalus</i> sp.	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	<i>Hemiurus levinseni</i>	0.19	0.07	0.14	0.00	0.00	0.00	0.00	0.03
	<i>Hysterothylacium aduncum</i>	0.41	0.38	0.46	0.23	0.51	0.41	0.13	0.19
	<i>Lecithaster gibbosus</i>	1.22	0.17	2.00	2.23	7.06	1.38	0.74	0.28
	<i>Parahemiurus merus</i>	0.03	0.10	0.16	0.00	0.00	0.00	0.00	0.03
	<i>Rhadinorhynchus trachuri</i>	0.00	0.07	1.24	0.08	0.00	0.09	0.04	0.06
Tetraphyllid cestode	0.00	0.10	0.73	0.46	0.29	0.76	0.52	0.00	
Total		32	29	37	13	35	34	23	31

**Table 4.** Marine parasite taxa from juvenile Upper Columbia River summer and fall Chinook salmon and Columbia River coho collected off Washington, USA.

Parasite species	Intermediate host	Reference
<i>Anisakis simplex</i>	Copepods, chaetognaths, euphausiids, and fish	Davey 1971; Hays et al. 1998; Marcogliese 1995
<i>Bothriocephalus</i> sp.	Cyclopoid and calanoid copepods	Marcogliese 1995
<i>Hemiurus levinseni</i>	Molluscs, copepods, and chaetognaths	Marcogliese 1995
<i>Hysterothylacium aduncum</i>	Calanoid copepods, chaetognaths, coelenterates, crab larvae, ctenophores, euphausiids, hyperiid amphipods, polychaetes, and fish	Marcogliese 1995
<i>Lecithaster gibbosus</i>	Calanoid copepods	Klimpel and Rückert 2005
<i>Lecithophyllum</i> sp.	Molluscs, copepods, and chaetognaths	Hoffman 1999
<i>Parahemiurus merus</i>	Calanoid copepods and chaetognaths	Koie 1993
<i>Rhadinorhynchus trachuri</i>	Copepods, amphipods, and euphausiids	Hoffman 1999
Tetraphyllid cestode	Copepods, euphausiids	Marcogliese 1995
<i>Tubulovesicula</i> sp.	Calanoid copepods and chaetognaths	Koie 1993

We observed a wide range of ocean conditions during the study period, with annual spring (April–June) mean SST ranging from 11.0 °C in 2008 to 13.5 °C in 2005. In addition there was a well-documented, anomalous subarctic intrusion of cold water in 2002 leading to SST 0.5 °C cooler than the historical mean (Freeland et al. 2003) and the warmest summer SST recorded off the Oregon coast (2005) since continuous observations began in 1961 (Pierce et al. 2006). On a basin scale, the PDO index revealed that our sampling period contained an equal number of “warm” ocean years as indicated by positive values (2003, 2004, 2005, and 2006) and “cold” ocean years as indicated by negative values (2002, 2007, 2008, and 2009).

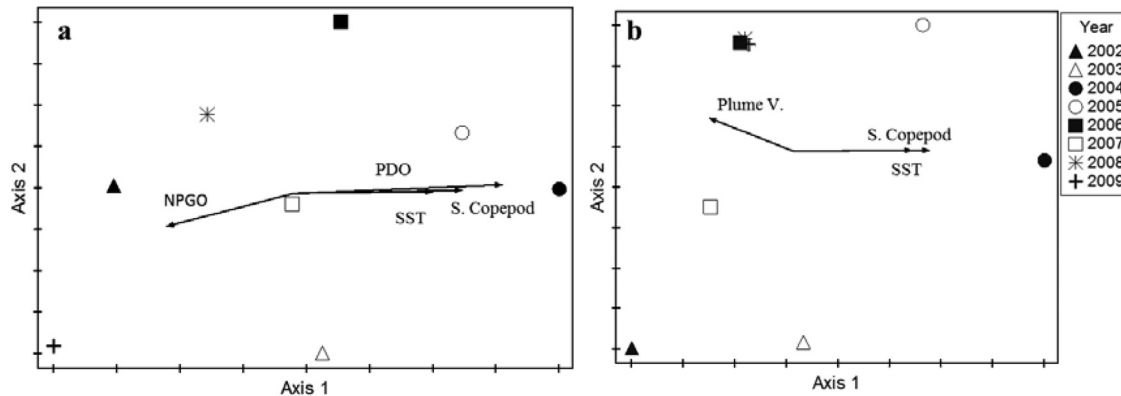
#### Correlations between parasite community and environmental variables

