CAUSES AND CONSEQUENCES OF DISPERSAL IN A MARINE PARASITE (*LEPEOPHTHEIRUS SALMONIS*)

by

Brendan Michael Connors
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Name:	Brendan Michael Connors
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Examining Committee:

Chair: Dr. E. Palsson, Assistant Professor, S.F.U

_____
Dr. L.M. Dill, Professor Emeritus, Senior Supervisor
Department of Biological Sciences, S.F.U.

_____
Dr. C. Orr, Executive Director
Watershed Watch Salmon Society

_____
Dr. B. Roitberg, Professor
Department of Biological Sciences, S.F.U.

_____
Dr. J.D. Reynolds, Professor
Department of Biological Sciences, S.F.U.

_____
Dr. M. Adamson, Professor
Department of Zoology, U.B.C.
Public examiner

_____
Dr. T.P. Quinn, Professor
School of Aquatic and Fishery Sciences, U. of Washington
External Examiner

Date Defended/Approved: _____

Abstract

Parasitism is the most common animal lifestyle yet surprisingly little is known about the role parasites play in the ecosystems in which they are embedded. This thesis examines the causes and consequences of the dispersal of a marine ectoparasite, the salmon louse (*Lepeophtheirus salmonis*), in an area of intensive salmon aquaculture where the transmission of lice from farmed salmon may have consequences for the dynamics of adjacent wild salmon populations. Salmon lice are capable of leaving one host in search of another as they approach sexual maturity; while previously thought to be an artefact of the confined conditions characteristic of experiments and salmon farms I show that this is common in nature with at least 50% of lice on juvenile pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon moving from one host to another as they mature. I demonstrate that the underlying drivers of this dispersal shift with ontogeny from competition for resources to access to mates. Movement among hosts increases the probability that a louse interacts with multiple hosts potentially increasing the extent of louse transmission from farmed to wild salmon and the spread of other pathogens if lice can act as vectors. In addition, the movement of lice among hosts may have important consequences for predator-prey interactions between salmonids during early marine life. Coho salmon smolts (*O. kisutch*) selectively prey upon infected pinks. I show that sea lice transfer from pinks to coho during these interactions and as a result coho experience a 2 to 3 fold increase in parasite exposure over what they would otherwise experience through passive exposure to infective larvae from farms. To test for a population level response to this increase in louse exposure I examined coho population dynamics spanning a region of exposure to lice from infected pink salmon and salmon farms and show that populations exposed to recurrent infestations were depressed 7 fold relative to adjacent unexposed populations. These findings highlight the ecosystem context in which louse transmission from farmed to wild fish occurs and suggest that species interactions and parasite behaviour may cause the effects of parasite transmission from farmed to wild fish to propagate up marine food webs with broader consequences than previously appreciated.

Keywords: parasite; Pacific salmon; predator-prey; aquaculture; habitat selection

Big fleas have little fleas,
Upon their backs to bite 'em,
And little fleas have lesser fleas,
and so, ad infinitum

- Ogden Nash (1971)

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Chapter 1

General Introduction

Parasites are a ubiquitous feature of life on Earth and all living organisms are influenced in one way or another by parasitism, either as host or parasite (Price 1980). It should therefore come as no surprise that parasites can drive evolutionary change (Blais et al. 2007) and population dynamics (Cattadori et al. 2005) and mediate the structure and function of ecosystems (Edmunds and Carpenter 2001). Parasites play a particularly prominent role in aquatic ecosystems where they can dominate the biomass and productivity of the food webs in which they occur (Kuris et al. 2008). However, because parasites are often inconspicuous relative to other members of aquatic communities research into the influence of parasites in aquatic environments has been limited to a few well-studied ecosystems (Lafferty et al. 2008). Human activities, including those in or adjacent to aquatic environments, can have a pronounced effect on the emergence of disease (including parasites; Daszak et al. 2000), with implications for human health (Jones et al. 2008) and wildlife (Dobson and Foufopoulos 2001). Because anthropogenic activities increasingly alter the distribution and abundance of parasites (McKenzie 2007, Morand and Krasnov 2010, Polley et al. 2010) the ability to predict and mitigate the consequences of emergent infections depends, in part, on our understanding of how human activities influence the role of parasites in ecosystems.

In Canada, no parasite has received more attention in recent years than the salmon louse (*Lepeophtheirus salmonis*), a marine copepod that parasitizes anadromous salmonids throughout the northern hemisphere (Costello 2006). Salmon lice have a direct lifecycle consisting of free living infective stages, attached chalimus stages that are physically tethered to host fish, and motile stages that are able to move freely over the surface of hosts as they approach sexual maturity (Johnson and Albright 1991b). The extensive marine migrations that characterize most anadromous salmonids keep juvenile hosts spatially and temporally separated from adult hosts during early marine life. This serves as a barrier to louse transmission between host age classes until they occur in sympatry either in the outer coastal environment or the open ocean (Krkosek et al. 2007b, Gottesfeld et al. 2009). Intensive open net pen salmon aquaculture can undermine this natural barrier to transmission by providing a year-round host population in the nearshore marine environment. In the late summer and

fall, returning adult salmon infect farm fish whose lice can subsequently spill over to sympatric wild juvenile salmonids the following spring (Marty et al. 2010). As a consequence, recurrent louse infestations that are orders of magnitude greater than in areas without aquaculture have been documented on juvenile salmon adjacent to farmed salmon (Costello 2009) and in some cases recurrent louse infestations are associated with depressed salmon populations (e.g., pink salmon; Krkosek et al. 2007a, Krkosek and Hilborn 2011). While progress has been made quantifying louse transmission and it's consequences for wild pink salmon (Krkosek 2010), 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, Marty et al. 2010). In addition, the broader ecosystem consequences of louse transmission, and the factors that mediate it, remain poorly understood.

As salmon lice mature they can leave the host on which they developed on seek a new host (Ritchie 1997, Hull et al. 1998). This thesis explores the causes of this behaviour and its consequences for wild Pacific salmon in areas of intensive salmon aquaculture. I begin, in Chapter 2, with an experimental investigation into when and why salmon lice leave the host they developed on in search of another. Although the ability of lice to move among hosts has been recognised for decades it has been generally thought to be an artefact of the confined conditions characteristic of experiments and salmon farms (e.g. Todd et al. 2005). In Chapter 3, I quantify the extent to which lice move among juvenile pink and chum salmon hosts during early marine life, and in Chapter 4 I examine the ability of lice to move from pink and chum salmon to their salmonid predators during predation events (i.e., the trophic transmission of lice). The observation that lice can escape the demise of their host by transferring from one host to another during predation directly leads to the next two chapters of my thesis in which I quantify the extent to which the trophic transmission of lice contributes to infection on predatory coho salmon (Chapter 5) and the extent, if any, to which it influences coho population dynamics (Chapter 6). In my final chapter I synthesize the individual findings of each chapter, suggest future research directions and outline the management and policy implications of this body of work.

Chapter 2

What's love got to do with it? Ontogenetic drivers of dispersal in a marine ectoparasite[1].

Abstract

Sex-biased dispersal is common in nature and can influence the way in which organisms are distributed throughout the environment with consequences at the individual, population, community and species level. Much of our understanding of what drives sex-biased dispersal stems from work on birds and mammals where dispersal tends to be female- and male- biased, respectively. Here I draw upon this large body of empirical and theoretical work on vertebrates to investigate what drives breeding dispersal in an ectoparasite, the salmon louse, *Lepeophtheirus salmonis*. I manipulated the density, sex and developmental stage of lice on pairs of juvenile pink salmon (*Oncorhynchus gorbuscha*) hosts and show that the probability of leaving a host is density dependent at the pre-adult I stage, and dependent on the presence of the opposite sex at pre-adult II and adult stages. Experiments in which louse movement was observed in groups of 25 individually infected hosts supported findings from individual experiments. Lice appeared to account for predation risk as they were 3 times more likely to disperse in the dark, when susceptibility to predation was low, than in the light. My results support the hypothesis that asymmetry in reproductive investment shapes patterns of sex-biased dispersal and highlight the potential for drivers of dispersal to change with ontogeny. These findings are the first to establish what drives dispersal in the ecologically and economically important salmon louse and highlight the generality of the role mate competition plays in driving sex-biased dispersal across the animal kingdom.

Introduction

Dispersal, the permanent movement of organisms from one habitat to another, is a fundamental life history response to spatio-temporal environmental variation (Clobert et al. 2001). Dispersal strategies evolve under selective pressures that both favour dispersal and select against it. Evolutionary stable

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[1] A version of this chapter is in press as Connors, B.M., Lagasse, C. and L.M. Dill. What's love got to do with it? Ontogenetic drives of dispersal in a marine ectoparasite. Behavioural Ecology.

patterns of dispersal are predicted to result from a balance between these forces. As selective pressures are often sex-specific, dispersal strategies can differ between the sexes, and indeed sex-biased dispersal is common in nature (Clobert et al. 2001). This has led to a large body of theoretical and empirical work aimed at understanding the proximate and ultimate drivers of sex-biased dispersal and their consequences at the individual, population and species level.

Advances in our understanding of what drives and maintains sex-biased dispersal have largely stemmed from contrasting patterns of dispersal in mammals and birds where a number of hypotheses have been developed to explain patterns of sex-biased dispersal including inbreeding avoidance, resource competition and local mate competition (Greenwood 1980, Perrin and Mazalov 2000). The direction of bias is predicted to depend on mating system; all three hypotheses predict male-biased dispersal in polygynous systems while in monogamous systems only the resource competition hypothesis predicts female-biased dispersal. While the vast majority of empirical and theoretical work has focused on birds and mammals, sex-biased dispersal has more recently been demonstrated in a handful of other taxa including fish (Hutchings and Gerber 2002, Croft et al. 2003), lizards (Olsson and Shine 2003) and invertebrates (Sundstrom et al. 2003, Beirinckx et al. 2006, Stevens et al. 2006, Bandilla et al. 2008). The majority of these studies involved detecting patterns of dispersal in the field with species that are polygynous and support the local mate competition hypothesis. There remains a paucity of controlled experimental investigation into what drives and maintains sex-biased dispersal outside of vertebrate taxa.

