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## **Growth and condition of juvenile coho salmon *Oncorhynchus kisutch* relate positively to species richness of trophically transmitted parasites**

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The aims of this study were first, to test the hypothesis that metrics of fish growth and condition relate positively to parasite species richness ( $S_R$ ) in a salmonid host; second, to identify whether  $S_R$  differs as a function of host origin; third, to identify whether acquisition of parasites through marine v. freshwater trophic interactions was related to growth and condition of juvenile salmonids. To evaluate these questions, species diversity of trophically transmitted parasites in juvenile coho salmon *Oncorhynchus kisutch* collected off the coast of the Oregon and Washington states, U.S.A. in June 2002 and 2004 were analysed. Fish infected with three or more parasite species scored highest in metrics of growth and condition. Fish originating from the Columbia River basin had lower  $S_R$  than those from the Oregon coast, Washington coast and Puget Sound, WA. Parasites obtained through freshwater or marine trophic interactions were equally important in the relationship between  $S_R$  and ocean growth and condition of juvenile *O. kisutch* salmon.

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Key words: fresh water; habitat quality; IGF1; marine; species diversity.

### **INTRODUCTION**

Parasites, by definition, survive at the expense of their host. Recent syntheses, however, have suggested that parasite diversity is highest in healthy ecosystems (Marcogliese, 2005; Hudson *et al.*, 2006). Hudson *et al.* (2006) asked ‘is a healthy ecosystem one that is rich in parasites?’ They suggested that a healthy ecosystem, which supports a high biodiversity of indigenous free-living fauna (Landsberg *et al.*, 1998), will

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also carry a diverse community of parasites species. While parasite community data support this conjecture (Marcogliese & Cone, 1996; Valtonen *et al.*, 1997; Dzikowsky *et al.*, 2003), no one has examined these findings in terms of the growth and condition of individual hosts.

Many parasites have life cycles that involve trophic transmission through a chain of intermediate host species. Therefore, each parasite species in a host reflects the presence of various organisms in the environment which support that parasite's life cycle (Marcogliese & Cone, 1996; Marcogliese, 2005). Removal of any one of the hosts required to complete a parasite's life cycle will lead to elimination of that parasite from the ecosystem. In this way, parasites appear to be more sensitive to environmental stressors than their hosts (Landsberg *et al.*, 1998), where environmental conditions associated with poor ecosystem health (*e.g.* sewage, eutrophication, thermal stress and urban development) lead to a reduction in free-living fauna and the associated parasite species (MacKenzie, 1999). This pattern has been well documented in numerous fish species from a variety of habitats. Parasite communities of two species of freshwater fishes perch *Perca fluviatilis* L. 1758 and roach *Rutilus rutilus* (L. 1758) were compared across four lakes in central Finland (Valtonen *et al.*, 1997). They found that the parasite communities of fishes captured at sites contaminated with chemical pollution from a nearby pulp mill were composed of significantly fewer species than those of fishes captured at unpolluted sites. Dzikowsky *et al.* (2003) documented a similar pattern in marine waters off the coast of Israel. They observed a complete absence of parasites in the gut of grey mullet *Liza aurata* (Risso 1810) captured in a heavily polluted bay. In contrast, a diverse community of intestinal helminths was observed in fish captured in an unpolluted reference site (Dzikowsky *et al.*, 2003). These and other studies add to the growing evidence that a healthy ecosystem is one that is rich in parasites (Marcogliese, 2005).

In this study, species diversity of trophically transmitted parasites was analysed in juvenile coho salmon *Oncorhynchus kisutch* (Walbaum 1792) to test the hypothesis that fish growth and condition are positively related to the number of trophically transmitted parasite species infecting them. For Pacific salmon *Oncorhynchus* spp., growth has been used as an indicator of condition and general health and is considered an important determinant of survival for juveniles after ocean entry through size-selective mortality (Fisher & Pearcy, 2005). It has been well documented that faster-growing *Oncorhynchus* spp. are at risk of predation for a shorter time than those growing more slowly (Pearcy, 1992; Duffy & Beauchamp, 2011). In addition, the condition and fitness of an individual *Oncorhynchus* spp. during early marine residency may relate to ability to survive the first marine winter (Beamish & Mahnken, 2001; Beamish *et al.*, 2004). Factors driving variability in growth rates among *Oncorhynchus* spp. are not completely understood. Environmental conditions associated with prey quality and composition, water temperature and man-made alterations appear to be related to growth and condition of *Oncorhynchus* spp. in both the fresh water (Richardson *et al.*, 1985; Groot & Margolis, 1991; Waples *et al.*, 2007) and marine environment (Davis & Myers, 1998; Beauchamp *et al.*, 2007; Trudel *et al.*, 2007; Peterson *et al.*, 2010).

Due to a diverse diet and a position in the food web as both predators and prey (Quinn, 2005), *Oncorhynchus* spp. serve as intermediate, paratenic (facultative) and definitive hosts to an array of parasites (Olson, 1978; Baldwin *et al.*, 2008). These parasites that are acquired through trophic interactions may remain with their host for weeks, months or years (Rohde, 1984; Moser, 1992; Marcogliese & Cone, 1997), causing little or no

apparent harm (Mosquera *et al.*, 2003). Juvenile *Oncorhynchus* spp. captured in the marine environment carry parasites obtained through consumption of infected intermediate hosts in both fresh water and salt water (Baldwin *et al.*, 2008). Thus, the parasite community of juvenile *Oncorhynchus* spp. during early marine residency is a product of trophic interactions across a wide range of habitats.

