# Predation intensifies parasite exposure in a salmonid food chain

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## Summary

**1.** Parasites can influence ecosystem structure, function and dynamics by mediating predator–prey interactions. Recurrent infestations of the salmon louse *Lepeophtheirus salmonis* associated with salmon aquaculture may mediate interactions between juvenile salmonids. Louse infection increases pink salmon *Oncorhynchus gorbuscha* susceptibility to predation, resulting in the trophic transmission of lice (with an adult male bias) to coho salmon *O. kisutch* predators. While experimental evidence is accumulating, the extent to which trophic transmission structures the distribution of lice among juvenile salmon in the wild is unknown.

**2.** We used a hierarchical modelling approach to examine the abundance and sex ratio of salmon lice on juvenile pink and coho salmon, collected from a region of salmon aquaculture during sea louse infestations, to test the hypothesis that trophic transmission of salmon lice increases infection on coho that feed upon infected pink salmon prey.

**3.** As predicted, coho had higher adult and pre-adult louse abundance than their pink salmon prey, and louse abundance was more adult male biased on predators than sympatric prey. We estimate that trophic transmission accounts for 53–67% of pre-adult and adult louse infection on coho.

**4.** *Synthesis and applications.* These results suggest that, by evading predation, salmon lice can accumulate up juvenile salmon food webs. Predators, such as coho, can experience a two- to three-fold increase in parasite exposure through predation on infected prey than would otherwise occur through passive exposure to infective larvae. Thus, predation may intensify parasite exposure and undermine the protection to ectoparasites conferred by the larger body size of predators. For larger predatory wild juvenile salmon, the risk of louse transmission from farmed salmon may therefore be greater than previously appreciated. These findings argue for an ecosystem perspective in monitoring and managing the marine environment in areas of intensive salmon aquaculture that includes the productivity and ecological interactions of all salmonid species.

**Key-words:** predator–prey, salmon, sea lice, trophic transmission

## Introduction

Parasites can alter the strength of inter- and intraspecific interactions, drive trophic cascades and influence ecosystem productivity (Poulin 1999; Lafferty *et al.* 2008). Accounting for parasites in food webs can lead to changes in species richness, food chain length and trophic levels (e.g. Huxham & Raffaelli 1995; Thompson, Mouritsen & Poulin 2005) as well as less intuitive changes in connectance (Lafferty, Dobson & Kuris 2006) and trophic energy flow (Mouritsen & Jensen 1994; Wood *et al.* 2007). This is particularly true in aquatic systems where parasites can dominate the biomass and productivity of the food webs in which they occur (Kuris *et al.* 2008). While interest in the role parasites play in aquatic food webs has increased in recent years (Byers 2009), investigations to date have been limited to a few well-studied coastal ecosystems (Lafferty *et al.* 2008).

Recurrent infestations of the salmon louse *Lepeophtheirus salmonis* Krøyer on juvenile pink salmon *Oncorhynchus gorbuscha* Walbaum have been reported in a region of coastal British Columbia (the Broughton Archipelago; Fig. 1) in 2001, 2002 and from 2004 to 2006 (Morton & Williams 2003; Morton *et al.* 2004; Krkosek, Lewis & Volpe 2005; Krkosek *et al.* 2006; Jones & Hargreaves 2009). These infestations have been orders of magnitude greater than those observed in other