Practically absent from studies of sex-biased dispersal are parasites (but see Bandilla et al. 2008). Yet parasites that can be facultatively transmitted, i.e., can decide to leave a host after having been obligately transmitted earlier in their lifecycle, offer a number of distinct advantages over free-living organisms in the study of dispersal: they are often short lived and occupy discrete habitats that are easily identified, replicated and amenable to experimental manipulation. One such parasite is the salmon louse, *Lepeophtheirus salmonis*, a directly transmitted ectoparasite that is ubiquitous on farmed and wild salmon in the northern hemisphere. Its lifecycle is characterized by two free-living naupliar stages followed by an infective copepodid stage which seeks out and attaches to a host fish. This is followed by four chalimus stages, which are physically tethered to the surface of the host, and then two pre-adult and one adult stage, which are collectively known as motile stages, because they can move between hosts (Johnson and Albright 1991b). Facultative, adult male-biased movement among hosts, analogous to breeding dispersal in free-living organisms, has been observed under experimental conditions (Hull et al. 1998, Connors et al. 2008b), on salmon farms (Ritchie 1997) and

in the wild (Krkosek et al. 2007b, Connors et al. 2010a), however, little is known about the underlying drivers of dispersal in motile lice.

Sea lice cost the global aquaculture industry in excess of $400 million USD annually (Costello 2009). Motile louse stages are the most pathogenic to hosts (Bjorn and Finstad 1998), may act as vectors of viral and bacterial pathogens (Nylund et al. 1991, Nylund et al. 1994, Barker et al. 2009), and their ability to move among hosts may play an important role in the transmission of lice from farmed to wild salmon (Connors et al. 2008b, Connors et al. 2010a). Thus, the movement of motile lice among hosts may have important economic and ecological consequences. Here, I empirically examine the relative importance of resources and access to mates in driving dispersal of motile stage *L. salmonis*, quantify a cost of moving among hosts, and provide insight into ontogenic changes in drivers of sex-biased dispersal.

Methods

COLLECTION AND MAINTENANCE:

Wild juvenile pink salmon (*Oncorhynchus gorbuscha*) were collected, examined for *L. salmonis* as described by Krkosek et al. (2005b) and sorted based on infection. Fish (Mean ± SD; FL: 68 ± 4 mm; girth: 11 ± 2 mm) were then held for a minimum of 24 hrs in a partitioned 2 x 0.5 x 0.5 m flow through trough and fed *ad libitum* twice daily. Experimental aquaria (see below) were held in flow through baths with water in each aquarium being 2/3 replaced every 24 hrs enabling temperature, salinity and dissolved oxygen to be maintained between 10-15°C, 29-32 and 8-10mg/l respectively (Connors et al. 2008a). Lice were removed from host fish as needed by transferring an infected host to a transparent bag with a small amount of seawater and then gently running one's fingers along the side of the host until the louse became dislodged.

INDIVIDUAL MOVEMENT EXPERIMENTS:

To test for an influence of access to mates and resources (i.e., density of conspecifics) on the propensity of lice to leave a host I established pairs of uninfected size matched (FL and girth) pink salmon fry, which were fin-clipped (tip of right or left pectoral fin), and placed in 10 L aquaria. After a 24 hr recovery period one fish was randomly chosen to be artificially infected by placing motile lice in 250 ml of seawater with the fish to be infected until the desired number, stage and sex of lice had attached (see experimental conditions below) while the other host was sham infected (i.e., placed in 250 ml of sea water for the same period of time as the to-be-infected fish).

Experimental conditions consisted of either a single louse sex or males and females together on a single host under two densities (2 or 4 lice host^{-1}/approximately 0.66 or 1.33 lice gram^{-1}) across the 3 motile stages, replicated a minimum of 10 times for each condition (Table 2.1). For adult females, only virgins were used, as verified by the absence of paired spermatophores (Ritchie et al. 1996). Trials were carried out under a 12:12 photoperiod with roughly half of all trials beginning during the 12 hr dark period and half starting during the 12 hr light period, allowing us to test for an influence of illumination on movement among hosts. Twice daily (~07:00 and ~19:00), for 7 days, tanks were removed from their water bath and the distribution of lice on hosts was recorded. At the end of each trial lice were removed and fish were released at their site of capture.

We analyzed the resulting dataset using generalized linear mixed effects models (GLMM) with binomial error (Pinheiro and Bates 2000). This allowed us to account for the fact that there was more than one louse observation per fish while testing for an influence of louse density, sex and presence of the opposite sex on the probability of leaving a host. Analysis began with the building of a maximal model with density, sex, presence of the opposite sex and all interactions as independent variables using maximum likelihood estimation. I then sequentially removed model terms testing their significance using likelihood ratio tests (Hilborn and Mangel 1997) until a minimum adequate model remained. I predicted that dispersal would be positively density dependent if it were driven by competition for resources, negatively density dependent if it were driven by the need to overcome host defences, and dependent on the presence of the opposite sex if it were driven by access to mates.

GROUP MOVEMENT EXPERIMENTS:

While the preceding experiments allowed for detailed replicated manipulations of fish and lice, juvenile salmonids are normally found in schools of tens to thousands (Groot and Margolis 1991). In order to more closely approximate natural conditions I therefore conducted a series of experiments that examined movement among hosts in larger groups. Wild caught juvenile pink salmon were examined for motile stage lice in transparent seawater filled bags and placed in 77 L aquaria until there were 25 fish with a single motile louse on each host and roughly equal numbers of each louse sex in each aquaria (Table 2.2). This was replicated 12 times with each trial running for 96 hrs at which point fish were removed and the distribution, sex and stage of lice noted. I determined if the distribution of motile lice at the end of the trials was aggregated and, if so, tested whether there were significantly more male-female pairings than expected based on chance alone using a chi-square test. I predicted that if dispersal were driven by competition for resources lice would remain evenly distributed among hosts at the end of the trials, if dispersal were driven by the need to overcome host

Table 2.1. The number of trials (n) for each experimental combination of sea louse developmental stage, sex (single sex, or both sexes) and density (number of lice host^{-1}, low: 2, high: 4) in individual movement experiments.

Stage	Sex	Density	n
Pre-adult I	male	low	10
Pre-adult I	male	high	11
Pre-adult I	female	low	12
Pre-adult I	female	high	11
Pre-adult I	male/female	low	12
Pre-adult I	male/female	high	10
Pre-adult II	male	low	11
Pre-adult II	male	high	11
Pre-adult II	female	low	10
Pre-adult II	female	high	10
Pre-adult II	male/female	low	14
Pre-adult II	male/female	high	12
Adult	male	low	10
Adult	male	high	10
Adult	female	low	10
Adult	female	high	12
Adult	male/female	low	11
Adult	male/female	high	11

defences lice would be aggregated on hosts at the end of the trials, and if dispersal were driven by access to mates, aggregation would result in more male-female pairs than expected based on chance alone. Furthermore, I predicted that if these drivers change with ontogeny they should be reflected by changes in these patterns as the proportion of lice in each trial shifted from being dominated by pre-adult I lice to pre-adult II and then adult lice.

PREDATION EXPERIMENTS:

The movement of parasites from one host to another is a risky endeavor. One such risk is predation from other organisms including their hosts; motile stage sea lice are of the same size class (Johnson and Albright 1991b) as juvenile pink salmon's primary prey (zooplankton; Groot and Margolis 1991) and motile lice are occasionally seen being consumed by juvenile salmon (personal observation). In light of the potential for hosts to act as predators I sought to examine the relative susceptibility of each motile stage and sex to predation by juvenile pink salmon.

Uninfected juvenile pink salmon were assigned to 8 L aquaria with a single motile louse added 2 hrs later. Half of the trials began under a 12 hr light cycle with the other half under a 12 hr dark cycle. Every 12 hrs tanks were observed to determine if the louse had attached to the fish or been consumed, with observations and switching of the light regime continuing every 12 hrs until attachment or consumption occurred. Fish were not fed during the course of this experiment and trials were replicated 9-13 times per stage, sex and light regime (Table 2.3).

Dissection to examine stomach contents confirmed consumption of lice by juvenile salmon in the first 10 trials where lice disappeared. In each of these 10 trials, a single louse was found, confirming consumption by the pink salmon. In the remaining trials, consumption was verified by examination of salmon feces for an undigested louse carapace, which was conspicuous compared to the rest of the faecal contents. There were 4 trials in which louse consumption could not be confirmed and these trials were excluded from subsequent analysis. The proportion of lice that were consumed by hosts was compared among sexes, stages and light regimes using chi-squared tests with Yates' correction for continuity when expected counts were less than 5. I predicted that if susceptibility to predation is a function of conspicuousness, lice would be more likely to be consumed during light periods and at larger sizes (i.e., developmental stages). All analyses were performed in R (R Development Core Team 2010).

Results

INDIVIDUAL MOVEMENT EXPERIMENTS:

In 4 of 12 high-density (4 lice host^{-1}) adult female trials the infected fish died and so these trials were excluded from the analysis. Louse movement was positively density dependent for pre-adult I lice (GLMM density term: $\chi^2_1 = 4.23$, $p = 0.039$; Figure 2.1) and dependent on the presence of the opposite sex for pre-adult II males (GLMM sex x presence of opposite sex interaction term: $\chi^2_1 = 5.68$, $p = 0.017$; Figure 2.1) and adult males (GLMM sex x presence of opposite sex interaction term: $\chi^2_1 = 3.98$, $p = 0.046$; Figure 2.1). Lice were significantly more likely to leave a host during a dark period than a light period (light: 26 of 101 movement events; dark: 75 of 101 movement events; $\chi^2_1 = 23.78$, $p < 0.0001$).