The hypothesis that metrics of fish condition and growth (Fulton's condition factor,  $K$ , ocean growth calculated from scales, insulin-like growth factor-1 and fork length,  $L_F$ ) are positively related to the number of trophically transmitted parasite species infecting fish was tested. Further, whether parasite species richness ( $S_R$ ) differed among source populations of *O. kisutch* and whether parasites obtained through trophic interactions in the marine environment were a better indicator of fish growth or condition than those obtained in freshwater environments was evaluated.

## MATERIALS AND METHODS

### FISH COLLECTION

This study is one component of a multidisciplinary project designed to examine the early ocean ecology of juvenile *Oncorhynchus* spp. and the factors that affect their marine survival (Fisher & Pearcy, 2005; Peterson *et al.*, 2010). Samples for this project were collected during 10 days in the second half of June 2002 and 2004. Sampling stations were located on eight transects from La Push, Washington to Newport, Oregon (Fig. 1). Stations on each transect began as close to shore as possible and ranged from 3 to 50 km offshore (Fisher *et al.*, 2007). Juvenile *O. kisutch* were collected during daylight hours using a Nordic 264-rope trawl towed at the surface. The mouth opening of the trawl was 20 m deep and 30 m wide when towed. Tows lasted 15–30 min at an approximate speed of 6.5 km h<sup>-1</sup>.

Yearling *O. kisutch* were distinguished from sub-adult or adult fish by  $L_F$  (Pearcy & Fisher, 1988; Fisher *et al.*, 2007). Blood was taken immediately from the caudal vein using a heparinized syringe and stored on ice for up to 2 h. Samples were then spun for 5 min in a microcentrifuge at 3000 g for 5 min. Blood plasma was collected and frozen at -20° C while at sea (up to 10 days) and then transferred and stored at -80° C in 1.5 ml cryo-tubes on land. Scales were taken only when scales were available from the preferred area above the lateral line midway between the dorsal and adipose-fins (Scarnecchia, 1979) and stored in envelopes. Fish were frozen onboard immediately after blood and scale samples were collected. In the laboratory, juvenile *O. kisutch* were partially thawed, re-measured ( $L_F$ ) and weighed ( $M$ , to the nearest 0.1 g).

### COLLECTIONS OF PARASITES AND ANALYSIS

A total of 411 juvenile *O. kisutch* were examined for trophically transmitted parasites. Parasite recovery from stomachs, intestines, body cavities and swim bladders followed standard necropsy procedures (Arthur & Albert, 1994). The majority of parasites were identified to species. To confirm the identity of some species, individual parasites were compared to specimens from the reference parasite collection of R. Olson and R. Baldwin at the Hatfield Marine Science Center and to type specimens from the U.S. National Parasite Collection (Beltsville, MD, U.S.A.). Parasites recovered that are known to utilize modes of transmission other than food web interactions were not included in analyses.

Parasite species richness, defined as the number of parasite species occurring in a sample (Poulin, 1998), was calculated for every fish and included both freshwater and marine parasites. In addition to  $S_R$ , four other metrics were calculated to describe the population of parasites infecting *O. kisutch*. These included the Shannon diversity index ( $H'$ ), which combines richness and evenness (Begon *et al.*, 1996); total number of parasite individuals infecting an individual fish; parasite prevalence, defined as the number of hosts infected by a particular parasite species

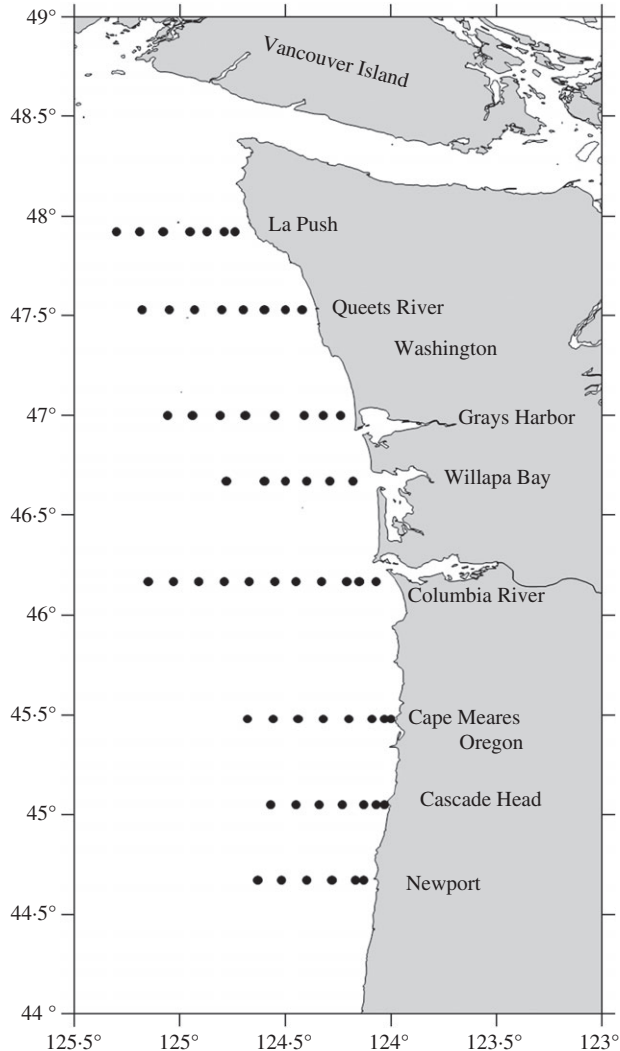


FIG. 1. Station locations along eight transects in the Northern California Current where juvenile *Oncorhynchus kisutch* were collected in 2002 and 2004 (●).

divided by the number of hosts examined (Bush *et al.*, 1997); intensity, defined as the number of individual parasites of a given species in a single infected host.

