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Parasitism and food web dynamics of juvenile Pacific salmon

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Abstract. There is an increasing realization of the diverse mechanisms by which parasites and pathogens influence the dynamics of host populations and communities. In multi-host systems, parasites may mediate food web dynamics with unexpected outcomes for host populations. Models have been used to explore the potential consequences of interactions between hosts, parasites and predators, but connections between theory and data are rare. Here, we consider sea louse parasites (*Lepeophtheirus salmonis*), which directly increase mortality of juvenile salmon hosts (*Oncorhynchus* spp.). We use mathematical models and field-based experiments to investigate how the indirect effects of parasitism via predation influence mortality of sympatric juvenile chum salmon (*O. keta*) and pink salmon (*O. gorbuscha*). Our experiments show that coho salmon predators (*O. kisutch*) selectively prey on pink salmon and on parasitized prey. Preference for pink salmon increased slightly when prey were parasitized by sea lice, although there was considerable uncertainty regarding this result. Despite this uncertainty, we show that even the small increase in preference that we observed may be biologically significant. We calculate a critical threshold of pink salmon abundance above which chum salmon may experience a parasite-mediated release from predation as predation shifts towards preferred prey species. This work highlights the importance of considering community interactions, such as predation, when assessing the risk that emerging parasites and pathogens pose to wildlife populations.

Key words: British Columbia; functional response; *Lepeophtheirus salmonis*; model averaging; *Oncorhynchus gorbuscha*; *Oncorhynchus keta*; *Oncorhynchus kisutch*; parasite-mediated behavior; predation; prey preference; salmon.

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INTRODUCTION

Predators kill their prey, whereas the effects of parasites on hosts are often sub-lethal. Therefore, the way in which parasites affect predator-prey interactions in food webs can have implications for host population dynamics and communities (Hatcher et al. 2012, 2014). In some cases, parasite-induced changes in host behavior that make prey more susceptible to predation may have evolved to facilitate transmission to a definitive host (e.g., Carney 1969, Lafferty and Morris 1996). However, there is growing recognition that parasites can influence food web dynamics of host populations more broadly (Hatcher et al. 2006, 2014). Parasite-induced changes to host behavior may increase predation by non-host species (e.g., Marriott et al. 1989), adding to direct effects of parasites on hosts. Alternatively, if parasites reduce predation, parasite-mediated relief from predation may offset direct effects of parasites on hosts. Whether parasites increase or decrease predation mortality of hosts therefore becomes a key question in determining the net impact of parasites on host populations.

Most theoretical models of predation and parasitism assume that predators will prefer parasitized prey because they may be easier to detect and catch (e.g., Lafferty 1992, Ives and Murray 1997, Kisdi et al. 2013, Toor and Best 2015). Empirical evidence of this has been reported for red grouse infested with nematodes (parasitized individuals appear to emit more scent and are more easily detected; Hudson et al. 1992) and selective predation of snowshoe hares infested with nematodes (Murray et al. 1997). Selective predation on parasitized prey can have implications for population dynamics, destabilizing predator-prey cycles (Ives and Murray 1997) and potentially improving the health of host populations by reducing the overall prevalence of parasites (Hudson et al. 1992, Packer et al. 2003). There are numerous studies using mathematical models to explore how predation and parasitism might interact (e.g., Lafferty 1992, Packer et al. 2003, Hatcher et al. 2014, Peacock et al. 2014), but connections between theory and data are rare, particularly for multi-host systems.

The impact of sea louse parasites (*Lepeophtheirus salmonis*) on juvenile salmon (*Oncorhynchus* spp.) in Pacific Canada has been an important conservation issue (Krkošek 2010). Sea lice are marine copepods that feed on the epidermis, blood and muscle of salmonid hosts. Sea lice develop through copepodid, chalimus and motile stages while attached to hosts, with virulence increasing with stage (Brauner et al. 2012). Infestation pressure is naturally quite low for wild juvenile salmon during their early marine phase (Gottesfeld et al. 2009) but has increased in recent decades due to the expansion of salmon aquaculture providing alternative hosts in coastal ecosystems (Frazer et al. 2012). Research on sea lice and juvenile salmon has focused on direct physiological effects of sea lice (e.g., Brauner et al. 2012), but ecological effects including parasite-induced changes to predation vulnerability may be important given the high levels of predation on juvenile salmon in the wild (Parker 1969, Groot and Margolis 1991). Krkošek et al. (2011) found that infested pink and chum salmon fry (*O. gorbuscha* and *O. keta*) were more vulnerable to predators as they accepted higher risk when foraging, had deviant schooling behavior, and were less likely to evade a predator strike relative to uninfested conspecifics. The cumulative effects of sea louse infestations and predation may therefore result in higher mortality of juvenile salmon due to sea lice than previously thought (Krkošek et al. 2011).

Indeed, the effect of sea lice on pink salmon survival is detectable at the population level; spawner-recruit analyses suggest that pink salmon survival declines with increasing sea louse infestations on out-migrating juveniles (Peacock et al. 2013); however, chum salmon survival does not (Peacock et al. 2014). Paradoxically, juvenile pink and chum salmon have very similar early life histories, with similar infestation levels during their seaward migration (Patanasatienkul et al. 2013) and similar rates of direct louse-induced mortality (Krkošek et al. 2009).

The way in which sea lice affect predation on mixed-species schools of pink and chum salmon may explain their different population-level responses. Juvenile coho salmon (*O. kisutch*) spend a year in freshwater before migrating to sea and are primary predators of juvenile pink and chum salmon (Parker 1969). Previous experimental work found that coho salmon predators preferentially consume pink salmon over chum salmon (Hargreaves and LeBrasseur 1985). A mathematical model tailored to the system suggested that if this preference were amplified by infestations, then sea lice may reduce predation on chum salmon (Peacock et al. 2014), offsetting the direct effects of parasitism and dampening the population-level impact. Previous studies of predation on infested juvenile salmon used only single-species schools of prey (Krkošek et al. 2011), so empirical evidence of sea lice changing predation dynamics in mixed-species schools is needed to substantiate this hypothesis. Here, we expand on previous modeling work and experimentally test for evidence of parasite-mediated changes to the food web dynamics of juvenile salmon. The results further our understanding of how sea lice affect juvenile Pacific salmon and are an example of the unexpected outcomes of parasitism in multi-host systems.