GROUP MOVEMENT EXPERIMENTS:

At the end of each trial, lice were aggregated among hosts and aggregations were roughly twice as likely to result in a male-female pairing than a same sex pairing ($\chi^2_1 = 4.74$, $p = 0.029$; Table 2.2).

Table 2.2. Number of pre-adult and adult lice at the beginning of each trial (1 louse fish^{-1}) and the number of opposite sex and same sex pairs observed on hosts at the end of each trial.

Trial	Pre-adult	Pre-adult II	Adult	Male	Female	Total	Opposite sex	Same sex
1	19	5	1	14	11	25	2	4
2	19	5	1	14	11	25	1	1
3	17	8	0	17	8	25	2	1
4	14	3	8	11	14	25	2	1
5	23	2	0	14	11	25	1	2
6	9	13	3	14	11	25	2	2
7	5	17	3	13	12	25	3	1
8	0	12	13	15	10	25	4	1
9	0	15	15	14	11	25	4	2
10	7	16	2	11	14	25	4	2
11	0	0	25	12	13	25	6	1
12	0	1	24	12	13	25	4	1

Table 2.3. Number of trials (n), number of lice consumed (eaten) and the number of lice that remained unattached or that successfully attached to hosts after 12 hrs of light or dark.

Sex/Stage	Light				Dark		
	n	Eaten	Unattach	Attach	n	Eaten	Unattach
Pre-adult I male	10	4	1	1	11	0	0
Pre-adult I female	9	6	1	1	10	0	0
Pre-adult IImale	10	4	2	2	11	0	0
Pre-adult II female	11	5	2	2	11	0	0
Adult male	10	2	1	0	10	0	0
Adult female	13	4	7	6	11	0	0
Total	63	25	14	12	64	0	0

The degree of aggregation (proportion of hosts with >1 louse) was positively correlated with the proportion of pre-adult II and adult lice at the beginning of the trial ($R^2 = 0.36$, $p = 0.023$; Figure 2.2). The proportion of pairings that were opposite sex pairings was also positively related to the proportion of lice in the trial that were pre-adult II and adult stages ($R^2 = 0.69$, $p < 0.001$; Figure 2.3).

PREDATION EXPERIMENTS:

Consumption of lice by pink salmon occurred in 25 out of the 63 trials that began in the light and in none of the trials that began in the dark ($\chi^2_1 = 67.17$, $p < 0.001$; Table 2.3). Excluding those trials where a louse was consumed, attachment occurred significantly more often in the first 12 hrs if the

trial began in the dark (dark: 64/64; light 24/38; $\chi^2_1 = 27.67$, p< 0.001). Of the 14 trials that began in the light, and in which lice remained unattached and uneaten after 12 hrs, lice were able to successfully attach to the host during the subsequent 12 hr dark period in all but two cases. The likelihood of being consumed by a pink salmon host did not differ by louse sex or stage ($\chi^2_5 = 4.94$, p = 0.462).

Discussion

I provide evidence to support the hypothesis that both competition for resources and access to mates influence dispersal in salmon lice and that the importance of these drivers shifts with ontogeny. In individual movement experiments, competition for resources drove dispersal at the pre-adult I stage while competition for mates drove dispersal at the pre-adult II and adult stage. These drivers were not sex specific for pre-adult I lice but at the pre-adult II stage males were less likely than females to disperse when the opposite sex was present and males were more likely than females to disperse in the absence of the opposite sex at the adult stage.

Sex-biased dispersal is predicted to arise when the benefit to cost ratio of dispersal differs between sexes. Predation did not differ by sea louse sex or stage, though susceptibility to predation was strongly influenced by light levels and lice appeared to take this into account as they were ~ 3 times more likely to move in the dark, when predation risk was lower than during light periods. These findings suggest that predation risk is incorporated into sea louse dispersal decisions and that the costs of movement among hosts do not vary significantly between sexes or stages. Similar behaviour is widespread in zooplankton, which undergo diurnal vertical migrations to avoid predation by fish (Lampert 1993), and has also been documented in some benthic invertebrates where males move into the water column in search of mates at night (Tully and Ceidigh 1987).

The absence of sex specific costs of movement among hosts suggest that sex-biased patterns of dispersal in lice result from sex specific benefits to movement. Salmon lice are polygynous and adult males provide no investment in offspring beyond sperm while adult females invest both time and energy. Male fitness is therefore dependent on access to mates while female fitness is contingent upon access to resources for egg production. The resulting asymmetry in reproductive investment likely underlies sex specific benefits of dispersal as lice approach sexual maturity. At the pre-adult I stage, when lice are ~ 33% (females) to 50% (males) of their adult size (Johnson and Albright 1991b), lice of both sexes should benefit by maximizing resources available for development to sexual maturity and so competition for host resources is an important driver of dispersal. Lice at the pre-adult II stage

10
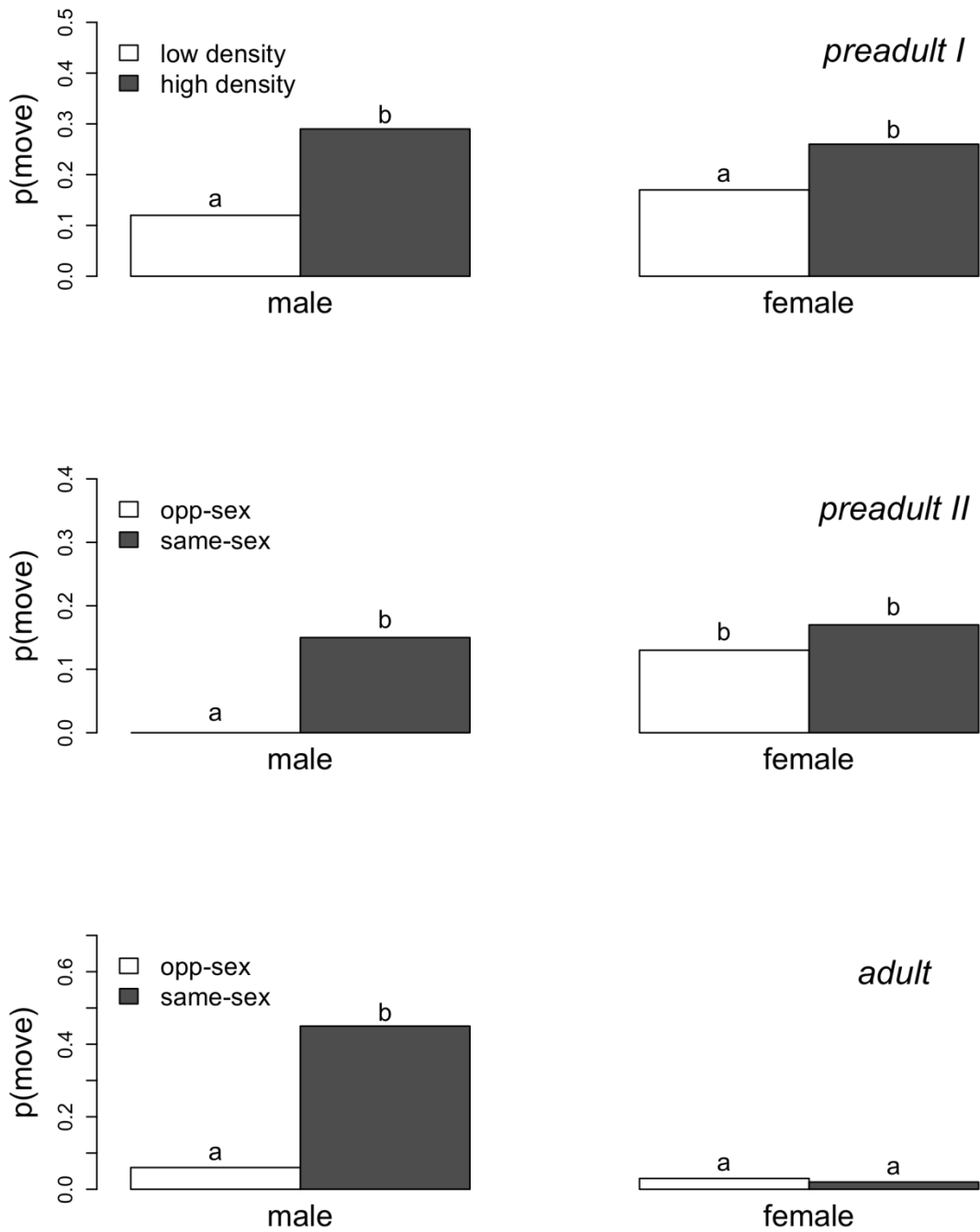
Figure 2.1. When do lice leave a host? The probability pre-adult I, II and adult lice left a host as a function of sex and density (pre-adult I) and presence or absence of the opposite sex (pre-adult II, adults). Bars sharing lowercase letters are not significantly different (based on generalized linear mixed effects analysis).
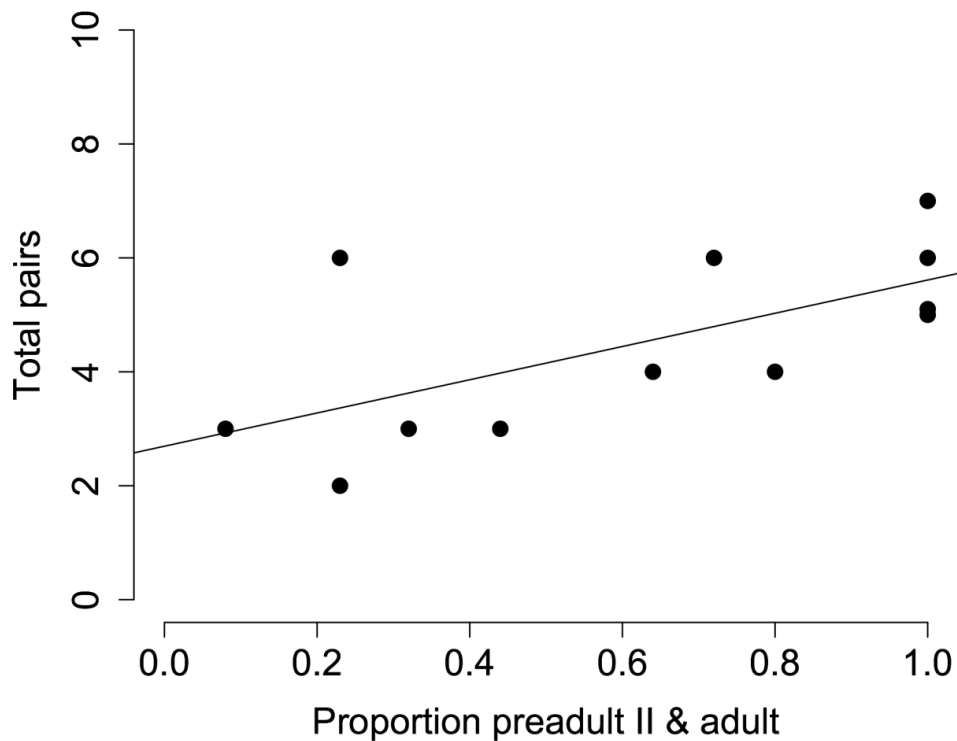
Figure 2.2. Relationship between the proportion of pre-adult II and adult lice in a group movement trial and the degree of aggregation (total pairs; number of hosts with >1 louse) at the end of the trial (y = 2.69 + 2.92 x, R^2 = 0.36, p = 0.022)