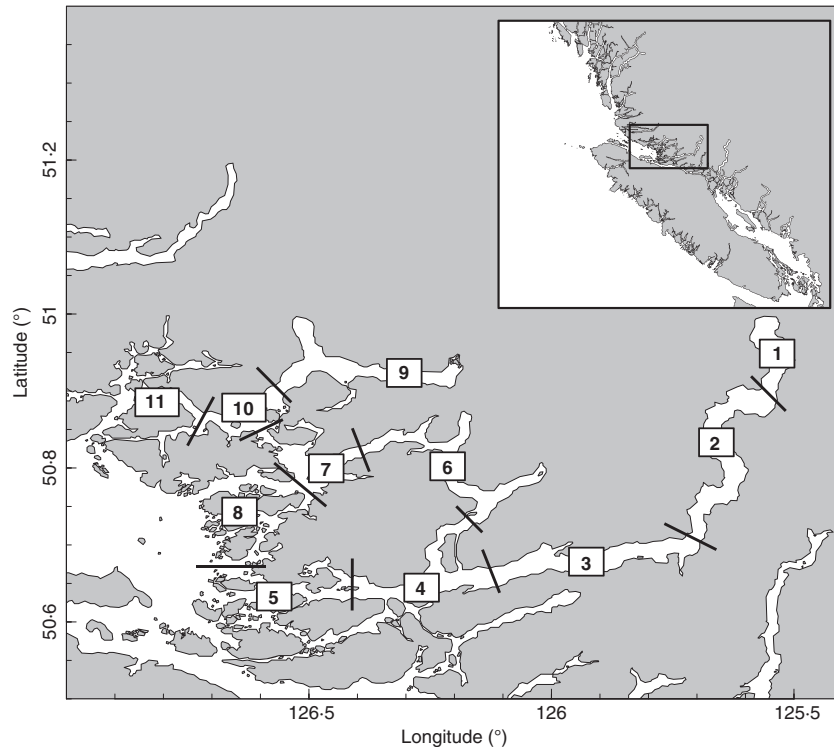*\*Correspondence author. E-mail: bconnors@sfu.ca*

**Fig. 1.** Study area and zones sampled for juvenile pink and coho salmon during spring of 2004 and 2005 (adapted from Jones & Hargreaves 2007). Black dots are approximate locations of salmon farm tenures in the region.

nearshore areas of the northeast Pacific where salmon louse abundance is low during the first few months of pink salmon marine life (Wertheimer *et al.* 2003; Morton *et al.* 2004; Gottesfeld *et al.* 2009). Recurrent infestations are associated with open net pen salmon aquaculture and depressed and declining pink salmon populations (Krkosek *et al.* 2007) although the relative contribution of lice from natural and anthropogenic sources and their impact on sympatric wild salmonids remains an area of ongoing debate (Costello 2009).

Juvenile coho salmon *O. kisutch* Walbaum are important predators of juvenile pinks in many areas throughout their range. Coho usually spend at least a year in freshwater and are approximately twice the size at marine entry as their pink salmon prey, which enter the marine environment shortly after emerging from the gravel. While these predator–prey interactions are intense, accounting for up to 70% of early marine mortality in pink salmon populations (Parker 1968), they are also short lived, lasting for only the first few months of marine life (i.e. April–July; Groot & Margolis 1991; Quinn 2005). Salmon louse infection has the potential to mediate coho–pink salmon interactions in two important ways. First, infection can increase juvenile pink salmon susceptibility to predators including juvenile coho (Costello 2006; Wagner, Fast & Johnson 2008; Krkosek *et al.* in press). Second, motile (i.e. adult and pre-adult) salmon louse stages respond to host predation by transferring from prey to predator, with adult males transferring more often than females (Connors, Krkosek & Dill 2008). These experimental findings suggest that when salmon lice are commonly found on juvenile pink salmon, selective

predation on infected individuals may result in the adult male biased transmission and accumulation of motile salmon lice on juvenile coho.

The transmission and accumulation of lice may have important consequences for early marine growth and survival of coho populations. However, the extent to which, if at all, trophic transmission influences the distribution of lice on salmonids that rear with and feed upon juvenile pink salmon is unknown. Here we report the results of field investigations into the distribution of salmon lice on juvenile salmon in an area of known louse infestations and provide evidence to support the hypothesis that trophic transmission commonly occurs when juvenile coho salmon are sympatric with infected juvenile pink salmon.