A GENERAL MODEL FOR PARASITE-MEDIATED PREDATION

We begin with a simple model for parasite-mediated predation and build upon previous simulation work (Peacock et al. 2014) by analytically determining the condition under which predation on chum salmon would be expected to decline with parasites. We then frame this condition in the context of predator preference and form the hypotheses to be tested in our experiments.

The functional response

A type II functional response describes an increase in predation rate with increasing prey abundance until a saturation point where predators are limited by the time it takes to handle and digest prey (Holling 1959). The functional response of a generalist predator depends on both the abundance of alternate prey species and the preference the predator displays for each species. The instantaneous rate of prey consumption by a single generalist predator on prey species N_i in the presence of alternate prey N_j is described by

$$f_i = \frac{a_i N_i}{1 + T_h(a_i N_i + a_j N_j)} \tag{1}$$

where a_i and a_j are the rates of successful attack resulting in capture, henceforth referred to as attack rates, and T_h is the handling time for predators to consume and digest prey (Holling 1959, Lawton et al. 1974). This type of functional response is common in piscivorous fishes such as coho salmon (Moustahfid et al. 2010), and has been applied previously to juvenile salmon (Krkošek et al. 2011, Peacock et al. 2014).

Attack rates may differ among prey species, in which case the predator is said to have a preference for the species with the higher attack rate (Chesson 1983). Due to previous evidence of selective predation on pink salmon (Hargreaves and LeBrasseur 1985), we chose the attack rate on pink salmon to be greater than the attack rate on chum salmon. Handling time may also differ between prey species, but here we assume that it is the same for both prey species because juvenile pink and chum salmon are morphologically and behaviorally similar. Throughout the paper, we use subscripts i and j to denote different prey species, and subscripts c and p to refer specifically to chum and pink salmon.

We included an effect of parasites on predation susceptibility of prey by incorporating a linear increase in the attack rate with the mean number of parasites per prey, x

$$a_i = \gamma_i(1 + \omega_i x) \tag{2}$$

where γ_i is the base attack rate on species i in the absence of parasites and ω_i is the per-parasite proportional increase in the attack rate on species i (Krkošek et al. 2011, Peacock et al. 2014). We assume that the number of parasites is the same on both prey species because no significant difference in infection levels between juvenile pink and chum salmon has been reported in the wild (Patanasatienkul et al. 2013, Peacock et al. 2014). The impact of parasites on host susceptibility to predation is likely non-linear, but a linear approximation is acceptable for low to moderate parasite abundances (see Appendix).

To determine the conditions under which predation on chum salmon might decline with parasites, we consider how the per-capita predation rate, $g_c = f_c/N_c$, changes with respect to the number of parasites. Inserting Eq. 2 into Eq. 1, and solving $dg_c/dx < 0$ leads to the following condition:

$$\frac{\omega_c}{\omega_p} < \frac{T_h \gamma_p N_p}{1 + T_h \gamma_p N_p}. \tag{3}$$

In words, Eq. 3 indicates that in order to observe a decline in predation on chum salmon with increasing number of parasites, the per-parasite increase in predation on chum salmon must be less than the per-parasite increase in predation on pink salmon (i.e., $\omega_c < \omega_p$). Under this condition, the attack rate on pink salmon would increase more quickly with the number of parasites than the attack rate on chum salmon (Appendix: Fig. A1). More specifically, Eq. 3 says that the ratio of ω_c/ω_p must be less than the proportion of time that predators would spend consuming pink salmon if there were no chum salmon present and no parasites. The more pink salmon there are in the environment (i.e., $N \rightarrow \infty$), the longer it takes predators to handle prey (i.e., $T_h \rightarrow \infty$), or the higher the base attack rate on pink salmon (i.e., $\gamma_p \to \infty$) the more occupied predators will be with their preferred prey, therefore requiring less of a difference in per-parasite increases in attack rates to see a decline in predation on chum salmon.

Prey preference

Rivers in coastal British Columbia see hundreds to millions of pink and chum salmon returning to spawn each fall (Fisheries and Oceans Canada 2011), and the following spring their offspring emerge from the gravel and migrate by the millions through coastal waters for a period of two to three months (Heard 1991). It is therefore reasonable to assume that during this time, N_p is large, and if γ_p and T_h are not too small (Krkošek et al. 2011) then we can approximate Eq. 3 by $\omega_c < \omega_p$ (we revisit this approximation later in light of our experimental results). This approximate condition can be stated in terms of the change in predators' preference for pink salmon with parasites. The preference for prey type j is defined as the probability that prey type j will be consumed next given equal availability of all prey types, and can be calculated as $\alpha_j = a_j / \sum_i a_i$ (Chesson 1983). Values of $\alpha_j > 0.5$ indicate a preference for species j. Incorporating the effect of parasites on the attack rate (Eq. 2), the preference for pink salmon when prey are infested with x lice is

$$\alpha = \frac{\gamma_p(1+\omega_p x)}{\gamma_c(1+\omega_c x)+\gamma_p(1+\omega_p x)}. \qquad (4)$$

The rate of change in preference with respect to the number of parasites is

$$\frac{d\alpha}{dx} = \frac{\gamma_c\gamma_p(\omega_p-\omega_c)}{\left[\gamma_c(1+\omega_c x)+\gamma_p(1+\omega_p x)\right]^2}. \qquad (5)$$

Therefore, the condition that $\omega_c < \omega_p$ is equivalent to $d\alpha/dx > 0$, i.e., that the preference for pink salmon increases with the number of parasites (Appendix: Fig. A1). In the following section, we describe a series of field-based experiments designed to test the hypothesis that predator preference for pink salmon increases with the number of parasites, and that predation mortality of chum salmon declines with infestations.

EMPIRICAL EVIDENCE FROM A JUVENILE SALMON FOOD WEB

Experimental methods

We conducted a series of field-based predation experiments in the Broughton Archipelago, Canada (126.5° W, 50.8° N; Appendix: Fig. A2) in the springs of 2013 and 2014. The goals of these experiments were (1) to test for species-selective predation by coho salmon on pink salmon, (2) to test for selective predation on parasitized prey, and (3) to determine if preference for pink salmon increases with parasitized prey. Experimental methods are briefly described here, with details in the Appendix.

We collected coho predators and pink and chum prey by beach seine and transported them to a floating research facility where they were housed in flow-through ocean enclosures until being used in experiments. Two days prior to an experiment, we haphazardly selected the required number of coho predators and transferred them to a separate ocean enclosure where they were deprived of food until experiments.