are closer to their adult size (females 60% of adult size, males 80%) and pre-adult II adult males can mate guard females until they are sexually mature. This suggests that at the pre-adult II stage, males should benefit to a greater extent than females by remaining on hosts with the opposite sex so as to ensure access to mates once they are sexually mature. Once lice are adults, males can mate repeatedly and so fitness is proportional to the total number of mates a male secures; females on the other hand only need to mate once (but see Todd et al. 2005) so fitness is proportional to investment in resource acquisition and the production of offspring. Adult males therefore benefit to a greater extent than adult females by dispersing from a host if there are no mates available. Group experiments, more closely mimicking natural conditions, confirmed the shift in drivers of dispersal observed in the individual trials. Lice were aggregated at the end of group trials and there was a positive relationship between the proportion of lice in the trial that were pre-adult II and adults and both the degree of aggregation and the proportion of aggregation events with the opposite sex.
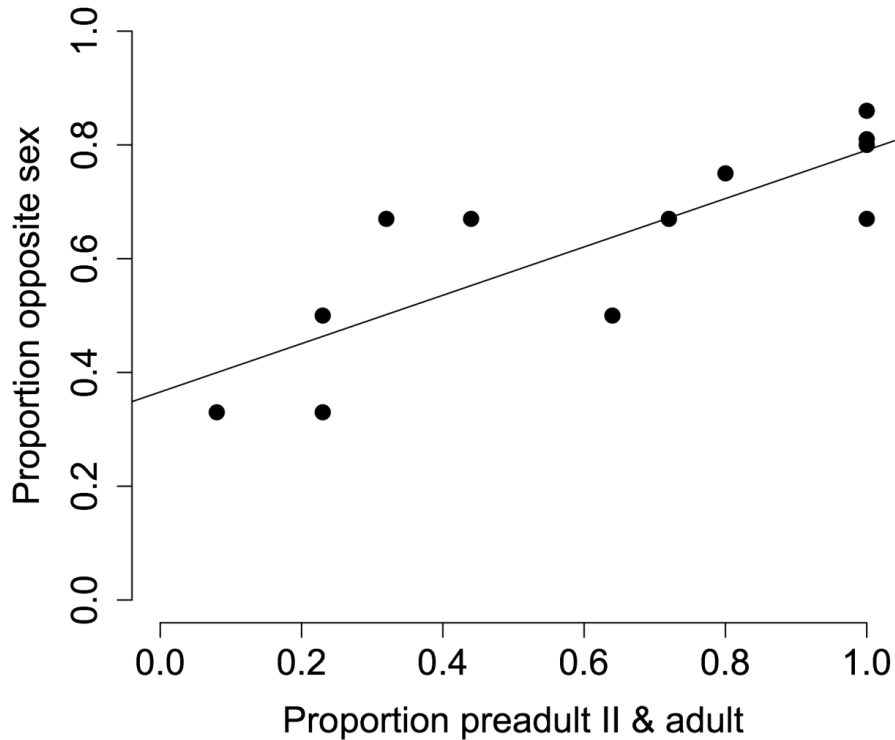
Figure 2.3. Relationship between the proportion of pre-adult II and adult lice in a group movement trial and the proportion of louse pairings on hosts at the end of the trial that were of opposite sex (y = 0.37 + 0.43 x, R^2 = 0.69, p < 0.001)

I assume that the juvenile pink salmon used in the experiments were homogenous in their suitability as hosts. This is likely an oversimplification as host compatibility, including immune response to infection and/or host behaviour could influence movement of lice among hosts by creating heterogeneous host environments. In an effort to control for the potentially confounding influence of host compatibility I randomly selected uninfected hosts from the field for the experiments, nonetheless, the influence of host compatibility on louse dispersal requires further research. I also assumed that louse densities were high enough to limit resources as has been suggested by observations of lice on farmed salmon (McKenzie et al. 2004). This appeared to be the case at the pre-adult I stage and although resources did not influence dispersal decisions at the pre-adult II and adult stages it is still likely that host resources were limiting as host mortality did occur in some high density treatments, at least for adult females.

Sex-biased dispersal can have important consequences for disease transmission and dynamics (e.g. Robertson et al. 2006) and sea lice are no exception. Motile lice may act as vectors of viral and bacterial pathogens, which could contribute to pathogen transmission among and between farmed and

wild hosts. These findings are the first to identify when and why lice move among hosts, and can advise the development of integrated pest management strategies on salmon farms which account for louse behaviour. In addition, an improved understanding of the drivers of louse dispersal may help to mitigate the impacts of louse transmission from farmed to wild salmon in areas of intensive salmon aquaculture. My findings, along with a growing number of investigations into sex-biased dispersal in invertebrates, fish and lizards have allowed researchers to overcome the confounding effects of phylogeny and social structure inherent in studies of dispersal in birds and mammals and highlight the ubiquity of the role mate competition plays in driving sex-biased dispersal across the animal kingdom.

Chapter 3

Quantifying salmon louse movement among hosts: implications for conservation and management

Abstract

Although parasites are a ubiquitous feature of most aquatic environments their role in ecosystems is often poorly understood. Nonetheless, as anthropogenic activities increasingly alter parasite dynamics there is an urgent need to better understand their ecological role. Interactions between farmed and wild salmon mediated by salmon lice (*Lepeophtheirus salmonis*) provide an opportunity to study how parasite behaviour influences the distribution and abundance of parasites among hosts. Salmon lice are able to leave one host in search of another as they approach sexual maturity. However, this movement is believed be an artefact of the confined conditions characteristic of the experiments and salmon farms where it has been observed. Here I show that lice commonly move among hosts in the wild, with at least 50% of the lice observed on juvenile pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon having developed on another host. The finding that lice readily move among hosts as they mature challenges our current understanding of sea louse-wild salmon interactions and suggests that: (a) per louse impacts on hosts may be greater than previously thought, and (b) increasing the probability of coming into contact with more than one host may increase the transmission and spread of viruses and bacteria common on farmed and wild salmon. These results highlight the role parasite behaviour may play in influencing the consequences of salmon louse infections on both farmed and wild salmon.

Introduction

Fish have on average as many parasites as they do predators (Lafferty 2008), yet while research into fish predators is voluminous, our understanding of the role of parasites in aquatic ecosystems is limited. This stems from the conspicuous nature of predators and the relative obscurity of parasites, despite the fact that, in some cases, parasites make up a substantial portion of the total biomass in aquatic ecosystems (Kuris et al. 2008). There is increasing evidence that parasites can shape the health, behaviour and dynamics of hosts and in turn structure the ecosystems in which they occur

(Thomas et al. 2005). In light of this there is an urgent need to better understand the role parasites play in natural systems and, given that human activities increasingly alter the distribution and abundance of parasites (e.g. Morand and Krasnov 2010, Polley et al. 2010), if and how human activities change parasite dynamics.

Owing to their commercial importance, broad distribution, and introductions around the globe, salmonids are one of the most intensively studied groups of fishes. One of the most important, and certainly best studied parasites of salmonids is the salmon louse (*Lepeophtheirus salmonis*). Salmon lice are naturally occurring ecotparasitic copepods that cost the global aquaculture industry in excess of $400 USD million annually and have become a conservation concern for wild salmon in areas of industrial salmon aquaculture (Costello 2009). Salmon louse transmission from farmed salmon can lead to epizootics on adjacent wild juvenile salmon and depressed wild salmon stocks (Krkosek et al. 2007a, Ford and Myers 2008, Connors et al. 2010b). Louse mediated interactions between farmed and wild fish have been well studied in coastal British Columbia, Canada; however, there is still a need to better understand what factors influence the transmission, spread and impact of louse transmission from farmed to wild salmon.