The NMS ordinations of the parasite assemblages of Chinook salmon (Fig. 2a; stress = 1.09 for 2D solution) and coho salmon (Fig. 2b; stress = 2.69 for 2D solution) revealed substantial interannual variation in parasite assemblages during the 8-year study. In addition, the multiresponse permutation procedure revealed that the parasite species composition and abundance were significantly different across years ( $P < 0.0001$ ). Mantel's test indicated that variation in the marine environment was significantly associated with variation in the parasite community of coho and Chinook salmon during the study period ( $P < 0.05$ ).

Axis 1 of NMS ordinations accounted for a majority of the interannual variation in the parasite community for both juvenile coho and Chinook salmon (coho: 52%, Chinook salmon: 64%). Axis 2 described a smaller proportion of the variance in salmon parasite communities (coho salmon: 33%, Chinook salmon: 18%). For this reason, Axis 1 was used as the primary index to describe variation in the parasite community. Strong relationships were observed between interannual variation in the parasite community (i.e., Axis 1 scores) and specific conditions in the marine environment (Fig. 2). For both coho and Chinook salmon, Axis 1 values were positively correlated with mean spring SST (April–June) and the Southern Copepod Index (April–June;  $P < 0.05$ ; Table 5; Fig. 3). In addition, for Chinook salmon, Axis 1 scores were associated with positive values of the PDO index and negative NPGO values. Axis 1 scores for coho salmon were negatively correlated to the volume of the Columbia River plume ( $P < 0.05$ ; Table 5).

Correlations between environmental variables and Axis 1 scores revealed associations between particular taxa in the parasite community and specific ocean conditions (Table 5). For both fish species, the abundances of a tetraphyllid cestode and the acanthocephalan *Rhadinorhynchus trachuri* were highest in late spring during years when the SST was warm and the biomass of southern-origin copepods was high ( $P < 0.05$  on Axis 1; Table 5). In contrast, both a cold SST and smaller biomass of southern copepods were associated

**Fig. 2.** Nonmetric multidimensional scaling analysis of (a) juvenile Upper Columbia River summer and fall Chinook salmon and (b) juvenile Columbia River coho salmon comparing similarity in parasite communities across years (April–June). Joint plots illustrate relationships between environmental variables and axis scores (cutoff  $r^2 = 0.50$ ). NPGO, North Pacific Gyre Oscillation; PDO, Pacific Decadal Oscillation; SST, sea-surface temperature; S. Copepod, Southern Copepod Index; Plume V., Columbia River plume volume.



**Table 5.** Pearson correlation coefficients between environmental variables and parasite species and axes scores of ordination of trophically transmitted parasites of juvenile Columbia River coho and Upper Columbia River summer and fall Chinook salmon.

Environmental variable	UCR Su–Fa Chinook salmon		Columbia River coho	
	Axis 1 (64%)	Axis 2 (18%)	Axis 1 (52%)	Axis 2 (33%)
PDO	<b>0.74</b>	0.07	0.48	–0.26
NPGO	<b>–0.71</b>	–0.36	–0.60	–0.42
SST	<b>0.91</b>	0.19	<b>0.81</b>	0.07
Cumulative upwelling	–0.60	0.20	0.55	0.54
Plume volume	–0.59	0.22	<b>–0.63</b>	0.40
Northern copepod anomaly	–0.51	–0.19	–0.41	–0.31
Southern copepod anomaly	<b>0.81</b>	0.12	<b>0.76</b>	0.08
Parasite species				
<i>Anisakis simplex</i>	<b>–0.86</b>	–0.23	–0.26	0.08
<i>Hemiurus levinseni</i>	0.24	–0.46	<b>0.65</b>	–0.45
<i>Hysterothylacium aduncum</i>	0.41	0.09	<b>–0.61</b>	0.27
<i>Lecithaster gibbosus</i>	0.60	<b>–0.82</b>	–0.13	<b>0.87</b>
<i>Parahemiurus merus</i>	0.48	–0.34	0.01	–0.45
<i>Rhadinorhynchus trachuri</i>	<b>0.67</b>	–0.20	<b>0.93</b>	0.25
Tetraphyllid cestode	<b>0.94</b>	0.40	<b>0.90</b>	0.35