Each experiment consisted of paired trials, one with pink and chum prey that were infested with sea lice and one with uninfested prey. Prior to an experiment, we sorted prey into lousy and clean infestation categories by examining each fish in a clear plastic bag with seawater using a 16× hand lens (Krkošek et al. 2005*b*). We classified prey as lousy if they were infested with at least one *L. salmonis* sea louse of a chalimus II or motile stage, and clean if they had no sea lice of any stage or species and no signs of louse-induced morbidity. We size-matched pink and chum within and between infestation categories to minimize the impact of prey size as a confounding factor (Hargreaves and LeBrasseur 1986). We recognize that there may be other factors that increase the susceptibility of certain individuals to infection and would thus be confounded with sea louse infestation. This is an unavoidable consequence of using naturally infested prey. We note, however, that the aggregation of sea lice among hosts is likely due to small-scale patchiness in the spatial distribution of infectious parasites and there is limited evidence for selection among host individuals by sea lice (Murray 2002).

We transferred equal numbers of sorted pink and chum prey to one side of a divided experimental net pen. We had two experimental net pens, one with clean prey and one with lousy prey, and we randomly assigned which of the two experimental net pens housed the lousy trial (see data in Supplement). The food-deprived coho predators were then transferred to the empty side of experimental net pens, and predators and prey acclimatized to the divided experimental net pens for a minimum of four hours and a maximum of 20 hours before trials began. The variation in acclimatization period was unavoidable due to the variable time required to collect and sort prey and the constraint of starting and ended trials during daylight hours only.

Trials began by dropping the divider of the net pen to allow coho predators access to the mixed school of pink and chum prey. For experiments in 2014, a one-hour observation period followed during which we recorded the number of prey successfully captured by coho predators. Trials ran for between 4 and 24 hours; the length of the trial was pre-determined, but varied among experiments depending on the number of predators and prey we had (described below). At the end of trials, we divided the net pens and separated the coho predators from the remaining pink and chum prey. We counted coho predators and returned them to the holding pen. We measured the remaining pink and chum prey and visually inspected them for sea lice and other markings (e.g., scars from lice or predation strikes) using a 16× hand lens (Krkošek et al. 2005*b*) and then released them near their location of capture.

The number of predators, number of prey, and the length of the trials varied depending on how many clean and lousy pink and chum prey we were able to obtain. Lousy prey were often limiting, as the natural prevalence of sea lice was low throughout the study. When trials were run with less than 100 prey, the lengths of the trials and/or number of predators were predetermined with the goal of having approximately one-third of the available prey consumed based on consumption rates in previous trials. The variable number of predators, prey and length of the trails did not affect the preference for pink salmon (see Appendix).

We ran a total of 27 experiments, all but one of which consisted of paired trials with lousy and clean prey. Within these experiments, we performed eight control trials without coho salmon predators. The objectives of control trials were (1) to test if mortality in the absence of predation due to handling or sea lice was substantial or different between prey species, (2) to test if size-matching between pink and chum salmon prey was effective, and (3) to assess observation error in counting prey in and out of net pens. Any difference between prey species in mortality from sources other than predation may have confounded a predator preference, as we did observe coho consuming moribund prey.

Data analysis

Assuming the only substantial mortality of pink and chum prey in experiments was due to predation (we verified this assumption in the control experiments), the rate of change in prey species i throughout an experiment can be described by the functional response introduced in Eq. 1

$$\frac{dN_i}{dt} = -C\frac{a_iN_i(t)}{1+T_h\left(a_iN_i(t)+a_jN_j(t)\right)} \qquad (6)$$

where $N_i(t)$ and $N_j(t)$ are the number of prey species i and j available at time t and C is the number of coho predators in the experiment. Although we do not have a direct measure of the attack rates, we can solve for a_i as a function of known variables by integrating the coupled equations for the change in prey, $dN_i(t)/dt$ and $dN_j(t)/dt$ (Lawton et al. 1974), obtaining

$$N_i(t) = N_i(0)\exp[-a_i\Big(tC - T_h[N_i(0) - N_i(t) + N_j(0) - N_j(t)]\Big)] \qquad (7)$$

where $N_i(0)$ is the number of prey species i at the beginning of the trial and $N_i(t)$ is the number of prey species i remaining at the end of the trial. A similar equation, with is and js exchanged, results for the remaining prey $N_j(t)$. Eq. 7 is known as the Random Predator Equation (Rogers 1972). Solving Eq. 7 for a_p and a_c, the attack rates on pink and chum, and taking the ratio of $a_p/(a_c + a_p)$, we arrive at an equation for the preference for pink salmon (Chesson 1983)

Table 1. Model selection statistics for analysis of experiments. Only models comprising 90% of the cumulative Akaike weight (Cum. w_i) are shown.

Response (distribution, link)	Predictors	K†	$\mathrm{AIC_c}$‡	Δ_i§	w_i¶	Cum. w_i
Preference (normal, logit)	null	4	80.93	0.00	0.588	0.588
	lice	5	81.65	0.71	0.412	1.000
Proportion remaining with predator scars (binomial, logit)	species + lice	7	380.84	0.00	0.544	0.544
	species × lice#	8	382.85	2.01	0.200	0.744
	species	6	383.03	2.19	0.182	0.926
Lice per fish (Poisson, log)	after × species#	6	6742.23	0.00	0.517	0.517
	after + species	5	6742.71	0.48	0.407	0.924
Predation mortality (binomial, logit)	species	6	561.74	0.00	0.628	0.628
	species + lice	7	563.99	2.25	0.204	0.832
	species × lice#	8	564.38	2.64	0.168	1.000

† K = number of parameters.
‡ $\mathrm{AIC_c} = \mathrm{AIC} + 2\mathrm{K}\,(\mathrm{K}+1)/(\mathrm{n}-\mathrm{K}-1)$.
§ $\Delta_i = \mathrm{AIC_c}(i) - \min(\mathrm{AIC_c})$.
¶ Akaike weights: $w_i = \exp(-0.5\Delta_i)/\sum_j \exp(-0.5\Delta_j)$.
# Interactive and additive effects included.

$$\alpha = \frac{\log\Big(N_p(t)/N_p(0)\Big)}{\log\Big(\frac{N_p(t)N_c(t)}{N_p(0)N_c(0)}\Big)}. \tag{8}$$

We calculated α for each experimental trial. Values of α are constrained between zero and one, where $\alpha > 0.5$ indicates selective predation on pink salmon and $\alpha < 0.5$ indicates selective predation on chum salmon.