Salmon lice are transmitted among hosts as infective copepodids. Once attached to a host, copepodids develop into chalimus stage lice (4 stages) which are tethered to the surface of the host before molting into pre-adult and then adult stages (Johnson and Albright 1991a). These later developmental stages (pre-adult I, II and adults), collectively known as motile stages, are the most pathogenic and are capable of moving among hosts (Ritchie 1997, Hull et al. 1998, Connors et al. 2008b). While it has been generally agreed that movement of motile lice among hosts can occur in artificial environments under high host density (e.g., on a salmon farm, or in the laboratory), the movement of motile lice among hosts in the wild has been considered to be of little importance (e.g. Todd et al. 2005). Accordingly, louse movement has not been considered or incorporated into efforts to predict, manage, and mitigate the impact of louse parasitism on salmon hosts. Recent work suggests that the ability to move among hosts may be more widespread than previously appreciated (Connors et al. 2010a) and may facilitate the spread of pathogens (Barker et al. 2009), highlighting the need to determine if, and to what extent, the movement of motile lice occurs among hosts in the wild.

The single greatest impediment to determining if the movement of motile lice among hosts occurs in the wild is determining if a motile louse that is observed on a host developed there, or developed on another host and subsequently dispersed to its current host. Salmon lice can damage the epithelium of their hosts as they develop (Wagner et al. 2008). This damage (Figure 3.1) can serve as a signature of
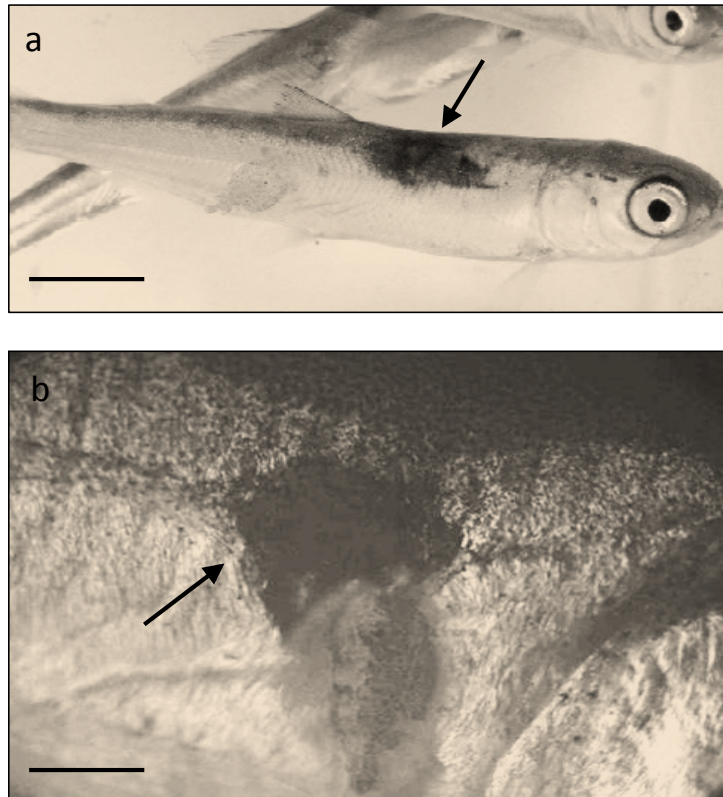
Figure 3.1. Scarring characteristic of developing chalimus stage *L. salmonis* on juvenile pink salmon. Scale bar is 10 mm in (a) and 2 mm in (b). Photo credit: Alexandra Morton

development which can be used to determine the probability a louse developed on the host on which it currently resides. Here I quantify epithelial damage characteristic of chalimus stage louse development on wild juvenile pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon, calculate the probability of leaving evidence of development on a host, and then estimate the extent to which salmon lice move among juvenile salmon in an area of intensive salmon aquaculture.

Methods

Juvenile pink (n = 73) and chum (n = 7) salmon (Mean +/- SD; FL: 59 +/- 8 mm) were collected by beach seine in May 2008, in the vicinity of Broughton Island, British Columbia, and examined (Krkosek et al. 2005b) to quantify the distribution of early infective stage lice (chalimus I/II) on the opercula, fins and body of the fish. A further 70 fish (31 chum, 39 pink; 60 +/- 7 mm FL) with a total of 119 chalimus I/II stage lice, and no evidence of scarring, were collected and held in pairs in 35, 10 L aquaria. Twice daily (0700 and 1700 hrs) fish were fed *ad libitum* and the location of lice on each

fish, along with scarring and development of lice, was noted. This was repeated until all lice had developed to the pre-adult I stage or perished. The proportions of lice that survived to the pre-adult I stage on the body, opercula and fins were compared using chi-square tests.

Based on the distribution of lice on the body, opercula and fins of hosts in the field I determined the probability an infective stage louse (chalimus I/II) occurred in region i of a host (Pr_i). From the development of lice on hosts in the lab I obtained the probability of surviving to the motile stage in each region ($Pr_{m,i}$). For those lice that were on the body of host fish I also calculated the probability of leaving epithelial damage (i.e., scarring; Figure 3.1) as a louse developed from the chalimus to pre-adult stage (Pr_s).

Based on these probabilities, if a motile louse is observed on a host then the probability it developed there is the probability of infecting each region times the probability of surviving to the motile stage in each region summed across regions:

Pr{developed on host|observed on host} =

$$(Pr_{m,body} \bullet Pr_{body}) + (Pr_{m,fin} \bullet Pr_{fins}) + (Pr_{m,opercula} \bullet Pr_{opercula}) \qquad \text{(eqn. 1)}$$

We can further refine this probability by accounting for scars that are characteristic of developing on the body. If a motile louse is observed on a host with a scar then the probability it developed on the host is the probability of surviving to the motile stage on the body times the probability of leaving a scar on the body, plus the probabilities of surviving to the motile stage on the opercula and fins:

Pr{developed on host|observed on host with scar} =

$$((Pr_{m,body} \bullet Pr_{body}) \bullet Pr_s) + (Pr_{m,fin} \bullet Pr_{fins}) + (Pr_{m,opercula} \bullet Pr_{opercula}) \qquad \text{(eqn. 2)}$$

It follows that if a motile louse is observed on a host *without* a scar on the body the probability it developed on the host is the probability of surviving to the motile stage on the body times the probability of not leaving a scar (i.e., 1- probability of leaving a scar), plus the probabilities of surviving to the motile stage on the opercula and fins:

Pr{developed on host|observed on host without scar} =

$$((Pr_{m,body} \bullet Pr_{body}) \bullet (1-Pr_s)) + (Pr_{m,fin} \bullet Pr_{fins}) + (Pr_{m,opercula} \bullet Pr_{opercula}) \qquad \text{(eqn. 3)}$$

Finally, if a motile louse is observed on a host without a scar on the body the probability it *did not* develop on the host is one minus the probability it developed on a host if it is observed on a host without scarring on the body:

Pr{did not develop on host|observed on host without scar} =

$$1- (((Pr_{m,body} \bullet Pr_{body}) \bullet (1-Pr_s)) + (Pr_{m,fin} \bullet Pr_{fins}) + (Pr_{m,opercula} \bullet Pr_{opercula})) \qquad \text{(eqn. 4)}$$

We compiled 8 years of field surveys of louse infection on juvenile pink and chum salmon during early marine life. Details of the surveys can be found in Morton and Williams (2003), Morton et al. (2004, 2005) and Krkosek et al. (2005, 2006). Briefly, juvenile salmon were caught by beach seine (1040 seine hauls) and lethally or non-lethally assessed for louse infection. These field surveys included quantifying epithelial damage characteristic of developing chalimus stage *L. salmonis* on the body of host fish (Figure 3.1). I then used the probability that if a motile louse is observed on a host without scarring, it developed on a host other than the one on which it is observed (i.e., equation 4) to estimate the proportion of lice at each sampling event (i.e., beach seine haul) that developed on a host other than the one on which they were observed. Specifically, the number of motile lice on a host minus the number of scars on the host times the probability derived from equation 4 was summed across all fish in a sample and divided by the total number of motile lice in the sample. This was done separately for each host species.

Using generalized linear mixed effects models (GLMM) with binomial error (Zuur et al. 2009) I examined whether the abundance of lice, sex ratio of adult lice (males:females), or host size in a sample influenced the degree of louse movement among hosts. Models included year as a random effect and the significance of each term was evaluated by likelihood ratio tests (Hilborn and Mangel 1997). All analyses were performed in R (R Development Core Team 2010).

Results

Chalimus stage lice were most commonly observed on the opercula (19%) followed by the body (37%) and then the fins (44%). Survival of lice from the chalimus to pre-adult stage differed significantly between the fins and the body (χ^2_1 = 9.96, p = 0.002) but not between the fins and the opercula (χ^2_1 = 3.16, p = 0.076) or between the opercula and body (χ^2_1 = 1.84, p= 0.175; Table 3.1).

Applying the probabilities from Table 3.1 to equation 4 I estimated the probability that a louse on a host with no scar developed on another host as 0.67. When this probability is applied to the 8 years of

field surveys I estimated that 53 +/- 1% (mean +/- SE) of motile lice observed on juvenile pink salmon and 55 +/- 1% of motile lice observed on chum salmon developed on a different host. The proportion of lice in a sample that had not developed on the host they were observed on was not related to the mean abundance of motile lice (GLMM, $\chi^2_1 = 0.136$, $p = 0.712$), the mean abundance of chalimus stage lice (GLMM, $\chi^2_1 = 0.244$, $p = 0.621$), the ratio of adult male to female lice (GLMM, $\chi^2_1 = 0.023$, $p = 0.879$) or the mean fork length of host fish (GLMM, $\chi^2_1 = 0.273$, $p = 0.601$).

Discussion

These results are the first to quantify motile salmon lice movement among juvenile salmon in coastal marine environments. This finding challenges the current understanding of sea louse-wild salmon interactions. It has been generally assumed that once a louse infects a host it remains there until it reproduces and dies. As a result of moving among hosts the dynamics of louse transmission between and among farmed and wild salmon may be altered in two important ways. First, instead of interacting with a single host fish after transmission and infection, the movement of lice among hosts may lead to interactions with multiple hosts as a louse develops and reproduces. Given that motile lice are the most pathogenic louse stage and that infection with even a single louse can influence juvenile salmon physiology, immunology, ecology and survival (e.g. Wagner et al. 2008, Krkosek et al. In Press), this suggests that more hosts may be impacted by louse transmission from farmed salmon than previously appreciated. Second, by increasing the probability of coming into contact with more than one host, the movement of motile lice among hosts has the potential to increase the transmission and spread of viruses and bacteria among farmed and wild salmon (e.g. Nylund et al. 1994).