#### CONDITION AND GROWTH ANALYSIS

$K$  was calculated for each fish as  $K = 100 M L_F^{-3}$ , where  $M$  is the wet mass in g and  $L_F$  is in cm. The  $L_F$  of juvenile *O. kisutch* at ocean entry was backcalculated from scale radius at the ocean entry check using the Fraser–Lee method (Ricker, 1992). These calculations used a  $y$  intercept of 34.16 mm, which was derived from a geometric mean regression of  $L_F$  on scale radius for 2834 juvenile fish caught in the ocean during 1981–2001 (Fisher & Pearcy, 2005).  $L_F$  at ocean entry was subtracted from  $L_F$  at ocean recovery to give an estimate of total ocean growth, from which the percentage of total length attributed to ocean growth (marine growth)

was calculated. Due to descaling of some fish, caused by the trawl, sample sizes were smaller for this analysis than for *K*. In the laboratory, plasma insulin-like growth factor-1 ( $G_{IGF}$ ) was quantified as described by Moriyama *et al.* (1994); its use as an indicator of recent growth in *O. kisutch* has been validated by Beckman *et al.* (2004).

## GENETIC ANALYSIS

Genetic data from Van Doornik *et al.* (2007) was used to examine the stock composition of *O. kisutch* in this study. A total of 327 fish from this study were genotyped, from fin clips, at 11 microsatellite DNA loci by Van Doornik *et al.* (2007). Estimates of stock composition were based on regional baseline genetic data (Van Doornik *et al.*, 2007) and computed using the genetic stock identification software ONCOR (Kalinowski *et al.*, 2007). Allocations to individual baseline populations were summed to estimate the proportional contributions of seven regional genetic stock groups to samples (Van Doornik *et al.*, 2007). Confidence intervals for stock composition estimates were derived by bootstrapping baseline and mixture data 100 times (Kalinowski *et al.*, 2007).

## STATISTICAL ANALYSIS

For each fish,  $S_R$ , as well as other metrics of parasite infection were compared to *K*, marine growth,  $G_{IGF}$  and  $L_F$  from the same fish. To compare growth rates of *O. kisutch* to parasite infection, each individual fish was grouped by its number of parasite species (*i.e.*  $S_R$ ). *F*-test for equality of variances was conducted to determine the need for transformations. Multi-factor analysis of variance (ANOVA) was used to test for an effect of  $S_R$  on *K*, marine growth,  $G_{IGF}$  and  $L_F$  while controlling for year and genetic stock composition (origin). Difference in *K*, marine growth,  $G_{IGF}$  and  $L_F$  across  $S_R$  groups were investigated further using one-way ANOVA followed by Fisher's protected least significant difference *post hoc* test using R statistical software (R Core Team; www.r-project.org). For these analyses, *K*, marine growth,  $G_{IGF}$  and  $L_F$  were compared among four parasite richness categories (0, 1, 2 and  $\geq 3$  species), which were chosen to keep sample sizes across categories consistent. In all *post hoc* tests, a Bonferroni correction was used, resulting in an adjusted level of 0.01 to achieve a *P*-value of 0.05 (*i.e.*  $\alpha = 0.05/4 = 0.01$ ) across multiple comparisons presented as realized experiment-wide error rate. Associations between indices of fish growth and both parasite diversity and total number of parasites were tested using regression analysis. A  $\chi^2$  test was used to test for differences in the contribution of marine *v.* freshwater parasites species across  $S_R$  groups.

Finally, to determine if associations between  $S_R$  and *O. kisutch* growth and condition were consistent in both hatchery-produced and naturally produced fish, they were separated by whether or not they had any type of hatchery marking [passive integrated transponder (PIT) tag, coded wire tag or adipose fin-clip]. Due to small sample sizes of some groups, data from 2002 and 2004 were combined for these analyses.

## RESULTS

### PARASITE FAUNA

A total of 21 trophically transmitted parasite taxa were recovered from 411 ocean-caught yearling *O. kisutch*, including 12 known marine and six known freshwater taxa (Table I). In addition to confirmed identifications, one unidentified cestode, one unidentified nematode and one unidentified larval trematode (metacercariae) were recovered. The total number of individual parasites ranged from one to 70 per host fish. Parasite species richness ranged from zero to five species per individual fish in 2002 and from zero to seven in 2004. Approximately one-third of the parasite taxa



TABLE I. Prevalence ( $P_r$ ) and mean  $\pm$  s.d. intensity ( $I$ ) of trophically transmitted freshwater and marine parasites recovered from *Oncorhynchus kisutch*