**Note:** Bold values are significant ( $P < 0.05$ ) at the 95% confidence interval. Variance in parasite community composition that was accounted for (%) by each axis is included in column heading. PDO, Pacific Decadal Oscillation; NPGO, North Pacific Gyre Oscillation; SST, sea-surface temperature.

with a higher abundance of the nematode *Anisakis simplex* in Chinook salmon ( $P < 0.05$  on Axis 1). In coho salmon, “cold” ocean conditions and high plume volume were associated with an increased abundance of the nematode *Hysterothylacium aduncum* ( $P < 0.05$  on Axis 1; Table 5). There was also a significant correlation between Axis 2 and one parasite species recovered from coho and Chinook salmon, the trematode *Lecithaster gibbosus* ( $P < 0.05$  on Axis 2; Table 5). However, Axis 2 scores were not significantly related with any of the environmental variables included in this study ( $P > 0.05$ ; Table 5).

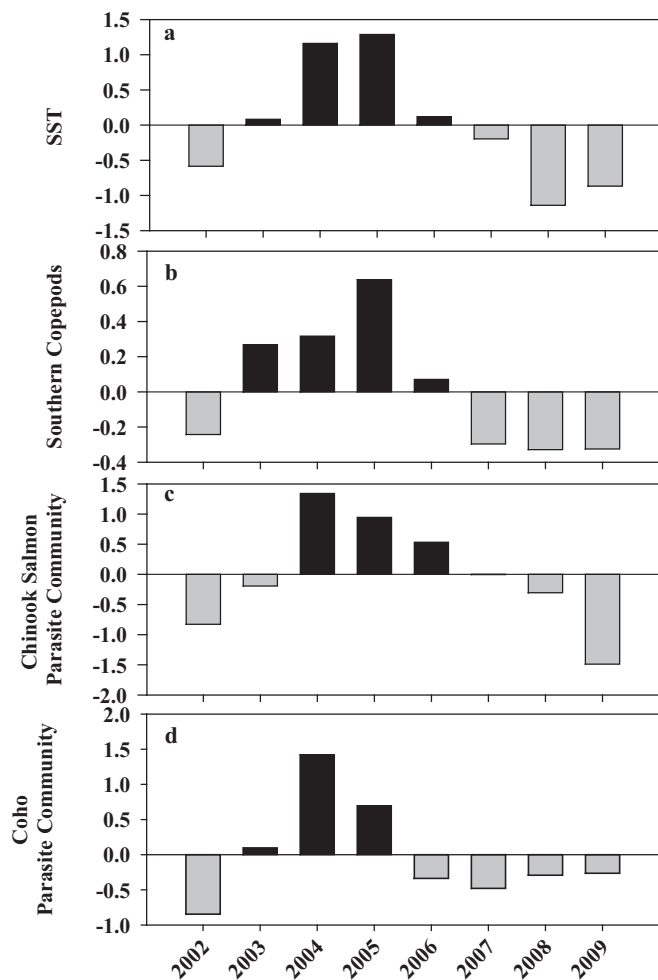
Interannual variation in mean fork length or condition factor of UCR Su–Fa Chinook salmon and Columbia River coho were not related to the parasite community as described by Axis 1 of the NMS ordinations ( $P > 0.05$ ; Fig. 4). With the exception of one parasite species recovered from coho salmon (*Parahemiurus merus*), fork length and condition factor of coho and Chinook salmon juveniles were not directly related to abundances of the parasite species they harbored (Table 6). The abundance of two parasite taxa recovered from Chinook salmon, *Rhadinorhynchus trachuri* and