An important parameter in the epidemiology of vector borne disease like malaria is the proportion of bites that lead to infection (i.e., b; Dobson 1988, Anderson and May 1991). A key component of b is the probability a vector bites an uninfected individual before biting an infected individual. As b increases the proportion of hosts infected in a population increases. If motile salmon lice act as vectors, all other things being equal, increased movement among hosts should lead to an increase in the probability of dispersing to an uninfected host from an infected one thereby increasing the proportion of hosts infected in a population. Consideration of the movement of lice among hosts within the epidemiological framework developed for vector borne disease may be a fruitful source of insight into the dynamics of pathogen transmission by lice among and between farmed and wild salmon.

Table 3.1. The distribution of chalimus I/II lice on the body, opercula and fins of wild caught juvenile pink and chum salmon (Pr_s), the probability of surviving to the pre-adult 1 stage (Pr_m), and the probability of leaving evidence of developing on the body (Pr_s) based on naturally infected fish maintained in the lab.

Location	Pr_i		Pr_m		Pr_s	
Body	0.37	(50/135)	0.83	(34/41)	1	(34/34)
Opercula	0.19	(25/135)	0.68	(32/47)	-	
Fins	0.44	(60/135)	0.45	(14/31)	-	

The analysis assumes the distribution of chalimus stage lice on the surface of the juvenile pink and chum salmon examined indicates the distribution of lice on hosts in general. Studies that have examined the distribution of lice on hosts have limited their investigations to motile stage lice (Jaworski and Holm 1992, Todd et al. 2000) so little is known about the distribution of early infective stages on the surface of host fish. The analysis also assumes the probability of damaging the epithelium of a host, and thus leaving a scar, is independent of louse density. It is possible that a host's tissue response may be related, either positively or inversely, to intensity of infection. But because little is known about host tissue damage as a function of intensity of infection it is not possible to determine if and to what extent this may influence the findings. Despite these limitations and uncertainties, my approach almost certainly underestimates movement of motile lice among hosts and should be considered the lower bound to the estimate because my approach (a) cannot differentiate between lice that moved to a host with existing scarring (caused by another louse that has since dispersed) and those that developed on the host on which they are observed, and (b) does not account for lice that have moved among hosts multiple times.

Motile lice move from one host to another in response to competition for resources (pre-adult I stage) and in search of mates (preadult II and adults; Connors et al. In press). These experimental findings predict that: (a) the proportion of pre-adult I lice in a sample of juvenile pink and chum that did not develop on the host on which they are observed should be positively related to motile abundance, and (b) the proportion of pre-adult II and adult lice that did not develop on the host on which they are observed should be negatively related to the abundance of pre-adult II and adult female lice in the sample. Unfortunately, because lice were not routinely identified to the pre-adult I and II level in the samples I was unable to test these predictions. Future field monitoring should consider identification of lice to the developmental stage to enable a finer scale examination of the movement of lice among hosts. I also suggest that the broad scale assaying of lice for viral and bacterial pathogens to determine if and to what extent lice act as vectors of pathogens in the natural environment should be a

research priority. In the meantime, these findings challenge the prevailing view in sea louse biology that a single louse interacts and impacts a single host and argue for a more comprehensive understanding of salmon louse behaviour in efforts to mitigate the impact of louse transmission among and between farmed and wild salmon.

Chapter 4

Salmon lice escape predation on their host[2]

Abstract

Parasites seldom have predators but often fall victim to those of their hosts. How parasites respond to host predation can have important consequences for both hosts and parasites, though empirical investigations are rare. The exposure of wild juvenile salmon to salmon lice (*Lepeophtheirus salmonis*) from salmon farms allowed us to study a novel ecological interaction: the response of lice to predation on their juvenile pink and chum salmon hosts by two salmonid predators – coho salmon [3]smolts and cutthroat trout. In ~70 % of trials in which a predator consumed a parasitized prey, lice escaped predation by swimming or moving directly onto the predator. This trophic transmission is strongly male-biased, probably because behaviour and morphology constrain female movement and transmission. These findings highlight the potential for salmon lice to be transmitted up marine food webs in areas of intensive salmon aquaculture, with implications for louse population dynamics and predatory salmonid health.

Introduction

Parasites are prisoners of their own habitat, and while few parasites have their own predators, they often fall victim to those of their hosts. Host predation can shape parasite life history by driving selection for (i) early maturity (Poulin 2007) ensuring a parasite reproduces before its host is eaten, (ii) manipulation of host behaviour to reduce the probability a host encounters a predator (Moore 2002), and (iii) parasitizing the predator itself, thus incorporating it into the parasite's lifecycle (Parker et al. 2003). These adaptive responses can then have important consequences for hosts by influencing parasite virulence (Ebert and Herre 1996), behaviour (Moore 2002) and distribution (Poulin 2007). Despite its importance, empirical investigations into how parasites respond to host predation are rare (but see Ponton et al. 2006).

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[2] A version of this chapter appears as Connors, B.M., Krkosek, M. and L.M. Dill. 2008. Sea lice escape predation on their host. Biology Letters 4: 455-457.

Empirical investigations into how parasites respond to host predation and the consequences of these are rare (but see Ponton et al. 2006). This is probably due to the logistical constraints of manipulating host, parasite and predator under experimental conditions. Opportunities to study evolutionary processes are often created by anthropogenic change (Palumbi 2001). The exposure to wild juvenile salmon to parasitic sea lice from salmon farms permits the study of a novel ecological interaction: that between predation among salmonids and parasitism by the sea louse.

Salmon lice are ubiquitous on farmed and wild adult salmon and trout throughout the oceans of the northern hemisphere (Costello 2006). Lice have a direct lifecycle consisting of noninfectious and infectious free-living stages, attached stages and motile stages (Johnson and Albright 1991b). Transmission occurs primarily when the infective stage seeks out and attaches to a host fish, although motiles can move directly among hosts (e.g., Hull et al. 1998). In areas without salmon farms, sea lice are less than 5% prevalent on juvenile pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon (Morton et al. 2004, Krkosek et al. 2007b), but in areas with farmed salmon they can be orders of magnitude more abundant (Krkosek et al. 2006).

During early marine life, juvenile pink and chum salmon experience high rates of predation from other, larger salmonids, including coho (*O. kisutch*) salmon smolts and anadromous cutthroat trout (*O. clarki*), both of which are also salmon louse hosts. Because infection with lice in unperturbed systems is rare until after 3 to 4 months of marine life (Krkosek et al 2007b), when predator-prey interactions between salmonids have ceased (Groot and Margolis 1991), salmon louse exposure to juvenile salmon caused by salmon farms allowed us to study the response of salmon lice to host predation by juvenile coho salmon and cutthroat trout. I report the results of experiments, designed to investigate how louse infection affects predation risk, that reveal an extraordinary behaviour of a parasite. Salmon lice respond to predation on their host by moving directly or swimming from prey to predator during predation.

Methods

We collected fish used in the experiments from marine waters of the Broughton Archipelago, British Columbia, Canada, during a period of salmon lice infestations of wild juvenile Pacific salmon. I used beach seines to collect juvenile pink and chum salmon (mean ± S.D.; 68 ± 9 mm FL) and beach seines and hook and line to collect two marine predators, coho salmon smolts (120 ± 11 mm FL; May 2005 and 2006) and cutthroat trout (226 ± 29 mm FL; May 2006). I examined all fish for motile lice

by viewing the fish in seawater-filled plastic bags similar to Krkosek et al. (2005) and then held them in floating pens for 24-48 hrs prior to experimentation.

In individual predation experiments, I paired size-matched pink salmon (one unparasitized and one parasitized with up to 3 motile lice) and left them undisturbed in a 10L aquarium for ~ 15 minutes before releasing them into a 1.5 x 1.5 x 1 m ocean enclosure with a single unparasitized cutthroat trout (n = 60). Trials ended when one prey had been consumed. I then coaxed the trout into a 10L aquarium where its entire surface was visually assessed for motile sea lice, which I removed and identified to stage and sex according to Johnson and Albright (1991b). To further estimate rates of trophic transmission I repeated this experiment with single parasitized juvenile pink salmon (n = 30).

The small ocean enclosures permitted us to closely observe louse behaviour during host predation. However, the enclosures did not represent the natural conditions in which predation occurs. I overcame this limitation by also conducting group predation trials in larger net pens where the prey were allowed to form a school. In these group predation experiments ~ 200 naturally infected juvenile pink or chum salmon (mean ± 95% bootstrap C.I.: 2 ± 0.33 motile lice fish^{-1}) were exposed to 40-50 coho salmon smolts (n = 8; 0.49 ± 0.1 motile lice fish^{-1}) or 50-100 less infected juvenile pink (when chum were prey) or chum (when pink were prey) salmon as a control (n = 4; 0.57 ± 0.04 motile sea lice fish^{-1}). I conducted the experiments in a 3 x 4 x 4 m marine net pen that was divided in half for ~2 hrs to separate prey and predators while the fish acclimatized to their new environment. The divider was removed and coho/control predators were allowed to feed on prey for 24-48 h. I examined predators and prey for motile lice before and after each trial as described above.