## Materials and methods

Salmon lice are a directly transmitted ectoparasitic caligid copepod ubiquitous on farmed and wild salmon throughout the northern hemisphere (Costello 2006). The salmon louse life cycle is characteristic of ectoparasitic copepods: free-living naupliar stages released from a pair of egg strings moult into an infective copepodid stage that seeks out and attaches to a host fish. Once on a host, copepodids moult into the first of four chalimus stages that are physically attached, via a frontal filament, to the host. The fourth chalimus stage moults into a preadult I and then II stage before reaching sexual maturity as an adult (Johnson & Albright 1991a). These last three stages are collectively referred to as motile because, as the name implies, they are capable of moving over the surface of host fish as well as among hosts (Ritchie 1997; Hull *et al.* 1998) and from prey to predator (Connors,

Krkosek & Dill 2008). Motile stages, which feed on mucus, scales and blood, are the most pathogenic to hosts (Wagner, Fast & Johnson 2008).

### FIELD DATA

Details of the field sampling have been described previously by Jones *et al.* (2006) and Jones & Hargreaves (2007). Briefly, juvenile salmon were collected in the Broughton Archipelago by beach and purse seine from May to July 2004 and 2005. Fish were individually bagged directly from the sampling net and immediately frozen for up to 57 months. Lice were then identified to species, stage and sex (motiles only) according to Johnson & Albright (1991b). The generalist sea louse *Caligus clemensi* Kabata was also identified and enumerated on hosts but not considered in the present analysis.

### DATASET STRUCTURE

We divided the dataset into salmon size classes consistent with previous experimental work on predator–prey interactions between juvenile pink and coho salmon (e.g. Hargreaves & Lebrasseur 1985; Connors, Krkosek & Dill 2008). The resulting dataset consisted of 4 juvenile salmon size classes (Table 1) allowing us to quantify and compare the distribution of salmon lice on predatory coho (large coho) to their pink salmon prey (small pinks). We also compared lice on large coho to pink salmon of a size class that are too large for coho to consume (large pinks), and to coho of a size class that are too small to consume pink salmon (small coho) thus accounting for any influence of species and size class *per se* on salmon louse abundance.

### LOUSE ABUNDANCE AND SEX RATIOS

Salmon louse abundance (lice per host) and louse sex ratios (males:females) were modelled separately using generalized linear mixed effects models (GLMMs) with Poisson (abundance) and binomial (sex ratio) error in R (R Development Core Team 2010). GLMMs allowed us to account for the nested nature of observations (i.e. parasites on fish nested within a sampling event, zone, and month) and the non-normal error distribution characteristic of count data. Sampling event, zone and month were treated as random effects assumed to be independently and identically normally distributed with a mean of zero and variance that is estimated. Salmon size class and gear type (beach or purse seine) were treated as fixed effects. Year was also treated as a fixed effect because with only two levels (2004 and 2005) we were unable to estimate among year variance sufficiently to treat it as a random effect (Gelman & Hill 2007). We accounted for overdispersion when present by correcting our standard errors using quasi-GLMMs with a dispersion parameter (Zuur *et al.* 2009). Parameters were estimated using Laplace approximation (Raudenbush, Yang & Yosef 2000).

Models with and without terms for salmon size classes, gear type and year were compared using AIC. The best supported model(s)

**Table 1.** Juvenile salmon size classes, corresponding fork lengths (mm) and number of individuals sampled and included in the analysis

| Size class | Mean FL (SE) | *n* |
|---|---|---|
| Coho > 100 mm FL | 118·2 (14·4) | 1211 |
| Coho < 80 mm FL | 62·7 (15·5) | 493 |
| Pinks > 100 mm FL | 106·6 (6·1) | 191 |
| Pinks < 80 mm FL | 59·7 (13·1) | 4063 |

were those with substantial support (i.e. ΔAIC ≤ 2; Burnham & Anderson 2004). When salmon size class was a term in the best supported model, parameters were contrasted between size classes by comparing parameter estimates and their confidence intervals. Size classes whose CIs did not overlap were considered statistically different. We predicted that if trophic transmission contributes to infection on predatory juvenile salmon then large coho should have significantly higher motile louse infection (but not copepodid and chalimus infection) than other size classes. Likewise, we predicted that large coho should have the most adult male- (but not preadult male-) biased sex ratio of the salmon size classes examined.