a tetraphyllid cestode, were significantly correlated to Chinook salmon adult returns to Priest Rapids Dam ( $r = -0.74$  and  $0.80$ , respectively;  $P < 0.05$ ; Table 6). In addition, indices of the parasite communities of juvenile coho and Chinook salmon (i.e., Axis 1 scores) were correlated with the number of adults returning to Priest Rapids Dam when lagged by 3 years ( $r = -0.943$ ;  $P < 0.05$ ; Fig. 5a). No significant relationships were observed when comparing Axis 1 scores with Chinook salmon adult returns at 2- or 4-year lags ( $r = -0.420$  and  $-0.320$ , respectively;  $P > 0.05$ ). For coho, Axis 1 scores were correlated with variation in the number of adults returning 1 year later ( $r = -0.671$ ;  $P < 0.05$ ; Fig. 5b).

## Discussion

We observed clear relationships between the species composition of trophically transmitted parasites in juvenile Columbia River coho and UCR Su–Fa Chinook salmon and variation in ocean conditions in the NCC, demonstrating for the first time a trophic linkage among ocean conditions, copepod communities, and

**Fig. 3.** Time series of (a) annual anomalies of SST ( $^{\circ}\text{C}$ ) averaged over April–June; (b) southern copepod biomass anomalies ( $\text{mg}\cdot\text{m}^{-3}$ ) from NH05 averaged over April–June; (c) Axis 1 scores from NMS of parasite community composition from Upper Columbia River summer and fall Chinook salmon; and (d) Axis 1 scores from NMS of parasite community composition from Columbia River coho salmon captured in June.



planktivorous prey of juvenile salmon. The assemblage of trophically transmitted parasites covaried with the PDO, SST, and the Southern Copepod Index as well as adult returns of Columbia River coho and UCR Su–Fa Chinook salmon. More specifically, when the biomass of lipid-poor, southern origin copepods was high during marine entry (April–June), yearling coho and Chinook salmon contained different trophically transmitted parasites and exhibited lower survival compared with years when the southern copepod biomass was low during April–June.

In the last decade, numerous studies have identified relationships among ocean transport mechanisms, copepod community composition, and salmon growth or abundance (Peterson and Schwing 2003; Mackas et al. 2007; Bi et al. 2011). These studies suggest that variation in copepod composition, likely driven by ocean transport (Keister et al. 2011), affects the prey of juvenile salmon during early marine residency. However, because copepods do not make up a large proportion of the diet of juvenile salmon, the mechanistic link among ocean conditions, juvenile salmon diets, and salmon survival has remained unclear. The trophically transmitted parasites analyzed in this study rely on zooplankton hosts for transmission (Marcogliese 1995) and require that juvenile salmon consume infected hosts (e.g., predatory

zooplankton, planktivorous fish). Therefore, the significant relationships among parasite community composition, copepod assemblage, and environmental conditions in the Northeast Pacific Ocean support the hypothesis that changes in ocean conditions that alter copepod species composition affect intermediate trophic levels that support juvenile salmon.