Chi-square tests were used to test for differences in the proportion of adult male and female sea lice trophically transmitted in individual predation experiments and generalized linear mixed-effects models (GLMM) to test for differences in the number of male and female sea lice on predators before and after predation on parasitized prey in the group predation experiments. The GLMM used a Poisson distribution for the dependent variable (sea louse abundance) and included before vs. after each trial as a fixed effect, the abundance of motile sea lice on prey before each trial as a covariate and replicate as a random effect. Differences in trophic transmission between sexes were evaluated by including a before vs. after predation x sex interaction term. Significant differences in trophic transmission between pink and chum hosts were not detected and so they were pooled in the final analysis. All analyses were performed in R (R Development Core Team 2010).
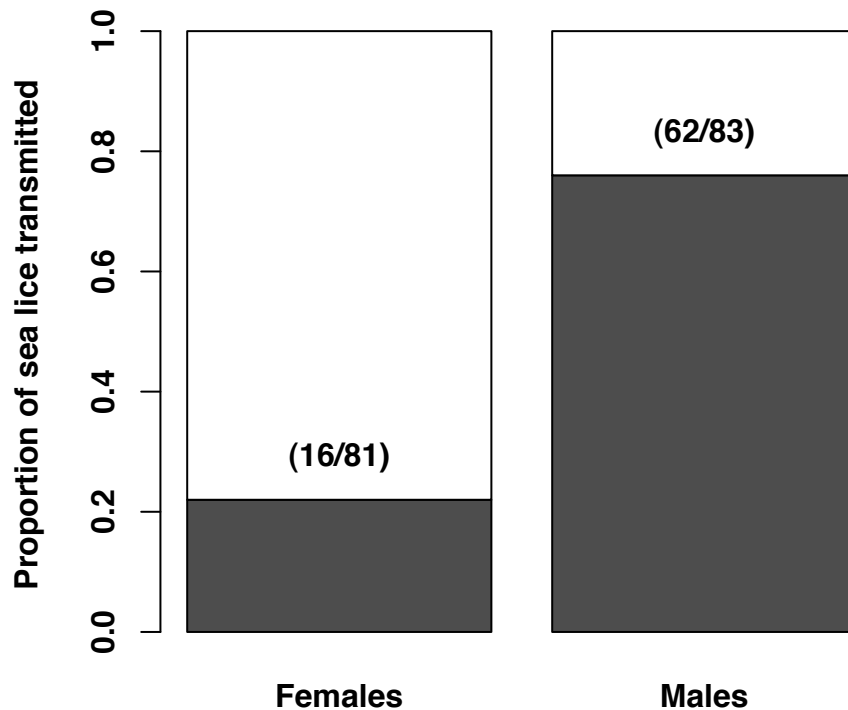
Figure 4.1 The proportion of available adult male and female *L. salmonis* trophically transmitted from infected juvenile pink salmon to cutthroat trout in individual predation experiments.

Results

In individual predation experiments, trophic transmission occurred in 70% of trials (52 of 74) when cutthroat trout consumed parasitized juvenile pink salmon. No lice were found on predators in trials when the unparasitized fish was consumed (n = 16). Adult male lice transferred 3.8 times more often than adult female lice (Chi-square test: χ^2_1 = 49.6, $p < 0.0001$; Figure 4.1). When it was directly observed (n = 17), lice swam from the host fish to the predator's dorsal or lateral surface, or moved directly from the captured prey onto the roof of the predator's mouth and then head.

A similar pattern emerged in the group predation experiments. Predation upon parasitized juvenile pink and chum salmon resulted in a significant increase in motile louse abundance on predators after 24-36 hrs (Z = 2.613, $p < 0.01$), with males transferring significantly more often than females (before vs. after predation x sex interaction, Z = 2.006, $p < 0.05$; Figure 4.2). Motile louse abundance on control fish did not increase after 24-36 hrs (Z = - 0.9295, $p > 0.05$).
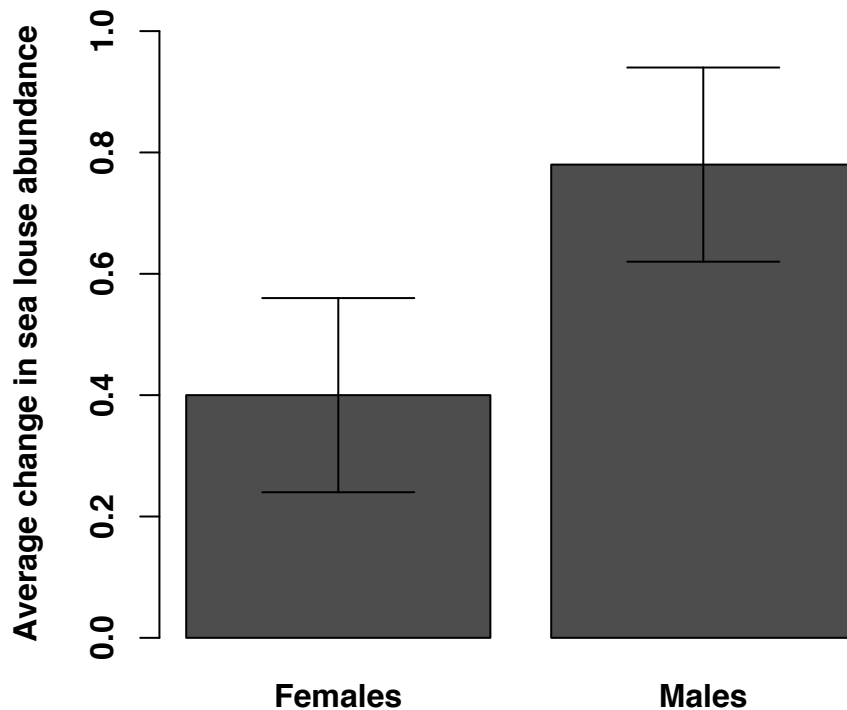
Figure 4.2 The average change in male and female *L. salmonis* abundance (± 1 S.E.) on coho salmon smolts after predation upon groups of parasitized pink and chum salmon.

Discussion

My results demonstrate that salmon lice can escape predation on their hosts by moving from prey to predator. This trophic transmission is strongly male-biased, suggesting that females do not exhibit this behaviour as frequently. Male-biased dispersal in free-living species is correlated with polygynous mating systems, where male reproductive success is limited by mating opportunities and female reproductive success is limited by investment in offspring (Clobert et al. 2001). Sea lice are polygynous and males provide no investment in offspring beyond sperm, whereas females invest both time and energy into producing eggs. As a result, male fitness is dependent on the total number of successful matings whereas female fitness is dependent on available energy reserves and nutrients for egg production. This has probably selected for sex-specific behavioural strategies where females remain on a host to sequester resources and males move among hosts to increase mate encounters. Experimental work supports these predictions (Hull et al. 1998). Morphological differences between sexes parallel differences in dispersal: females are larger and have expanded genital segments

(Johnson and Albright 1991b). These differences in behaviour and morphology may restrict motile female movement among hosts, thereby constraining their ability to escape predation on their hosts.

There are few empirical examples of parasites escaping host predation. Ponton et al. (2006) demonstrated that parasitic gordian worms escape host predation by wriggling out of the predator's mouth, gills or nose ~ 23% of the time their cricket host was preyed upon. Ticks and fleas are also commonly observed leaving a dying host, presumably increasing the probability of ending up on a scavenger or predator. What is extraordinary about the trophic transmission of sea lice is the frequency at which it occurs (e.g. ~ 70% of predation events in individual trials) and the fact that lice end up on a suitable host. Whether or not trophic transmission of lice is accompanied by an increase in fitness in contingent upon mating opportunities on their new hosts. These may be limited by increased male-male mate competition as a result of male-biased salon louse populations on the predatory salmonids with consequences for louse population dynamics.

The trophic transmission of lice may also affect the health of predatory salmonid populations sympatric with infested juvenile pink and chum salmon. Sea louse pathogenicity is intensity dependent (Pike and Wadsworth 2000) and because coho smolts and cutthroat trout are orders of magnitude larger than juvenile pink and chums during early marine residence, they are likely to be less negatively affected by the transmission of lice via free living infectious stages from wild and farmed hosts then are their small prey. However, predation on infested juvenile pink and chum may result in the accumulation of motile lice, the stage most pathogenic to hosts, in numbers sufficient to compromise the health of predatory salmonid populations. These results therefore also have a conservation message: the addition of salmon farms to coastal waters where wild salmonids rear and interact may have important indirect health consequences for larger predatory salmonid hosts than just the direct transmission of parasite larvae. However, if lice make prey easier for predators to capture, then the increased exposure to motile lice may be compensated for by an increased availability of prey. The capture and handling of prey by predators was similar in small enclosures, larger net pens, and in annual field surveys in the region. These similarities in predator-prey behaviour across scales of observation suggest the trophic transmission of sea lice is prevalent among wild juvenile salmonids in areas of intensive salmon aquaculture.

Chapter 5

Predation intensifies parasite exposure in a salmonid food web[4]

Abstract

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. I 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. 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. I estimate that trophic transmission accounts for 53 to 67% of pre-adult and adult louse infection on coho. These results suggest that, by evading predation, salmon lice can accumulate up juvenile salmon food webs. Predators, such as coho, can experience a 2 to 3 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 to monitoring and managing the marine environment in areas of intensive salmon aquaculture that includes the productivity and ecological interactions of all salmonid species.

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[4] A version of this chapter appears as Connors, B.M., Hargreaves, N.B., Jones, S.R.M, and L.M. 2010. Dill. Predation intensifies parasite exposure in a salmonid food chain. Journal of Applied Ecology 47: 1365-1371.