As infection increases on small pinks their susceptibility to predation should increase. Increased susceptibility to predation should lead to increased transmission of lice to large coho and thus the disparity in motile infection between small pinks and large coho should increase. In order to test this prediction we fit a line to the relationship between mean abundance of motile lice on large coho and motile abundance on sympatric small pinks (i.e. same zone, month and year). We then compared the slope of this relationship to the slope of the same relationship between large and small pinks. This allowed us to test if motile abundance increased at a greater rate on juvenile salmon feeding on infected pink salmon (i.e. large coho) than on similar sized salmon not subject to trophic transmission (i.e. large pinks). Slopes were compared using analysis of variance and the analysis was repeated for adult louse sex ratio.

### CONTRIBUTION OF TROPHIC TRANSMISSION TO INFECTION

Assuming that changes in chalimus to motile abundance on pinks and small coho result from processes independent of trophic transmission and therefore reflect the expected change on large coho in the absence of trophic transmission, we estimated the contribution of trophic transmission to motile infection on large coho as:

$$y_i = 1 - (\alpha_i / \beta) \qquad \text{eqn 1}$$

where *y* is the proportion of motile lice on large coho that were trophically transmitted, $\alpha$ is the change in chalimus to motile infection on size class *i* (small pinks, large pinks or small coho) and $\beta$ is the change in chalimus to motile infection on large coho.

## Results

### LOUSE ABUNDANCE AND SEX RATIOS

A total of 5958 juvenile pink and coho salmon were collected, examined for lice and used in the analysis (Table 1; Table S1, Supporting Information). The best-supported models of louse abundance and adult louse sex ratio included salmon size class. However, the best-supported model for pre-adult sex ratios did not (Table 2; for a summary of all models considered see Table S2, Supporting Information).

Copepodid abundance did not differ between large coho, small coho or large pinks but was lower on small pinks than on large pinks (Table 2; Fig. 2). Chalimus stage abundance was lower on small coho than on all other size classes and did not differ between large pinks, large coho or small coho (Table 2; Fig. 2). Motile salmon louse abundance was greatest on large coho followed by large pinks, small pinks and small coho (Table 2; Fig. 2). Pre-adult louse sex ratios did not differ

**Table 2.** GLMM parameter estimates from best supported models of motile, copepodid (cop) and chalimus (chal) stage louse abundance and pre-adult and adult louse sex ratios. Note parameter estimates are on the $\log_e$ scale

| Dependant variable | Parameter | Estimate | SE |
|---|---|---|---|
| Motile | Coho >100 mm FL | 0·26 | 0·10 |
| Motile | Coho <80 mm FL | −1·89 | 0·12 |
| Motile | Pinks >100 mm FL | −0·78 | 0·11 |
| Motile | Pinks <80 mm FL | −1·32 | 0·10 |
| Motile | Year | −1·23 | 0·13 |
| Motile | Gear type | −0·23 | 0·03 |
| Cop | Coho >100 mm FL | −2·69 | 0·08 |
| Cop | Coho <80 mm FL | −2·76 | 0·08 |
| Cop | Pinks >100 mm FL | −3·01 | 0·10 |
| Cop | Pinks <80 mm FL | −2·47 | 0·07 |
| Cop | Year | −1·58 | 0·10 |
| Chal | Coho >100 mm FL | −1·71 | 0·15 |
| Chal | Coho <80 mm FL | −3·11 | 0·20 |
| Chal | Pinks >100 mm FL | −1·63 | 0·18 |
| Chal | Pinks <80 mm FL | −2·27 | 0·15 |
| Chal | Year | −1·03 | 0·16 |
| Chal | Gear type | −0·81 | 0·13 |
| Pre-adult sex ratio | Year | −0·33 | 0·04 |
| Adult sex ratio | Coho >100 mm FL | 0·83 | 0·09 |
| Adult sex ratio | Coho <80 mm FL | 0·08 | 0·22 |
| Adult sex ratio | Pinks >100 mm FL | 0·10 | 0·11 |
| Adult sex ratio | Pinks <80 mm FL | 0·40 | 0·09 |
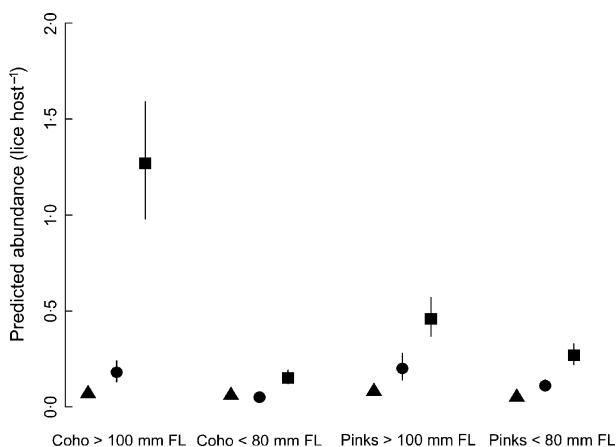