To determine if preference for pink salmon prey (α) increased when prey were parasitized, we fit a linear mixed-effects model with a fixed-effect for treatment (lousy or clean) and random effects for experiment number and coho group. The random effects accounted for possible variation among experiments conducted on different days due to weather, the age and size of prey, etc., and for possible variation among the coho groups collected from different areas at different times (Appendix: Table A1). We applied a logit transformation to α, which satisfied the assumptions of the linear model.

The predation scars on surviving prey and changes in louse abundances during experiments also carried information about predator preference. We estimated the proportion of remaining prey that had predator scars using a binomial generalized linear mixed-effects model (GLMM; logit link), with fixed effects for prey species and treatment (lousy or clean trial) plus an interaction term that allowed for a disproportionate effect of sea lice on one species. To account for non-independence of observations, we included nested random effects for trial within experiment number within coho group. We also included an observation-level random effect to account for overdispersion in the proportion of remaining prey with predator scars (Warton and Hui 2011).

We estimated the number of sea lice on prey using a Poisson GLMM (log link) with fixed effects for prey species and a factor indicating whether the data refer to before or after experiments, plus an interaction term, and a random effect for experiment number nested within coho group. Although sea lice are often overdispersed on hosts (Murray 2002), we were dealing with a group of hosts that had been sorted and had low but non-zero infestation intensity that was better represented by the Poisson.

Finally, we estimated the predation mortality of both pink and chum as a function of the mean number of lice per pink or chum at the beginning of each trial. The proportion of available prey that were consumed was estimated using a binomial GLMM (logit link function) with fixed effects for prey species and the mean number of lice per fish, plus an interaction term that allowed for a disproportionate effect of sea lice on predation mortality of one species. We also included nested random effects for trial within experiment number within coho group, accounting for the non-independence of pink and chum predation mortality estimates from the same trial/experiment/coho group. Again, we included an observation-level random effect to deal with overdispersion in the proportion of prey consumed by predators (Warton and Hui 2011).

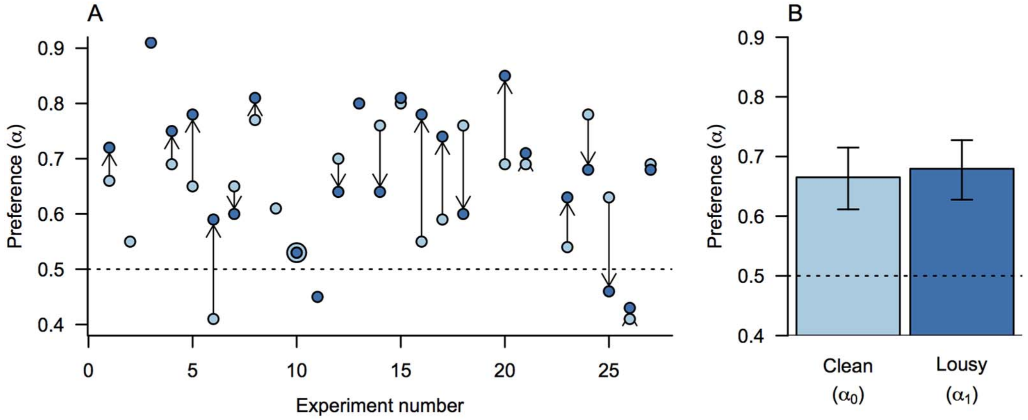

Fig. 1. (A) A predator preference for pink salmon was evident across experiments, with $\alpha > 0.5$ (dotted line) in 40/45 of the trials. Preference was higher in lousy trials (dark blue points) than clean trials (light blue points) in 12 experiments. Arrows indicate the direction of change in preference with parasites. (B) The model-averaged estimate (with 95% CI) of preference was higher in lousy trials than in clean trials, although there was considerable uncertainty in estimates.

For each set of models described above we fit all nested models and compared them using AIC_c (Table 1). In all cases, no single model had overwhelming support so we based our inference on the weighted average prediction of top models comprising 90% of the cumulative Akaike weight (Burnham and Anderson 2002), thereby accounting for both parameter uncertainty and model uncertainty. We report model-averaged predictions, as opposed to model-averaged parameters, to avoid errors in model-averaged parameters that can result from collinearity among predictors and different methods of averaging parameters (i.e., "natural average" vs. "zero method"; Grueber et al. 2011). All models were fit in R (R Core Team 2014), using the library lme4 for mixed-effects models (Bates et al. 2014) and AICcmodavg for model averaging (Mazerolle 2014).

Results

We conducted 45 predation trials and eight control trails, involving a total of 524 different coho predators and 3674 pink and chum prey. The eight control trials without coho predators had no substantial mortality of pink and chum salmon (see Appendix). A total of 911 pink salmon were consumed during predation experiments, while only 564 chum salmon were consumed. Coho predators showed a preference for consuming pink salmon ($\alpha > 0.5$) in 40 out of the 45 predation trials (Fig. 1A; see Supplement for data). In trials with clean prey, the model-averaged preference was $\alpha_0 = 0.665$ (0.611, 0.715; mean and 95% CI), indicating an overall preference for pink salmon prey over chum salmon (Fig. 1B). There was considerable uncertainty as to whether this preference changed when prey were infested with sea lice. We averaged predictions for preference over models that did and did not include an effect of sea lice as there was no obvious support from the data for a single top model (see Table 1 for model selection statistics and Table 2 for parameter estimates from the top models). The model averaged estimate of preference for pink salmon increased only slightly in lousy trials to $\alpha_1 = 0.680$ (0.628, 0.727), and confidence intervals for preference in clean trials overlapped the estimate for preference in lousy trials (Fig. 1B).

Fresh predation scars were clearly identified on surviving prey as semi-circular tooth marks, often accompanied by hemorrhaging (Appendix: Fig. A5). The proportion of remaining prey that had predator scars was higher for pink salmon and higher when prey were infested with sea lice (Fig. 2A) with a weak interaction between prey species and lice suggesting that the difference in predation scars between pink and chum salmon was higher when prey were infested (Tables 1

Table 2. Parameter estimates on the scale of the linear predictor from the top models for each of the response variables we considered. See Figs. 1–3 for model predictions on the scale of the response.