Parasite taxa	Yearling <i>O. kisutch</i>			
	2002 ( $n = 217$ )		2004 ( $n = 194$ )	
	$P_r$ (%)	Mean $\pm$ s.d. $I$	$P_r$ (%)	Mean $\pm$ s.d. $I$
Fresh water				
<i>Crepidostomum</i> sp.			1.0	3.0 $\pm$ 1.4
<i>Cucullanus</i> sp.	1.8	1.0 $\pm$ 0.0		
<i>Deropegus aspina</i>	39.2	11.6 $\pm$ 18.9	33.5	10.4 $\pm$ 27.3
<i>Neoechinorhynchus</i> sp.			0.5	1.0 $\pm$ 0.0
<i>Plagioporus shawi</i>	19.8	9.1 $\pm$ 11.7	30.4	19.8 $\pm$ 31.6
<i>Salvelinema</i> sp.	1.8	34.5 $\pm$ 61.1	1.5	10.0 $\pm$ 7.9
Marine				
<i>Anisakis</i> spp.	9.7	1.1 $\pm$ 0.4	3.1	1.2 $\pm$ 0.4
<i>Bothriocephalus</i> sp.	1.8	1.3 $\pm$ 0.5		
<i>Contraceacum</i> sp.			0.5	1.0 $\pm$ 0.0
<i>Corynosoma</i> sp.	0.5	1.0 $\pm$ 0.0		
<i>Hemiurus levinseni</i>	6.9	1.8 $\pm$ 1.6	10.8	1.9 $\pm$ 1.6
<i>Hysterothylacium aduncum</i>	9.2	1.4 $\pm$ 0.7	8.2	1.2 $\pm$ 0.4
<i>Lecithaster gibbosus</i>	19.8	3.7 $\pm$ 10.5	11.3	2.1 $\pm$ 2.0
<i>Lecithophylum</i> sp.			0.5	1.0 $\pm$ 0.0
<i>Parahemiurus merus</i>	1.8	1.0 $\pm$ 0.0	5.7	1.1 $\pm$ 0.3
<i>Rhadinorhynchus trachuri</i>	1.8	2.0 $\pm$ 2.0	37.1	3.3 $\pm$ 2.6
Tetraphyllid cestode	0.9	1.0 $\pm$ 0.0	27.3	2.1 $\pm$ 1.9
<i>Tubulovesicula</i> sp.	0.5	2.0 $\pm$ 0.0	1.5	1.0 $\pm$ 0.0
Unknown				
Unknown cestode	1.4	2.7 $\pm$ 2.1	1.0	2.0 $\pm$ 1.4
Unidentifiable nematode	1.8	1.0 $\pm$ 0.0	1.0	1.0 $\pm$ 0.0
Unidentifiable trematode	0.9	1.5 $\pm$ 0.7	0.5	1.0 $\pm$ 0.0

recovered in this study had infected fish through trophic interactions in the freshwater environment. The proportion of marine *v.* freshwater parasites was not significantly different for any  $S_R$  group in either year of this study (Fig. 2;  $\chi^2$  test,  $P > 0.05$ ).

#### PARASITE SPECIES RICHNESS *v.* GROWTH AND CONDITION

Data included in comparisons of  $S_R$  and growth and condition were not skewed; therefore, no transformations were used. Indices of fish growth and condition ( $K$ , marine growth and  $G_{IGF}$ ) were associated with  $S_R$  of individual *O. kisutch* while controlling for the effect of year and origin (Table II; multi-factor ANOVA,  $P < 0.05$ ). There was no effect of  $S_R$  on  $L_F$  (Table II;  $P > 0.05$ ).

Fish condition was significantly different between  $S_R$  groups in both 2002 and 2004 [Fig. 3(a), (b); ANOVA, 2002:  $F = 5.5$ , d.f. = 3, 212,  $P < 0.05$ ; 2004:  $F = 10.9$ , d.f. = 3, 190,  $P < 0.05$ ]. Mean  $K$  was significantly higher among fish with three or more parasite species than among those with two, one or no parasite species recovered (Fisher's PLSD,  $P < 0.05$ ) in 2002 and 2004. Significant differences in marine growth were also found between  $S_R$  groups in both years [Fig. 3(c), (d); ANOVA, 2002:  $F = 4.6$ ,

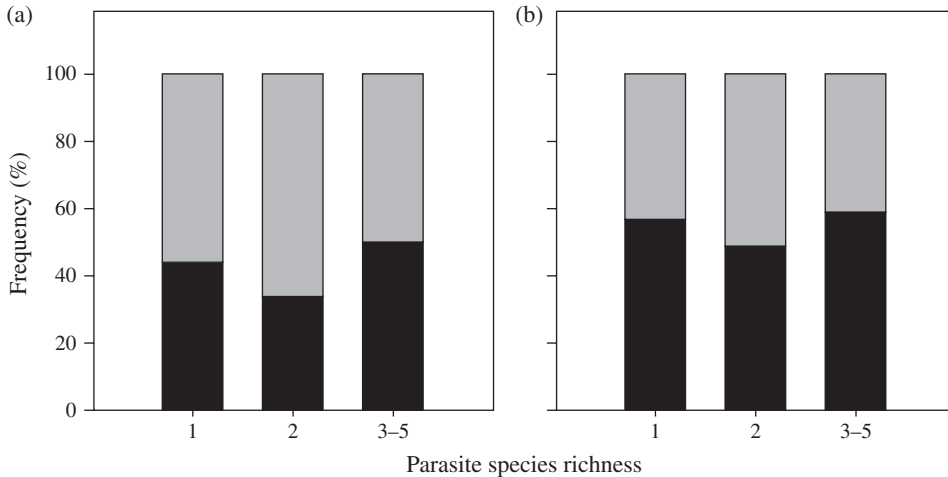


FIG. 2. Relative frequency freshwater parasites (□) to marine parasites (■) from June (a) 2002 and (b) 2004 yearling *Oncorhynchus kisutch* infected with different numbers of trophically transmitted parasite species.

d.f. = 3, 152,  $P < 0.05$ ; 2004:  $F = 6.6$ , d.f. = 3, 104,  $P < 0.05$ ]. Here, fish infected with three or more parasite species had significantly greater marine growth than fish with fewer than two parasite species (Fisher's PLSD,  $P < 0.05$ ). In addition,  $G_{IGF}$  levels which serve as a proxy for recent growth were significantly different between  $S_R$  groups in both years [Fig. 3(e), (f); ANOVA, 2002:  $F = 3.1$ , d.f. = 3, 179,  $P < 0.05$ ; 2004:  $F = 7.1$ , d.f. = 3, 169,  $P < 0.05$ ]; fish infected with three or more parasite species had significantly higher  $G_{IGF}$  levels than uninfected fish (Fisher's PLSD,  $P < 0.05$ ). Shannon diversity index and the total number of parasites infecting a fish were not related to  $K$ ,  $G_{IGF}$  or  $L_F$  in either study year ( $r^2 = 0.002-0.149$ ,  $P > 0.05$ ).