**Fig. 2.** Predicted copepodid (triangle), chalimus (circle), and motile (square) abundance (±95% CI) for each juvenile salmon size class. Values are transformed parameter estimates (i.e. $e^{(\text{predicted abundance} \pm \text{CI})}$) from best fit GLMMs hence they are lower than observed abundance (see Fig. S1) and conceptually represent relative differences in abundance between trophic groups once variation attributable to gear type, year, month, zone and sampling date is accounted for.

between salmon size classes, however, adult louse sex ratios were more male biased on large coho than on all other size classes. Adult louse sex ratios did not differ between large and small pinks and small coho (Table 2; Fig. 3).

As motile abundance increased on small pinks, motile abundance increased approximately twice as quickly on large coho than it did on large pinks ($F_{2,46} = 27.53$, $P < 0.001$; Fig. 4).
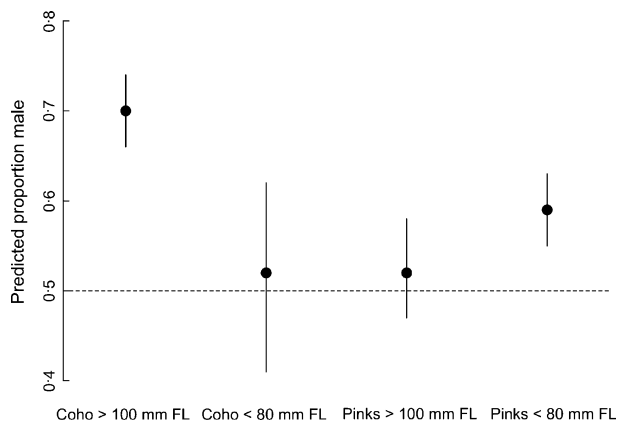


**Fig. 3.** Predicted proportion of adult salmon lice that are male (± 95% CI) for each juvenile salmon size class.
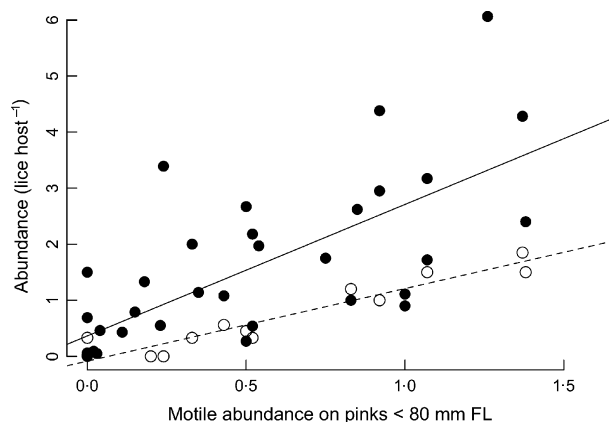


**Fig. 4.** Relationship between mean motile abundance on juvenile pink salmon less than 80 mm FL and sympatric coho greater then 100 mm FL (solid circles) and pinks greater than 100 mm FL (open circles). Lines are best-fit regression lines for coho (solid line: $y = 0.36 + 2.35x$, $P < 0.001$) and pinks (dashed line: $y = −0.08 + 1.29x$, $P < 0.001$). The slope of the relationship is $\sim 2$ times greater on coho than on pinks (slope coefficient $\pm$ 1SE; coho: $2.35 \pm 0.38$, pinks: $1.29 \pm 0.15$).