					95% CI		
Response and model	w_i†	Fixed effect‡	Estimate	SE	Lower	Upper	Overlap§
logit pref. for pink							
1	0.59	(intercept)	0.720	0.106	0.513	0.927	*
2	0.41	(intercept)	0.638	0.120	0.403	0.874	*
		treatment = lice	0.159	0.116	−0.069	0.387	
logit proportion of remaining prey with predation scars							
1	0.59	(intercept)	−2.402	0.187	−2.770	−2.035	*
		species = pink	0.406	0.143	0.125	0.687	*
		treatment = lice	0.369	0.165	0.045	0.694	*
2	0.22	(intercept)	−2.349	0.203	−2.747	−1.952	*
		species = pink	0.301	0.217	−0.124	0.726	
		treatment = lice	0.279	0.216	−0.145	0.703	
		pink:lice interaction	0.185	0.287	−0.377	0.748	
3	0.20	(intercept)	−2.212	0.169	−2.542	−1.882	*
		species = pink	0.400	0.143	0.120	0.680	*
log number of sea lice per fish							
1	0.56	(intercept)	0.191	0.030	0.132	0.250	*
		after	−0.116	0.048	−0.210	−0.021	*
		species = pink	−0.043	0.043	−0.127	0.041	
		after:pink interaction	−0.118	0.075	−0.266	0.029	
2	0.44	(intercept)	0.210	0.027	0.156	0.263	*
		after	−0.165	0.037	−0.237	−0.092	*
		species = pink	−0.081	0.035	−0.150	−0.012	*
logit proportion of available prey consumed							
1	0.63	(intercept)	−0.876	0.163	−1.196	−0.556	*
		species = pink	0.896	0.103	0.695	1.098	*
2	0.20	(intercept)	−0.858	0.173	−1.196	−0.520	*
		species = pink	0.895	0.103	0.694	1.097	*
		mean lice per fish	−0.030	0.091	−0.209	0.149	
3	0.17	(intercept)	−0.783	0.180	−1.136	−0.431	*
		species = pink	0.749	0.143	0.469	1.029	*
		mean lice per fish	−0.150	0.123	−0.391	0.091	
		pink:lice interaction	0.243	0.169	−0.089	0.575	

† Akaike weights normalized to include only the top models comprising 90% total Akaike weight from Table 1.

‡ The (intercept) refers to the parameter estimate for the base factor level while other parameters indicate the change for the specified factor level (e.g., "species = pink") or the slope with respect to the continuous variable (e.g., "mean lice per fish"). Base factor levels are "treatment = no lice," "species = chum," and "before" predation experiments.

§ Asterisks denote parameters for which the 95% CI does not overlap zero.

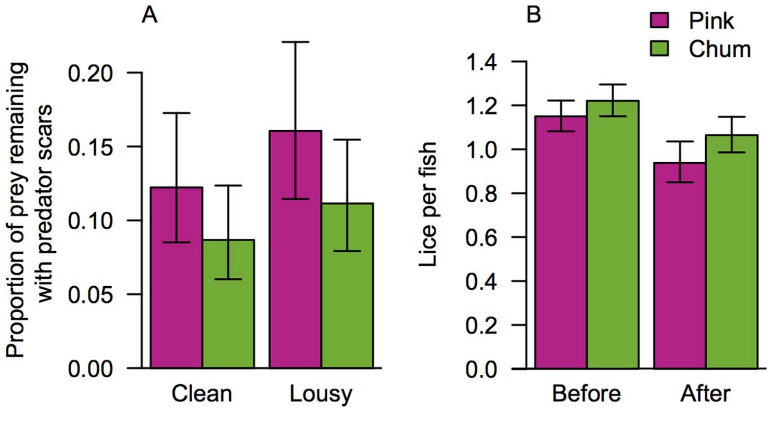

Fig. 2. (A) The proportion of remaining prey (with 95% CI) that had predator scars was higher for pink salmon than for chum salmon and higher in trials where prey were lousy. (B) The estimated number of lice per fish (with 95% CI) was slightly higher for chum salmon both before and after experiments, but decreased during experiments for both pink and chum.

and 2). This suggests that the observed species-selective predation on pink salmon was not the result of chum salmon escaping predators, but that pink salmon were more likely to be targeted by predators.

The number of chalimus- and motile-stage sea lice on prey was lower after experiments (Fig. 2B and Table 2). Furthermore, at the end of experiments, the number of sea lice on pink salmon was lower than the number of sea lice on chum salmon (Fig. 2B). In control experiments, the number of lice did not differ between prey species or before and after experiments (see Appendix for details). Therefore the pattern of reduced infestations after predation experiments with a stronger effect for pink salmon suggests selective predation of infested prey.

As the analysis of preference would suggest, the predation mortality of chum salmon was lower than the predation mortality of pink salmon (Fig. 3A). There was little evidence that sea lice affected the predation mortality of pink and chum salmon differently, although the suite of top models did include an interaction by which the predation mortality of pink salmon increased with the mean sea lice per fish at the start of the trial, but the predation mortality of chum salmon decreased with sea lice (Table 2). The model-averaged odds ratio, describing the increase in the odds of predation corresponding to an increase in one sea louse per fish, was 1.01 (95% CI: 0.93, 1.09) for pink salmon and 0.97 (0.88, 1.06) for chum salmon.

There was considerable uncertainty in the estimated predation mortality, particularly at high louse abundances because the range of infestation pressure we observed was limited; most prey in the lousy infestation category had just one sea louse of chalimus II or motile stage (Fig. 3A). At the peak of sea louse infestations in the study area, louse abundance was much higher (Fig. 3C). Nonetheless, the difference in predation mortality of pink and chum salmon (Fig. 3A) is consistent with the estimates of population-level mortality (Peacock et al. 2013, 2014; Fig. 3D–E), while individual-level direct louse-induced mortality (Krkošek et al. 2009; Fig. 3B) and the abundance of lice (Peacock et al. 2014; Fig. 3C) have been similar between the species.

Relating results to functional response model

An increase in preference for pink salmon with parasites was an approximate condition for predation on chum salmon to decline with parasites, but this approximation held only for large N_p. Given the relatively small increase in preference with parasites that we observed, we consider the full condition given by Eq. 3 to determine what abundance of pink salmon is required for Eq. 3 to be satisfied.