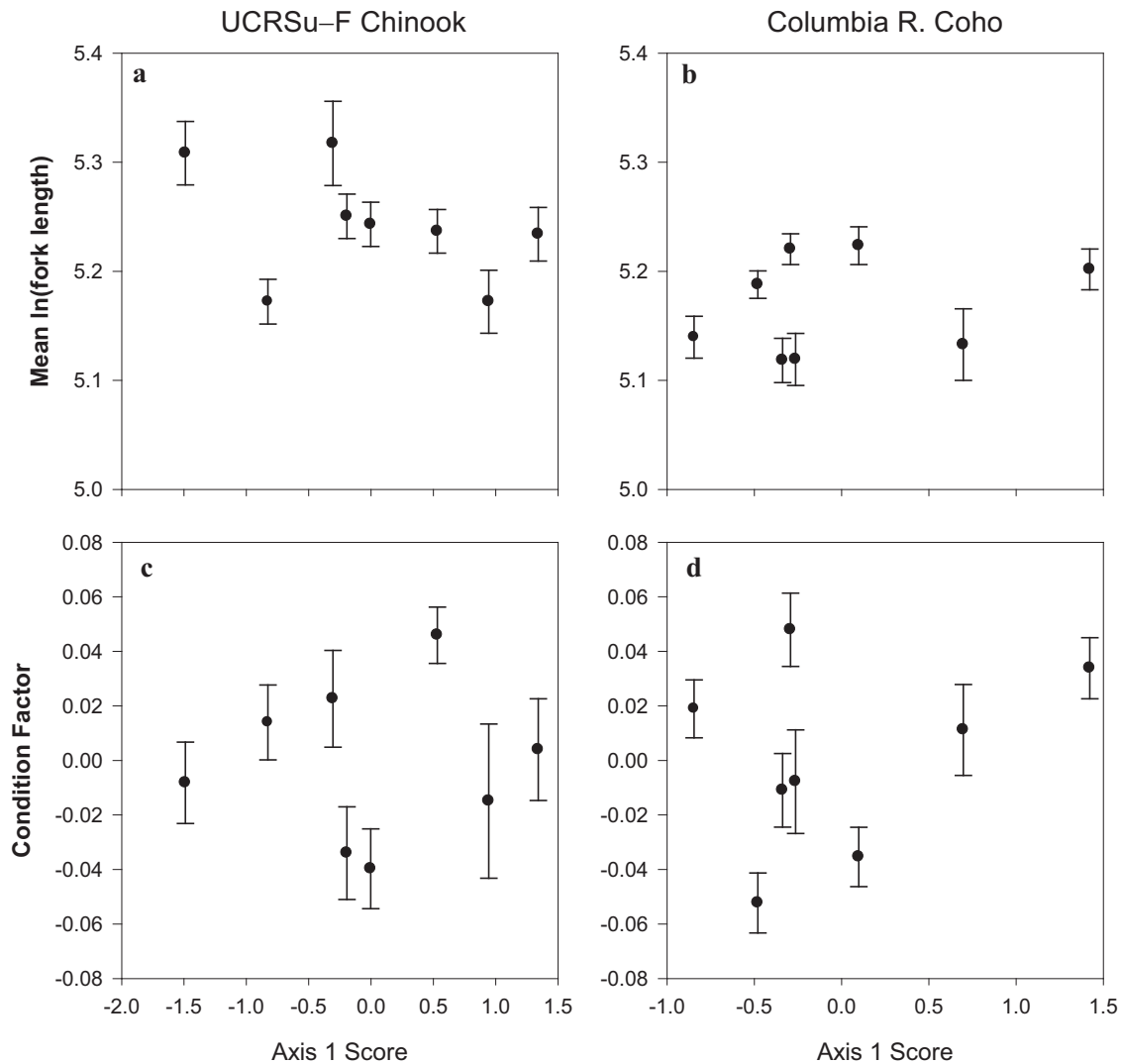
SST and the Southern Copepod Index in late spring were the best predictors of variation in the parasite community of juvenile coho and UCR Su–Fa Chinook salmon. These results suggest that variation in these physical and biological indices reflect variation in salmon trophic interactions during the first weeks to months at sea. Specifically, the positive associations among SST, the Southern Copepod Index, and the abundance of two parasite taxa, the acanthocephalan *R. trachuri* and a larval tetraphyllid cestode, likely represent compositional changes in the food web at lower trophic levels (i.e., copepods). The fact that many parasites are transmitted via predator–prey interactions through a variety of hosts suggests that differences in parasite assemblages reflect variation in species composition at one or more levels of the food web (Zander et al. 2000; Marcogliese 2002). In other words, parasites such as the acanthocephalan and the tetraphyllid cestode that are associated with lipid-poor, “warm-water” copepods in this study appear to be transferred to the prey of salmon, such as euphausiids and fish, in higher abundances in years of “warm” ocean conditions compared with years of “cold” ocean conditions. In addition, acanthocephalans in the genus *Rhadinorhynchus* have been commonly recovered from offshore fishes in the Pacific Ocean (George-Nascimento 2000; Jacobson et al. 2012), providing more evidence of onshore transport of offshore zooplankton species, including warm-water copepod species, during years of warm ocean conditions. Thus, parasite communities serve as indicators of a change in the copepod community in warm and cold years that can be detected within salmon and more directly link copepods and juvenile salmon.