#### PARASITE SPECIES RICHNESS AND FISH ORIGIN

Juvenile *O. kisutch* captured in this study originated from six different regions but were dominated by Columbia River (43%), Oregon coast (27%) and Washington coast (23%) stocks. Genetic stock composition (origin) had a significant effect on  $K$  and ocean growth calculated from scales (Table II; multi-factor ANOVA,  $P < 0.05$ ). In addition, genetic stock composition differed among samples grouped by  $S_R$  (Fig. 4). In 2002, the proportion of *O. kisutch* that originated from the Columbia River was lowest in the highest species richness category, whereas Oregon coast salmon made up the greatest proportion of fish in the highest species richness category (Fig. 4). Only 13% of fish in the high  $S_R$  group were estimated to be from the Columbia River, in contrast to 52% from the Oregon coast (Fig. 4). The 95% c.i. for the Columbia River proportion of uninfected fish (35-64%; Table III) did not overlap with that for the high species richness group (0-29%; Table III). In 2004, the pattern was similar, with the smallest proportion of Columbia River fish (26%) in the highest  $S_R$  group, and larger proportions of these fish in the uninfected group (46%) and the group infected with one parasite species (56%). In 2004, however, the 95% c.i. for estimated proportions of Columbia River fish for all the four species richness groups overlapped (Table III).



TABLE II. Multi-factor analysis of variance (ANOVA) for an effect of trophically transmitted parasite species richness ( $S_R$ ), fish origin (genetic stock composition) and year on Fulton's condition factor ( $K$ ), ocean growth calculated from scales, insulin-like growth factor-1 ( $G_{IGF}$ ) and fork length ( $L_F$ , mm) of juvenile *Oncorhynchus kisutch* sampled in the Northern California Current during June of 2002 and 2004

Source	Source	d.f.	Sum of squares	Mean squares	F ratio	P-Value
K	Parasite species richness ( $S_R$ )	6	0.5000	0.083	5.89	<0.001
	Origin ( $O$ )	5	0.2350	0.047	3.33	<0.01
	Year ( $Y$ )	1	0.0750	0.075	5.32	<0.05
	$Y \times P$ interaction	4	0.1410	0.035	2.49	<0.05
	$P \times O$ interaction	14	0.1940	0.014	0.98	>0.05
	$Y \times O$ interaction	4	0.0680	0.017	1.20	>0.05
	Error	291	4.1180	0.014		
	Total	325	5.3310			
Ocean growth	Parasite species richness ( $S_R$ )	6	0.3886	0.06476	4.94	<0.001
	Origin ( $O$ )	4	0.1505	0.03763	2.87	<0.05
	Year ( $Y$ )	1	0.0154	0.01538	1.17	>0.05
	$Y \times P$ interaction	4	0.0395	0.00987	0.75	>0.05
	$P \times O$ interaction	14	0.1843	0.01317	1.00	>0.05
	$Y \times O$ interaction	3	0.0665	0.02218	1.69	>0.05
	Error	176	2.3071	0.01311		451
	Total	208	3.1519	0.1761		
$G_{IGF}$	Parasite species richness ( $S_R$ )	6	13 400	2233.3	4.42	<0.001
	Origin ( $O$ )	5	4414	882.7	1.75	>0.05
	Year ( $Y$ )	1	25	25.3	0.05	>0.05
	$Y \times P$ interaction	5	1222	224.4	0.48	>0.05
	$P \times O$ interaction	16	12 371	773.2	1.53	>0.05
	$Y \times O$ interaction	4	608	152	0.30	>0.05
	Error	251	126 750	505		
	Total	288	158 790	4815.9		
$L_F$	Parasite species richness ( $S_R$ )	6	9193	1532	1.37	>0.05
	Origin ( $O$ )	5	35 724	7145	6.40	<0.001
	Year ( $Y$ )	1	4757	4757	4.26	<0.05
	$Y \times P$ interaction	5	9802	1960	1.76	0.123
	$P \times O$ interaction	14	6023	430	0.39	>0.05
	$Y \times O$ interaction	3	9196	3065	2.75	<0.05
	Error	221	246 805	1117		
	Total	255	321 500	20 006		

Comparisons of hatchery (marked) and naturally (non-marked) produced *O. kisutch* revealed that in marked *O. kisutch*  $K$ ,  $G_{IGF}$  and  $L_F$  were all significantly higher in the higher species richness groups (ANOVA,  $K$ :  $F = 4.8$ , d.f. = 3, 187,  $P < 0.05$ ;  $G_{IGF}$ :  $F = 14.8$ , d.f. = 3, 161,  $P < 0.05$ ;  $L_F$ :  $F = 4.4$ , d.f. = 3, 187,  $P < 0.05$ ). The same trend was observed for total ocean growth in marked *O. kisutch*, but the difference was not statistically significant (ANOVA,  $P > 0.05$ ). In unmarked *O. kisutch*, both  $K$  and total ocean growth were significantly higher in the higher species richness groups (ANOVA,  $K$ :  $F = 4.9$ , d.f. = 3, 216,  $P < 0.05$ ; marine growth:  $F = 16.4$ , d.f. = 3, 117,  $P < 0.05$ ). There was a similar but non-significant trend for  $G_{IGF}$  to be highest in the highest  $S_R$  group and no differences in  $L_F$  among species richness groups in unmarked *O. kisutch* (ANOVA,  $P > 0.05$ ).