First, we consider the equation for preference in terms of the base attack rates, γ_p and γ_c, and per-parasite proportional increases in attack rates, ω_p and ω_c. For the trials with clean prey, we substitute $x = 0$ into Eq. 4 to yield the equation for the preference for pink salmon in the absence of sea lice

$$\alpha_0 = \frac{\gamma_p}{\gamma_p + \gamma_c} \tag{9}$$

The corresponding equation for preference in lousy trials, denoted α_1, with pink and chum infested with x parasites is given by Eq. 4. Solving Eq. 9 for γ_c and substituting into Eq. 4 we arrive at the following expression for ω_c:

$$\omega_c = \frac{\alpha_0 - \alpha_1}{x\alpha_1(1-\alpha_0)} + \frac{\alpha_0(1-\alpha_1)}{\alpha_1(1-\alpha_0)}\omega_p \tag{10}$$

Our estimates of $\alpha_0 = 0.665$ and $\alpha_1 = 0.680$ yield an intercept in Eq. 10 that is negative and a slope that is less than one. In that case, ω_c is less than ω_p for all positive values of ω_p, and the condition in Eq. 3 is met as N_p approaches infinity. Given our estimates of α_0 and α_1, what is the minimum N_p for the condition in Eq. 3 to be met? If the intercept of Eq. 10 is negative, as our estimates suggest, then we know that

$$\frac{\omega_c}{\omega_p} < \frac{\alpha_0(1-\alpha_1)}{\alpha_1(1-\alpha_0)}, \tag{11}$$

and we can write the full condition for predation on chum salmon to decline with parasites in terms of our estimates of preference

$$\frac{\alpha_0(1-\alpha_1)}{\alpha_1(1-\alpha_0)} < \frac{T_h N_p \gamma_p}{1 + T_h N_p \gamma_p}. \tag{12}$$

Rearranging Eq. 12, we arrive at an equation for the minimum number of pink salmon, N_p^*, required for predation on chum salmon to decline with increasing parasites

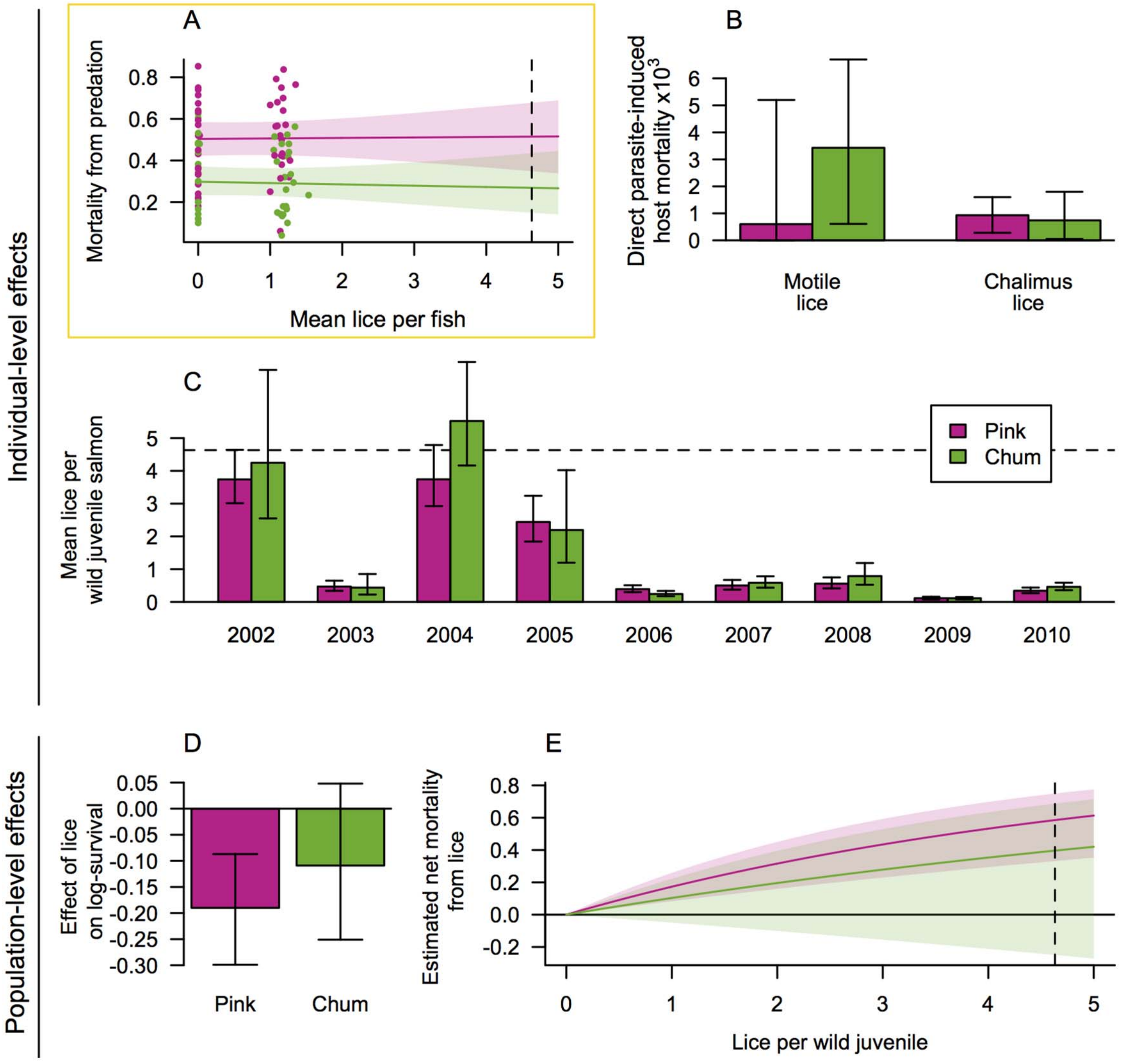

Fig. 3. This study investigated the effect of sea lice on predation mortality in mixed-species schools of pink and chum salmon (A; yellow box), which is just one factor contributing to the effect of sea lice on wild pink and chum salmon populations. Other studies have investigated: (B) Rates of direct parasite-induced mortality per chalimus- and motile-stage louse from a survival analysis of captive juvenile wild salmon (Krkošek et al. 2009). (C) The mean number of sea lice per juvenile wild salmon, estimated from monitoring data (Peacock et al. 2013; Supplement). (D) The population-level effect of sea lice estimated from spawner-recruit data using a Ricker model: $\log(R/S) = r - bS - cL$, where R are recruits, S are spawners, and L is the mean number of sea lice* per juvenile wild salmon (Peacock et al. 2013, 2014). (E) The predicted mortality due to lice ($1 - \exp(cL)$) over louse abundance. In all panels, shaded regions and error bars are 95% confidence intervals. *The x-axis of A is extended to show louse abundances corresponding to peak epizootics in 2004 (dashed line in panels A, C and E). Louse abundance includes chalimus II and motile stages in A, all louse stages in C, D and E (see Supplement).