Our results provide evidence that both local (SST) and basin-scale (PDO, NPGO) indicators of ocean conditions are related to the parasite composition of salmon prey. However, a dominant physical process in the NCC, seasonal upwelling, was not significantly correlated to the parasite community composition of juvenile coho or UCR Su–Fa Chinook salmon. While metrics of coastal upwelling strength provide good indicators of cross-shelf water transport (Austin and Lentz 2002; Keister et al. 2009), the current study highlights the fact that upwelling strength alone may not serve as a good predictor of local food-web structure. Rather, underlying basin-scale processes that determine the origin of source waters that feed the NCC (either from the north bringing cold-water boreal copepod species or from the west–southwest bringing warm water subtropical species) may be of equal importance in shaping food-web structure during late spring and early summer (Hooft and Peterson 2006; Keister et al. 2009; Bi et al. 2011).

Results from this study also suggest that the interaction between the fluvial and marine environments at the mouth of the Columbia River may be important in shaping the composition of planktivorous salmon prey during early marine residence. During the period of peak ocean immigration for juvenile salmon (April–June), shifts in the parasite community of juvenile coho were correlated with the volume of the Columbia River plume. In the current study, the volume of the Columbia River plume was positively related to the abundance of the nematode *H. aduncum* in juvenile coho, which is known to infect salmon in the Columbia River estuary (Claxton et al. 2013) as well as in the ocean. These results suggest that presence of *H. aduncum* alone may serve as an indicator of variation in feeding rate or prey composition associated with the size of the Columbia River plume or associated fronts. Currently, we are unable to determine if the infections occurred in the estuary, plume, or nearshore environment. However, increased abundance of *H. aduncum* in amphipods and fish captured along frontal regions compared with those captured in nonfrontal



**Fig. 4.** Relationship between (a, b) fork length and (c, d) condition factor and Axis 1 scores from NMS ordinations of marine parasite community observed in juvenile Chinook and coho salmon. Bars indicate standard error values.



**Table 6.** Pearson correlation coefficients between abundance of parasite species on mean fork length (FL), condition factor (CF), and survival indices of coho and Chinook salmon.

Parasite species	UCR Su-F Chinook			Columbia River coho		
	FL	CF	Survival	FL	CF	Survival
<i>Anisakis simplex</i>	0.60	0.01	0.60	-0.30	-0.12	-0.11
<i>Hemiurus levinseni</i>	-0.40	0.08	0.05	0.58	0.09	-0.40
<i>Hysterothylacium aduncum</i>	-0.51	0.12	-0.21	0.01	0.08	0.60
<i>Lecithaster gibbosus</i>	-0.27	0.65	-0.29	-0.56	0.06	-0.04
<i>Parahemiurus merus</i>	-0.03	-0.18	-0.37	<b>0.74</b>	-0.23	0.10
<i>Rhadinorhynchus trachuri</i>	-0.04	0.00	<b>-0.74</b>	0.25	0.38	-0.54
Tetraphyllid cestode	0.01	-0.14	<b>-0.80</b>	0.08	0.47	-0.52