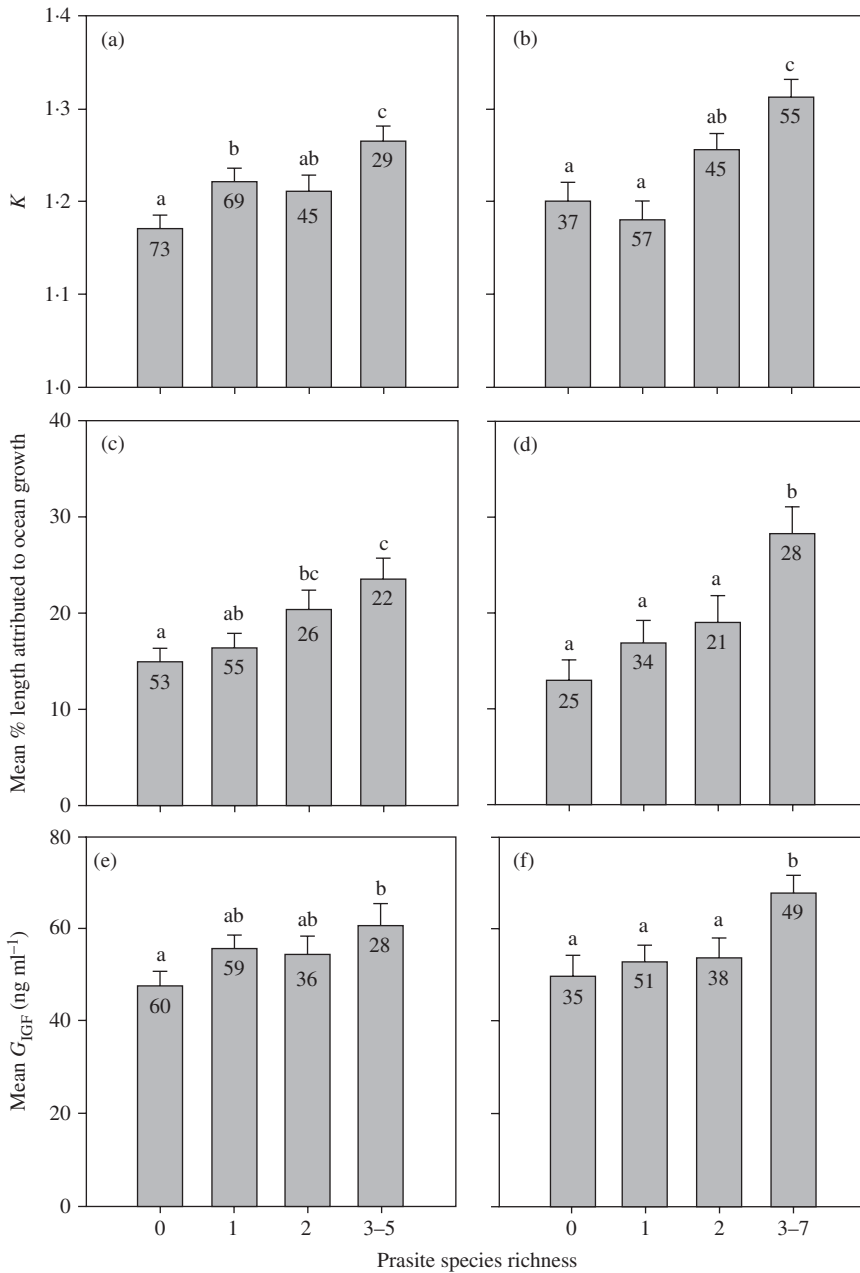


FIG. 3. Mean + S.E. (a, b) Fulton's condition factor ( $K$ ), (c, d) ocean growth calculated from scales and (e, f) insulin-like growth factor-1 ( $G_{IGF}$ ) for yearling *Oncorhynchus kisutch* infected with different numbers of tropically transmitted parasite species in June of (a, c, e) 2002 and (b, d, f) 2004 sampled in the Northern California Current. Sample sizes are indicated within each bar. Letters above bars are associated with pair-wise comparisons. Bars which do not share a lowercase letter are significantly different than each other ( $P < 0.05$ ).

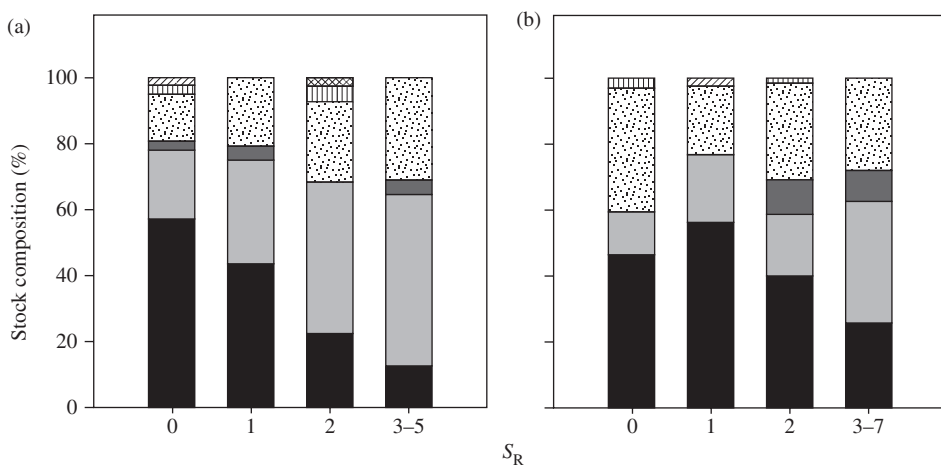


FIG. 4. Stock composition of parasite species richness ( $S_R$ ) groups from June (a) 2002 and (b) 2004 yearling *Oncorhynchus kisutch*. Stock groups are Columbia River (■), north and central Oregon coast (■), Puget Sound (■), Washington coast (□), south British Columbia (▨), central California (▩) and south Oregon and north California (▧).