$$N_p^* = \frac{\alpha_0(1-\alpha_1)}{T_h \gamma_p(\alpha_1 - \alpha_0)}. \tag{13}$$

The calculation of N_p^* from Eq. 13 requires estimates for the handling time, T_h, and base attack rate on pink salmon, γ_p (Fig. 4). To get an

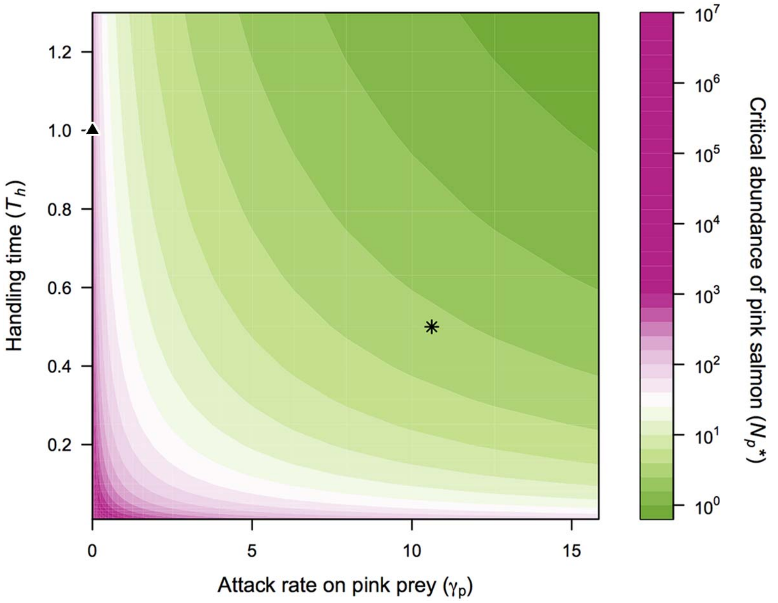

Fig. 4. The condition for predation on chum salmon to decline with parasites depended on the attack rate on pink salmon in the absence of parasites (γ_p; x-axis), the handling time of prey (T_h; y-axis) and the number of pink salmon available to predators (N_p^*; filled contours). Approximate estimates of γ_p and T_h from our experiments suggested that the condition was met for $N_p^* \geq 3$ pink salmon (star), while previous population-level estimates of those parameters suggest this critical value of pink salmon is much higher at $N_p^* \geq 4$ million pink salmon (black triangle).

estimate of handling time, we consider the maximum number of prey the average coho could consume in a day. In our experiments, the mean number of prey consumed per predator per day ranged from 0.25 to 10, but was biased high in shorter experiments (see Supplement for data). Considering the 24-hour experiments only, predators consumed an average of 1.88 prey each. This was consistent with observations by Hargreaves and LeBrasseur (1985) who found that coho consumed an average of 2–3 pink or chum salmon per day at the beginning of their experiments (as experiments progressed and coho grew, this increased to ~6 prey per day) and observations from Krkošek et al. (2011), who estimated that coho consumed approximately one prey per day in their group predation experiments. Based on this information, we assumed that the average coho satiates at two prey per day and set $T_h = 0.5$ days.

To get an approximate estimate of the successful attack rate on pink salmon in the absence of parasites, γ_p, we can use our recorded observations from the first hour of experiments, where we noted each successful attack on the school of prey by a coho predator ($n = 12$ trials; Appendix: Table A4). Based on these observations, the average attack rate per coho predator was 16.0 day^{-1} (range 4.8–24.0 day^{-1}). We were not able to distinguish between pink and chum prey in these observations, so we denote this overall attack rate as $\bar{\gamma} = \gamma_p + \gamma_c$. We can use our estimate of preference in the absence of parasites from the number of each prey species consumed to calculate the attack rate on chum salmon in terms of preference and the attack rate on pink salmon: $\gamma_c = \gamma_p (1 - \alpha_0)/\alpha_0$. It follows that $\gamma_p = \bar{\gamma}\alpha_0$, or $\gamma_p = 10.6$ day^{-1}. Using these estimates of $T_h = 0.5$ days and $\gamma_p = 10.6$ day^{-1}, the critical number of pink salmon in the school from Eq. 13 is $N_p^* \approx 3$ (Fig. 4).

The parameter estimates for handling time and attack rate derived from our experiments reflect the scale of a single school of pink and chum prey with a single group of coho predators over a maximum period of 24 hours. Previous studies have considered the population-level impacts of parasite-mediated predation over the entire juvenile salmon migration of ~3 months (Krkošek et al. 2011, Peacock et al. 2014). At this population scale, Krkošek et al. (2011) estimated $T_h = 1$ day and a much smaller attack rate of $\gamma_p = 3.4 \times 10^{-6}$ day^{-1}. These population-level parameters result in a very different estimate of $N_p^* \approx 4$ million pink salmon. Although this estimate may seem large, at the population-scale it is not unreasonable that there would be millions of juvenile pink salmon transiting through coastal waters during the spring migration. Estimates of abundance from river surveys indicate that returns of adult pink salmon to rivers in the Broughton Archipelago may be as high as ~2 million spawners (Fisheries and Oceans Canada 2011, Peacock et al. 2013: Fig. 6a), and the survival rate of salmon from juveniles to adults is relatively low (Parker 1968) suggesting that there would be many millions of juveniles migrating in the spring.

Discussion

Parasite infestations can have diverse outcomes for host populations depending on how parasites affect host interactions in the broader community (Hatcher et al. 2012). Theoretical studies have suggested that predation can play an important role in mediating host-parasite interactions (Ives and Murray 1997), particularly if predators display selective predation on parasitized prey (Hall et al. 2005). However, empirical work on the interactions between generalist parasites and predators in multi-host systems has been rare.

In this study, we investigated how parasites influenced selective predation in a juvenile salmon food web. We found that predators preferentially consumed pink salmon and preferentially consumed both pink and chum infested with sea lice, but there was uncertainty regarding how the predator preference for pink salmon changed with parasite infestation. The small increase in preference for pink salmon when prey were infested with sea lice was not statistically significant, but may be biologically significant. Our calculations suggest that, given this small increase in preference, predation on chum salmon may decline with sea lice if enough pink salmon are present to occupy choosy predators.