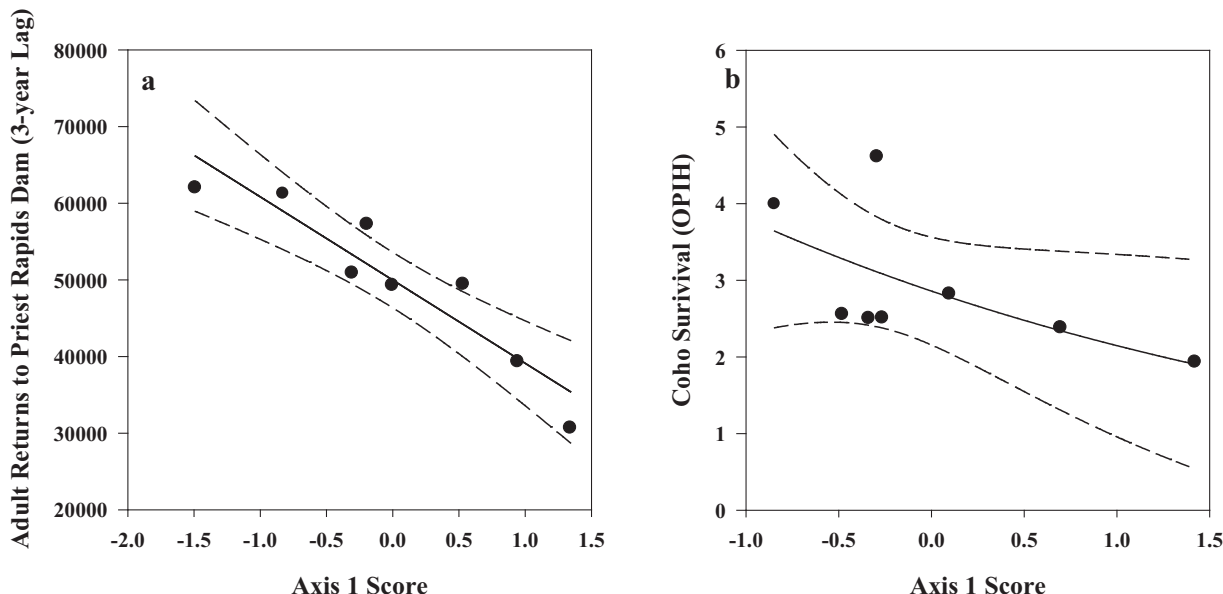
**Note:** Bold values are significant ( $P < 0.05$ ) at the 95% confidence interval.

areas provides support for the notion that *H. aduncum* may represent feeding in the plume frontal regions (Klimpel and Rückert 2005). In contrast, relationships between the parasite community and plume volume were not observed in UCR Su-Fa Chinook salmon. This could be a result of differences in habitat use, diet, or both, between juvenile coho and UCR Su-Fa Chinook salmon (Baldwin et al. 2008; Daly et al. 2009; Miller and Brodeur 2007).

Parasite community analysis provided evidence that fluctuations in the copepod community composition covaries with the parasite composition of salmon prey. It is unknown whether the

observed variation in parasite community composition is indicative of shifts in salmon prey or variation at lower trophic levels (i.e., the prey of salmon prey) or a combination of both. However, our results provide information on some specific aspects of salmon diet. All 10 of the parasite taxa recovered in the current study require a zooplankton host at some point in their life cycle, and each taxon has been found in copepods (Table 3). Therefore, we consider variations in copepod species composition an important source of the variation we observed in salmon parasites. In addition, one nematode, *A. simplex*, has the ability to move through

Fig. 5. Relationship between (a) Chinook salmon adult returns to Priest Rapids Dam (3-year lag;  $r^2 = 0.89$ ) and (b) Oregon Production Index Hatchery (OPIH) (1-year lag;  $r^2 = 0.45$ ) and Axis 1 scores from NMS ordinations of marine parasite community observed in juveniles. Dashed lines indicate 95% confidence intervals.



an indeterminate number of fish hosts without maturing. This nematode's ability to be transferred from one intermediate host to another (fish to fish via predation) explains why piscivorous fish are often found with many larvae of this species in the viscera (Koe 1993), as they inherit the parasite communities of the fish prey they consume (Bush et al. 1997). This feature of the nematode life cycle has enabled detection of piscivory in many species of marine fish (Pascual et al. 1996; Blaylock et al. 1998; Petrić et al. 2011) beyond the 12–24 h time frame of traditional diet analysis. Results from the current study suggest that increased abundance of *A. simplex* in years of cold SSTs may be the result of increased piscivory by juvenile salmon during the weeks or months prior to capture. Fish prey typically provide higher caloric value per gram than invertebrate prey consumed by juvenile salmon (Davis et al. 2005). Therefore, increased abundance of *A. simplex* in years of favorable ocean conditions provides additional support for the hypothesis that variation in the quality (energetic value) and (or) species composition of prey influences early marine survival.