There was a weak but non-significant difference in the slopes of the relationships between large coho and small pink adult louse sex ratio and large pink and small pink adult louse sex ratio ($F_{2,46} = 2.55$, $P = 0.09$).

## CONTRIBUTION OF TROPHIC TRANSMISSION TO INFECTION

The changes in predicted chalimus to motile abundance on small pinks, large pinks and small coho were 2·61, 2·34 and 3·37 respectively. In contrast, predicted motile louse abundance was 7·17 times higher than chalimus abundance on large coho. Assuming that changes in chalimus to motile abundance on pinks and small coho reflect the expected change on large coho in the absence of trophic transmission, equation 1 estimates that trophic transmission accounts for 53% (based on small coho) to 67% (based on large pinks) of motile infection on large coho. This suggests trophic transmission increases

infection on coho sympatric with infected prey by two- to threefold.

## Discussion

Our findings suggest that trophic transmission of salmon lice from juvenile pink salmon to their coho predators occurs in nature. This highlights that predation may intensify parasite exposure and undermine the protection to ectoparasites conferred by the larger body size of predators. Three lines of evidence support this conclusion. (i) Motile abundance, but not copepodid or chalimus abundance, was significantly higher on large coho than on sympatric juvenile salmon size classes. This difference could not be attributed to species or size class because the observed differences held true for comparisons with large and small pinks as well as small coho. (ii) The sex ratio of motile lice on large coho was significantly more adult male biased but not pre-adult male biased than on sympatric juvenile salmon size classes. This supports the prediction from experimental work that adult salmon louse abundance should be more male biased on predators than prey because of an increased ability of adult males to successfully transfer from prey to predator host during predation (Connors, Krkosek & Dill 2008). This is likely to be due to differences in louse behaviour and morphology which restrict adult female movement among hosts (Hull *et al.* 1998). Unlike adults, pre-adult lice do not exhibit differences in movement among hosts and their trophic transmission is not sex biased (BMC, unpublished data). (iii) As motile abundance increased on small pinks the disparity between motile abundance on sympatric large coho and small pinks increased. This held true even after controlling for host size; the slope of the relationship was significantly greater for large coho than for large pinks. This pattern suggests that as prey become more infected, increased susceptibility to predation and trophic transmission cause motile lice to accumulate on predators. Though a similar pattern was observed for the adult louse sex ratios, it was non-significant, perhaps because of adult male lice moving among hosts in search of mating opportunities (Hull *et al.* 1998).

The sex ratio of adult lice on wild salmonids is usually adult female biased (see Table S3 in Supporting Information for a summary of published sex ratios) presumably because females live longer than males. However, in the present study sex ratios were either 50:50 or male biased. The fact that small pinks have the most adult male biased sex ratio, aside from large coho, is intriguing. Owing to their large size (adult females are ~twice the size of adult males, Johnson & Albright 1991b), adult female lice are likely to be the most pathogenic stage and sex to host fish, and male biased sex ratios on small pinks may result from adult female induced host mortality. Scale development, which occurs at a smaller size in coho than pinks (Kaeriyama 1989) may buffer the influence of adult female induced mortality on small coho and help to explain why small coho have a sex ratio that is closer to unity than do pinks. It should be noted that many of the sex ratios summarized in Table S2 are from mature fish that have been in the marine environment for considerably longer than the fish considered in the present

study. Nonetheless, the atypical adult male biased sex ratio observed on large coho in the present study lends further support the hypothesis that adult male biased trophic transmission contributes to infection on predatory coho smolts.