## DISCUSSION

As hypothesized, growth and condition of yearling *O. kisutch* were greatest among those fish with the most diverse freshwater and marine trophically transmitted parasite fauna. Previous work has suggested that natural, unpolluted or healthy ecosystems carry a diverse fauna of parasites (Marcogliese & Cone, 1996; Halmetoja *et al.*, 2000; Huspeni & Lafferty, 2004), implying that high  $S_R$  may be associated with unaltered, unpolluted habitats. Results from this study support this premise and take it one step further by demonstrating that individual juvenile *O. kisutch* that exhibit greater growth and better condition also have higher parasites species richness than juvenile *O. kisutch* with slower growth or lower condition. These results may appear counterintuitive because parasites by definition should harm their hosts. Harm can vary from easily observed severe pathology to subtle, undetectable effects (Goater *et al.*, 2013); however, it is typically intensity-dependent. While high intensities of infection could have unmeasured pathological effects other than reduced growth or condition, our results suggest that diversity of parasites, but not their overall abundance, is related to fish growth and condition.

It is well known that the diets of fish can be deduced from trophically transmitted parasites (Margolis, 1965; Baldwin *et al.*, 2008; Valtonen *et al.*, 2010) and because most parasites are associated with a specific ecological niche and diet (Marcogliese, 2002), high diversity in host parasite fauna is often a result of a diverse host diet (Olson, 1978; Campbell *et al.*, 1980; Jennings & Hendrickson, 1982; Poulin, 1998). In this way, a diverse community of trophically transmitted parasites should indicate a host individual that has consumed a diversity of prey (in this case across freshwater, estuarine and marine habitats). The current results on  $S_R$  reinforce the importance of a diverse diet for juvenile *O. kisutch*, which during seaward migrations and early ocean life could lead to rapid ocean growth and, simultaneously, recruitment of a diverse parasite fauna.

TABLE III. Estimated proportion stock composition and 95% c.i. to trophically transmitted parasite species richness ( $S_R$ ) of yearling *Oncorhynchus kisutch* sampled in the Northern California Current during June 2002 and 2004. Confidence intervals are from 100 bootstrap resamplings of baseline and mixture genotypes. Stock groups are Columbia River (Columbia), north and central Oregon coast (N-COR), Puget sound (PS), Washington coast (WaC), south British Columbia (SBC), central California (CCa) and south Oregon and north California (Sor-NCa)

		2002					
$S_R$	0	1	2	3-5			
$n$	57	48	35	23			
Stock assignment	Estimate	95% c.i.	Estimate	95% c.i.	Estimate	95% c.i.	
SBC	0.03	(0.00, 0.10)	0.00	(0.00, 0.08)	0.05	(0.00, 0.16)	
PS	0.03	(0.00, 0.11)	0.04	(0.00, 0.24)	0.00	(0.00, 0.22)	
WaC	0.14	(0.06, 0.28)	0.21	(0.06, 0.35)	0.24	(0.06, 0.36)	
Columbia	0.57	(0.35, 0.64)	0.43	(0.20, 0.48)	0.22	(0.07, 0.36)	
N-COR	0.21	(0.10, 0.39)	0.32	(0.19, 0.51)	0.46	(0.27, 0.64)	
SOR-NCa	0.02	(0.00, 0.07)	0.00	(0.00, 0.00)	0.00	(0.00, 0.03)	
CCa	0.00	(0.00, 0.00)	0.00	(0.00, 0.00)	0.03	(0.00, 0.06)	
2004							
$S_R$	0	1	2	3-7			
$n$	31	47	40	46			
Stock assignment	Estimate	95% c.i.	Estimate	95% c.i.	Estimate	95% c.i.	
SBC	0.03	(0.00, 0.17)	0.00	(0.00, 0.06)	0.02	(0.00, 0.13)	
PS	0.00	(0.00, 0.14)	0.00	(0.00, 0.15)	0.10	(0.00, 0.25)	
WaC	0.37	(0.07, 0.50)	0.21	(0.05, 0.31)	0.29	(0.13, 0.49)	
Columbia	0.46	(0.22, 0.64)	0.56	(0.34, 0.69)	0.40	(0.18, 0.52)	
N-COR	0.13	(0.06, 0.39)	0.21	(0.10, 0.38)	0.19	(0.03, 0.37)	
SOR-NCa	0.00	(0.00, 0.06)	0.02	(0.00, 0.06)	0.00	(0.00, 0.05)	
CCa	0.00	(0.00, 0.00)	0.00	(0.00, 0.00)	0.00	(0.00, 0.00)	

The abundance and species composition of parasites that rely on food web interactions to complete their life cycle are determined in large part by the presence and diversity of free-living organisms in the environment, as well as by host foraging (Zander, 1998; Zander *et al.*, 2000). Therefore, environmental stressors which alter biodiversity and food web structure may affect the number of parasite species present (Williams *et al.*, 1992; Marcogliese, 2004, 2005). Environmental factors that affect parasite abundance and species richness in the freshwater environment, such as acidification, domestic sewage, thermal effluents and agricultural toxins (Landsberg *et al.*, 1998), have also been shown to affect fish health (Austin, 1998; Liney *et al.*, 2006). Together, these studies suggest that a fish living in a poor habitat may have both poor growth and condition and low species diversity of trophically transmitted parasites.