Food quality and consumption rate are important determinants of growth, and fast-growing salmon are at lower risk of predation than those growing more slowly (Percy 1992; Duffy and Beauchamp 2011). In addition, growth of juvenile salmon during early marine residency may relate to a critical level of fat content that a juvenile salmon must obtain during the summer to survive the first marine winter (Beamish and Mahnken 2001). In the current study we did not observe a significant relationship between fish size or condition and variation in the parasite community. This finding is possibly a result of a temporal or spatial mismatch between variation in ocean conditions that affect the copepod and parasite assemblages off the Washington coast and the resulting growth that these juvenile salmon may experience. While our results suggest that the trophic interactions of juvenile salmon are related to variation in the copepod community in early summer, the marine growth interval to June may be too short to detect significant interannual variation in growth. Yearling Columbia River coho and Chinook salmon enter the ocean at different times during the spring and display a diversity of dispersal patterns throughout the summer, including both rapid northward migrants as well as individuals that remain in southern areas throughout the summer (Fisher et al. 2014). In addition, the mean

date of peak catch for yearling UCR Su–Fa Chinook salmon in the lower Columbia River estuary is 27 May with a standard deviation of 14 days (L. Weitkamp, NOAA NWFSC, unpublished data). Thus, the majority of UCR Su–Fa Chinook salmon that we sampled in the ocean in late June resided in the ocean for only 3 to 4 weeks.

We have determined that the parasite community within juvenile salmon after early marine residence covaries with copepod community composition and ocean conditions. We do not consider the variation in observed adult salmon abundance to be the direct result of the different parasite communities. Rather, we suggest that variation in the parasite community serves as a proxy for variation in the composition of salmon prey and (or) variation in the diet of planktivorous salmon prey. An alternative explanation is that variation in ocean conditions that alter the copepod community assemblage may also be related to changes in the assemblage of juvenile salmon predators. Thus, variation in the copepod community may not directly influence growth and survival but rather covary with shifts in the predator community (abundance, species composition, or feeding rate). However, studies designed to compare predation on salmon by predatory fishes have reported little evidence of juvenile salmon in the stomachs of piscivorous fishes (Brodeur et al. 1987; Emmett and Krutzikowsky 2008), and overall lower and mid-level trophic indicators appear to serve as better predictors of salmon survival than abundance measures of predatory fish and seabirds (Thompson et al. 2012).

Ocean conditions were important in describing variation in the parasite community of both Columbia River coho and UCR Su–Fa Chinook salmon; however, these stocks exhibited notable differences in the parasites they carried and the relationships these parasites had with ocean conditions. These stock-specific differences may be driven by a variety of factors. Documenting the parasite communities and diets of juvenile salmon across a range of habitats throughout their outmigration (freshwater, estuarine, and marine) could provide a tool for understanding fine-scale temporal or spatial differences in the life history of specific stocks of coho and Chinook salmon.

In summary, we observed significant relationships between variation in the trophically transmitted parasite community of juvenile salmon and ocean conditions in early summer. These findings are consistent with the hypothesis that basin- and local-

scale variation in ocean conditions that alter zooplankton community composition also affects lower trophic levels that support juvenile salmon during early marine residency. Parasite communities of juvenile coho and Chinook salmon that were associated with greater adult returns of these two stocks occurred when SST was low, the biomass of subtropical copepods was low, and the plume volume was large in spring and very early summer. Correlations among a warm-water, lipid-poor copepod community, trophically transmitted parasites, and salmon survival provides additional, novel evidence that interannual variation in the composition of lower trophic levels is likely an important component of salmon survival.

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