The observed patterns of infection could be driven by differences in louse development from stage-to-stage if they are species *and* size class specific (i.e. unique to each salmon size class). A pattern of infection similar to the one reported here (i.e. higher adult-male biased abundance on large coho) could occur if salmon louse survival from chalimus to motile stages were higher on large coho than on the other size classes and if adult male but not pre-adult male survival were higher than that of females only on larger coho. We cannot explicitly rule out this possibility, but consider it highly unlikely, and know of no evidence of sex specific differences in salmon louse survival as a function of host size despite over two decades of investigation into louse development and survival.

Differences in residency time could also account for the observed differences in motile salmon louse abundance if large coho, but not small coho, migrated out of the Broughton Archipelago at a slower rate than pinks. However, little is known about juvenile salmon residency time in the Broughton and residency times of coho in relation to pinks in other regions can be longer (Jaenicke & Celewycz 1994), shorter (Hartt & Dell 1986) or of equal length (Orsi *et al.* 2002). Despite the variability in residency time observed elsewhere, the similarity in chalimus stage abundance on pinks and coho suggests that increased residency by coho was not likely to have occurred in 2004 and 2005.

Using the proportional change in chalimus to motile abundance on pinks and small coho as a proxy for the expected change on large coho in the absence of trophic transmission, we estimated that trophic transmission accounts for 53–67% of the total motile lice on large coho. This approach assumes changes in abundance from attached to motile stages on pink salmon and small coho are of the same magnitude on large coho in the absence of trophic transmission. The similarity in the proportional change in chalimus to motile abundance on small coho and large and small pinks supports this assumption but further investigation into louse survival on hosts of different sizes and species is warranted. Because adult males are known to move among hosts our approach probably underestimates the true extent to which trophic transmission occurs. Despite these limitations our estimates suggest that trophic transmission contributes substantially to the louse burdens large coho experience during early marine life, increasing infection two- to threefold.

Pacific salmon can strongly influence the flow of nutrients and energy from marine to terrestrial ecosystems (Schindler *et al.* 2003) and changes in their survival and abundance may substantially alter the productivity of coastal environments. While it is well recognized that high numbers of motile stage lice can cause host morbidity and mortality (Costello 2006; Wagner, Fast & Johnson 2008), louse burdens at much lower levels (e.g. as low as 0·1 lice g$^{-1}$) can lead to changes in host physiology, biochemistry and immunology which may underlie observed changes in host behaviour with infection

(e.g. Wagner *et al.* 2003; Webster, Dill & Butterworth 2007). However, we caution extrapolation of these findings to coho because the influence of salmon louse infection on host physiology can be host species dependent and to date investigation into coho–salmon louse interactions have been limited to host physiology and biochemistry at abundances lower than those reported here (e.g. Fast *et al.* 2002; Jones *et al.* 2007).

Our finding that predation may intensify parasite exposure and undermine the protection to ectoparasites conferred by the larger body size of predators challenges our current understanding of salmon louse-juvenile Pacific salmon interactions. Current management of salmon lice on juvenile pacific salmon in areas of intensive salmon aquaculture focuses almost exclusively on pink salmon because of their small size at marine entry. Our findings strongly advocate for a shift in the management of lice on wild salmon to include (i) laboratory and field based studies of juvenile coho-salmon louse interactions, (ii) quantitative examination of coho population dynamics in areas of recurrent salmon louse infestations, and (iii) a more comprehensive ecosystem perspective to management and monitoring that includes the ecological interactions and productivity of all salmonid species.

## Acknowledgements

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Fig. S1.** Pre-adult, adult and total motile salmon louse abundance (±95% bootstrap CIs) on pinks < 80 mm FL (prey) and coho > 100 mm FL (predators) sampled in 2004 (a) and 2005 (b). Open circles are female lice and closed circles are male lice in the pre-adult and adult panels.

**Table S1.** Summary of sample sizes and mean abundance of salmon louse developmental stages (±95% bootstrap CIs) by salmon size class, year, month and zone.

**Table S2.** Summary of GLMMs considered. Best-fit models are highlighted.

**Table S3.** Summary of published data on adult male and female salmon lice enumerated on wild salmonids.

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