Occupation of poor-quality habitat prior to capture may have contributed to the strong relationship between metrics of fish growth and condition and  $S_R$  revealed in this study. Fish with low parasite diversity, which also had lower rates of ocean growth and condition, may have originated from or been reared in sub-optimal ecosystems. In addition, fish from poor-quality habitats may have had poor body condition and were thus unable to forage as efficiently as fish from better quality habitats, even after entering the marine environment. Together, these direct (foraging behaviour) and indirect (environmental) factors are known to affect parasite diversity within a host (González & Poulin, 2005; Valtonen *et al.*, 2010), and a combination of the two probably contributed to the finding of  $S_R$  increasing with growth and condition.

Columbia River *O. kisutch* made up a substantial proportion of the fish with low values for  $S_R$ , growth and condition (Fig. 4). Although the process that drives this trend is unknown, it suggests that Columbia River fish may have experienced less diverse feeding opportunities than fish originating in other systems. Alternatively, these fish may have been exposed to other stressors such as extreme temperatures, pH imbalance or pollution, each of which could lead to lower growth and lower  $S_R$  (Landsberg *et al.*, 1998). For example, Marcogliese & Cone (1996) found a decrease in  $S_R$  in American eels *Anguilla rostrata* (LeSueur 1817), associated with increased acidity in streams in Nova Scotia; however, they did not examine relationships between the health or condition of the host and  $S_R$ . This study highlights variability in parasite diversity associated with fish from different origins. Additional work aimed at clarifying the life cycles of trophically transmitted parasites would allow for a better understanding of trophic interactions which lead to differences in parasite assemblage discussed here.

It is also noteworthy that a large proportion of *O. kisutch* juveniles in the study area were the result of hatchery production (Teel *et al.*, 2003); therefore, it is worth considering the feeding behaviour of these fish. Brodeur *et al.* (1992) hypothesized that hatchery-reared salmonids may develop an 'inflexible search image' during rearing. After release, such a development could impair the success of hatchery fishes in identifying prey, compared with naturally produced salmon. In addition, it is likely that in *O. kisutch* not reared on live prey, parasite communities would be restricted to species encountered after release. In this study with data from 2002 and 2004 combined, only 15 marked *O. kisutch* contained three or more trophically transmitted parasite taxa, compared with 61 unmarked *O. kisutch* that fell into this highest species richness group. Similar trends of increased growth and condition with higher  $S_R$  were found in both marked and unmarked *O. kisutch* despite small sample sizes of some

groups and combined data from 2002 and 2004. To determine precisely how these parasite communities may differ would require isolation of known hatchery and naturally produced fish and comparison of their respective trophically transmitted parasite communities.

Additional research is needed to determine why juvenile *O. kisutch* with low  $S_R$  exhibit less growth and lower condition as reported herein. While this study is novel in being the first to report high parasite diversity associated with hosts exhibiting higher condition and growth rates, these findings were based on observational rather than on experimental data and included only 2 years of data. For these reasons, the precise factors that drive differences in host performance and parasite diversity are not clear. While a longer time series would be necessary to adequately identify patterns of inter-annual variability in parasite diversity relative to fish growth and condition, the fact that a multi-factor ANOVA identified a significant interaction between year and parasites supports the conclusion that high  $S_R$  was associated with high growth in individual fish in 2 years of variable levels of  $S_R$ . Studies on the diet of juvenile *O. kisutch* in the Northern California Current report a diverse diet with a high abundance of decapods, euphausiids, hyperiid amphipods and larval and juvenile fish species (Schabetsberger *et al.*, 2003; Brodeur *et al.*, 2007; Baldwin *et al.*, 2008). To date, no study has identified an association between a specific prey item and high growth and condition of juvenile *O. kisutch* in the marine environment. A study that incorporates a longer time series, with precise measurements of ocean entry-timing, and measurements of prey availability would further clarify the potential benefits of feeding on a diversity of prey during this critical period of the salmonid life cycle.

Species richness of trophically transmitted parasites has the potential to be a useful indicator of fish health or overall condition and may provide insight into the trophic interactions of juvenile salmonids and other fishes that lead to successful growth. Perhaps of greater importance are the implications these results have for identifying potential habitats of concern. The link between fish health and habitat degradation has been well documented (Adams, 2002; Quinn, 2005). Likewise, studies have associated habitat degradation to a decrease in diversity of endoparasites (MacKenzie, 1999), and  $S_R$  has been suggested as an indicator of ecosystem health (Marcogliese, 2005). This study takes the next logical step by providing evidence that high parasite species diversity can be an indicator of individual fish growth and condition.

Future work characterizing specific environmental conditions or behaviours associated with metrics of fish growth,  $K$  and  $S_R$  would dramatically enhance the ability of scientists and managers to assess the state of a variety of ecosystems and other fish populations. This information would help identify specific habitats or trophic interactions that are more or less suitable for the rapid growth important for fish survival. Similar patterns between parasite diversity and host condition metrics may be found in other organisms as well. Future work could reveal if the relationship between parasite species diversity and host growth and condition is specific to *O. kisutch*, extends to other fish species or is observable across a diverse array of host organisms.

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