The minimum number of pink salmon required to observe a decline in predation on chum salmon with parasites was highly dependent on the scale at which we considered parameter estimates. Observations from our experiments suggest that this critical abundance of pink salmon is as low as three, while parameters from other population-level studies (Krkošek et al. 2011, Peacock et al. 2014) put the minimum number of pink salmon in the millions. This difference reflects the importance of scale when interpreting the results of experiments such as ours. A type II functional response describing the consumption rate of individual predators over increasing abundance of prey may not be directly applicable at the population scale. For social species like juvenile salmon that migrate or hunt in groups, the number of groups, not individuals, may be the appropriate unit when considering population dynamics (Fryxell et al. 2007). The number of groups may not increase linearly with the number of individuals and, in our system, the relative numbers of pink and chum salmon may vary considerably among schools. Therefore, it may not be trivial to understand population-level responses from individual-level experiments. In interpreting our results, we have implicitly assumed that the responses at the level of single schools of predators and prey would be observed at the population-scale, but more careful consideration of how these effects scale up should be incorporated into in future work.

Our results clearly indicate that coho predators preferentially consume pink salmon over chum salmon, consistent with a previous study reporting species-selective predation by coho salmon (Hargreaves and LeBrasseur 1985). In the absence of sea louse infestations, the predation mortality of pink salmon was significantly higher than that of chum salmon (Fig. 3A). The preference for pink salmon did not change significantly in trials with lousy prey, but there was a trend towards increased preference with sea lice. When prey were infested, predation mortality of pink salmon tended to increase, as expected from previous work indicating that sea lice make juvenile salmon more vulnerable to predation (Krkošek et al. 2011), but predation mortality of chum salmon tended to decline (Fig. 3A). Although the increase in predator preference for pink salmon with parasites was small and uncertain, it does point to a mechanism that may explain the different population-level responses of pink and chum salmon. The effect of sea lice on predation of pink and chum salmon is consistent with observed population-level effects (Fig. 3A and E).

Our experimental data did not offer clear support for a single hypothesis regarding prey preference or estimates of predation mortality, and so we used model averaging to account for the uncertainty in both parameter values and model selection (Burnham and Anderson 2002). In this way, we avoided overestimating effect sizes, as would have occurred if we had used the full models to draw inference. For example, the impact of sea lice on predator preference (Fig. 1) was larger if the effect was estimated only from model that included treatment (i.e., lousy or clean trial) as a covariate. However, there was only a 41.2% chance that was the correct model over the null model with no effect of sea lice (Table 1). Evidence of a change in preference with sea lice was weaker when accounting for this model uncertainty by averaging the predicted preference between the null model and the model including lice as a factor. We acknowledge that the use of AIC for mixed-effects models is an active area of research and that there are concerns regarding model-averaged parameter estimates for models with multiple predictor variables (e.g., different parameter estimates among models for the same predictor due to collinearity among predictors; Grueber et al. 2011). To avoid some of these pitfalls, we maintained the same random-effect structures among all models we compared and mainly reported model-averaged predictions rather than model-averaged parameters.

Several limitations in experiments may underlie the uncertainty in our parameter estimates. Our experiments included a limited number of predators and prey, which may have increased variability in consumption of each prey species among trials due to the unavoidable stochastic nature of the order in which predators will encounter the different prey species. Future work over a wider range of prey abundances with higher replication would allow parameterization of the functional response parameters directly, and allow a more direct test of how these parameters differ for different prey species. We used naturally-infested pink and chum salmon, and so the effect-size in our experiments was limited by the level of infestation in the wild. At the time of experiments, sea lice were not abundant on juvenile wild salmon. As a result, prey in lousy trials often had just one chalimus II stage louse, which may have had little effect on prey susceptibility to predation (Krkošek et al. 2011, Brauner et al. 2012). Effect sizes may have been much larger for infestation levels such as those measured in the early 2000s (Fig. 3C), but that was extrapolating beyond the range of our data (Fig. 3A).

The ways in which generalist parasites affect food web dynamics is gaining attention (e.g., Hatcher et al. 2006, 2012), but the impact that parasites can have on interactions in host communities has long been recognized. In particular, parasite-mediated apparent competition, by which generalist parasites cause declines for host species that are more vulnerable to infection or have lower growth rates (Hudson and Greenman 1998), has been cited as a major factor shaping the structure of ecological communities (Bonsall and Hassell 1997). For juvenile salmon, parasite-mediated apparent competition could explain the observed differences in population-level survival of pink and chum salmon if high chum salmon abundance caused a rise in parasite numbers overall that had a disproportionate negative impact on sympatric pink salmon. However, experimental work has shown that, if anything, chum salmon incur higher direct parasite-induced mortality (Krkošek et al. 2009; Fig. 3B). Further, pink salmon are the more abundant species in Broughton Archipelago, where population-level impacts have been estimated. The main source of sea lice on juvenile pink and chum salmon in our study area is farmed salmon in open-net pens along the migration route (Krkošek et al. 2006), with secondary infection among juvenile salmon being lower, particularly at the beginning of the migration when juvenile salmon are most vulnerable to sea lice (Krkošek et al. 2005*a*). It therefore seems unlikely that apparent competition is a reason why pink salmon seem to be more affected by sea lice at the population level, though this hypothesis may warrant further investigation.

Conclusions

We have shown that sea louse parasites can alter the food web dynamics of their juvenile salmon hosts and potentially shift predation towards preferred prey, leading to unexpected outcomes of parasite infestations for salmon populations. Initial research on sea lice and juvenile salmon focused on direct effects of parasites on host physiology (Brauner et al. 2012) and mortality in isolation (Morton and Routledge 2005, Krkošek et al. 2009). In the wild, host survival is also influenced by community interactions and the ecological effects that parasites might have on processes such as competition and predation are of key importance (Hatcher et al. 2006).

In general, where predators display species-selective predation, even a small increase in prey preference with parasites can result in parasite-mediated release from predation for less-desirable prey under the right conditions. This is contrary to conventional thinking, which posits that parasites make hosts more vulnerable to predation by altering host behavior or other traits (Hudson et al. 1992). Indeed, it was initially reported that sea lice increase predation susceptibility of both juvenile pink and chum salmon (Krkošek et al. 2011). However, as we have found, this straightforward interpretation can be complicated in multi-host systems with generalist predators, where parasites may alter food web dynamics. In such cases, the potential for interactions among host species through predation needs to be considered. This study contributes to an increasing realization of the diverse mechanisms by which parasites influence the dynamics of host populations and communities.

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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

The Appendix and the Supplement are available online: http://dx.doi.org/10.1890/ES15-00337.1.sm