Introduction

Parasites can alter the strength of inter- and intra-specific 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 and Raffaelli 1995, Thompson et al. 2005) as well as less intuitive changes in connectance (Lafferty et al. 2006) and trophic energy flow (Mouritsen and 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*) on juvenile pink salmon (*Oncorhynchus gorbuscha*) have been reported in a region of coastal British Columbia (the Broughton Archipelago; Figure 5.1) in 2001, 2002 and from 2004 to 2006 (Morton and Williams 2003, Morton et al. 2004, Krkosek et al. 2005a, Krkosek et al. 2006, Jones and Hargreaves 2009). These infestations have been orders of magnitude greater than those observed in other 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, Krkosek et al. 2007b, Peet 2007, Gottesfeld et al. 2009). Recurrent infestations are associated with open net pen salmon aquaculture and depressed and declining pink salmon populations (Krkosek et al. 2007a) 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*) 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, possibly 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 and 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, such as juvenile coho (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 et al. 2008b).
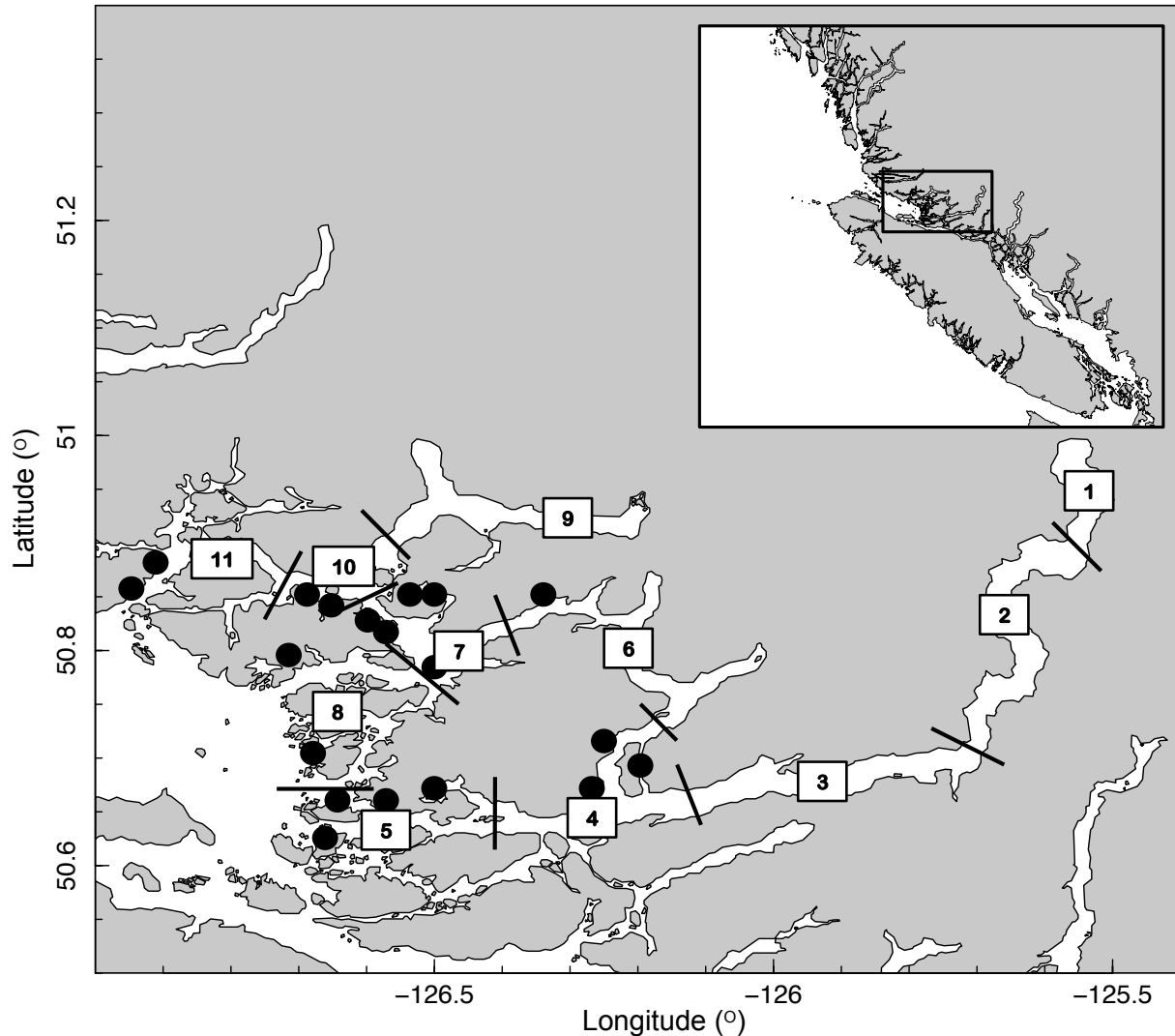
Figure 5.1. Study area and zones sampled for juvenile pink and coho salmon during spring of 2004 and 2005 (adapted from Jones and Hargreaves 2007). Black dots are approximate locations of salmon farm tenures in the region.

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 I 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.

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 lifecycle is characteristic of ectoparasitic copepods: free-living naupliar stages released from a pair of egg strings molt into an infective copepodid stage that seeks out and attaches to a host fish. Once on a host, copepodids molt into the first of four chalimus stages that are physically attached, via a frontal filament, to the host. The fourth chalimus stage molts into a pre-adult I and then II stage before reaching sexual maturity as an adult (Johnson and 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 et al. 2008b). Motile stages, which feed on mucus, scales and blood, are the most pathogenic to hosts (Pike and Wadsworth 2000, Johnson et al. 2004, Wagner et al. 2008).

FIELD DATA

Details of the field sampling have been described previously by Jones et al. (2006) and Jones and 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 and Albright (1991b). The generalist sea louse *Caligus clemensi* 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 (Parker 1971, Hargreaves and Lebrasseur 1985, 1986, Connors et al. 2008b, Krkosek et al. In Press). The resulting dataset consisted of 4 juvenile salmon size classes (Table 5.1) allowing us to quantify and compare the distribution of lice on predatory coho (large coho) to their pink salmon prey (small pinks). I 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.

Table 5.1. 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

LOUSE ABUNDANCE AND SEX RATIOS

Salmon louse abundance (lice host[-1]) 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) I was unable to estimate among year variance sufficiently to treat it as a random effect (Gelman and Hill 2007). I accounted for overdispersion when present by correcting standard errors using quasi-GLMMs with a dispersion parameter (Zuur et al. 2009). Parameters were estimated using Laplace approximation (Raudenbush et al. 2000).

Models with and without terms for salmon size classes, gear type and year were compared using AIC. The best supported model(s) were those with substantial support (i.e. $\Delta AIC \leq 2$; Burnham and 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 confidence intervals did not overlap were considered statistically different. I 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, I predicted that large coho should have the most adult male- (but not pre-adult 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 I 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). I 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, I estimated the contribution of trophic transmission to motile infection on large coho as:

$$y_i = 1 - (\alpha_i / \beta) \hspace{4cm} \text{(eqn. 1)}$$

where y is the proportion of motile lice on large coho that were trophically transmitted, α is the change in chalimus to motile infection on size class *i* (small pinks, large pinks or small coho) and β 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 5.1). 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 include terms for salmon size class (Table 5.2).

Copepodid abundance did not differ between large coho, small coho or large pinks but was lower on small pinks than on large pinks (Table 5.2; Figure 5.2). 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 5.2; Figure 5.2). Motile salmon louse abundance was greatest on large coho followed by large pinks, small pinks and small coho (Table 5.2; Figure 5.2). Pre-adult louse sex ratios did not differ 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 5.2; Figure 5.3)

As motile abundance increased on small pinks, motile abundance increased approximately twice as quickly on large coho than it did on large pinks ($F_{2,46} = 27.53$, $p < 0.001$; Figure 5.4). 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 2 to 3 fold.

Discussion

My 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 against ectoparasites conferred by the larger body size of predators. Three lines of evidence support this conclusion. (1) 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. (2) 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 et al. 2008b). 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). (3) As motile abundance increased on small pinks the disparity between

Table 5.2. 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

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 (Table 5.3) 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 and Albright 1991b), adult female lice are likely to be the most pathogenic stage and sex to host fish, and male-biased sex

Table 5.3. Summary of published data on adult male and female salmon lice enumerated on wild salmonids. Counts of males and females are total lice identified on each species of host in a given study. Sex ratio is the number of males identified in the total sample divided by the number of adult females. Host size ranges are approximate fork length.

Host species	Males	Females	Sex ratio	Host size (mm)	Hosts sampled	Reference
O. gorbuscha	581	583	0.50	430-570	132	(Beamish et al. 2005)
O. nerka	780	1054	0.43	510-750	124	(Beamish et al. 2005)
O. keta	139	148	0.48	670-810	62	(Beamish et al. 2005)
O. tshawytscha	535	814	0.40	200-830	140	(Beamish et al. 2005)
O. kisutch	582	855	0.41	510-780	208	(Beamish et al. 2005)
S. trutta	560	980	0.36	220-520	78	(Birkeland 1996)
S. salar	455	1752	0.21	380-850	69	(Jacobsen and Gaard 1997)
S. trutta	13	26	0.33	160-400	60	(Schram et al. 1998)
S. trutta	166	228	0.42	50-480	146	(Schram et al. 1998)
S. trutta	120	116	0.51	140-590	184	(Schram et al. 1998)
S. trutta	62	167	0.27	180-650	111	(Schram et al. 1998)
S. trutta	82	370	0.18	240-690	105	(Tingley et al. 1997)
S. trutta	189	659	0.22	220-790	190	(Tingley et al. 1997)
S. trutta	189	94	0.67	na	160	(Tully and Whelan 1993)
O. tshawytscha	239	575	0.29	470-950	69	(Gottesfeld et al. 2009)
O. kisutch	423	494	0.46	600-660	101	(Gottesfeld et al. 2009)
O. gorbuscha	49	147	0.25	na	1633	(Butterworth et al. 2008)
S. salar	83	129	0.39	na	56	(Bristow et al. 1996, Todd et al. 2000)
S. salar	53	85	0.38	na	20	(Todd et al. 2000)
S. salar	223	347	0.39	na	25	(Todd et al. 2000)
S. salar	156	371	0.30	na	28	(Todd et al. 2000)
S. salar	381	739	0.34	na	41	(Todd et al. 2000)
S. salar	12	136	0.08	440-1110	31	(Bristow et al. 1996)
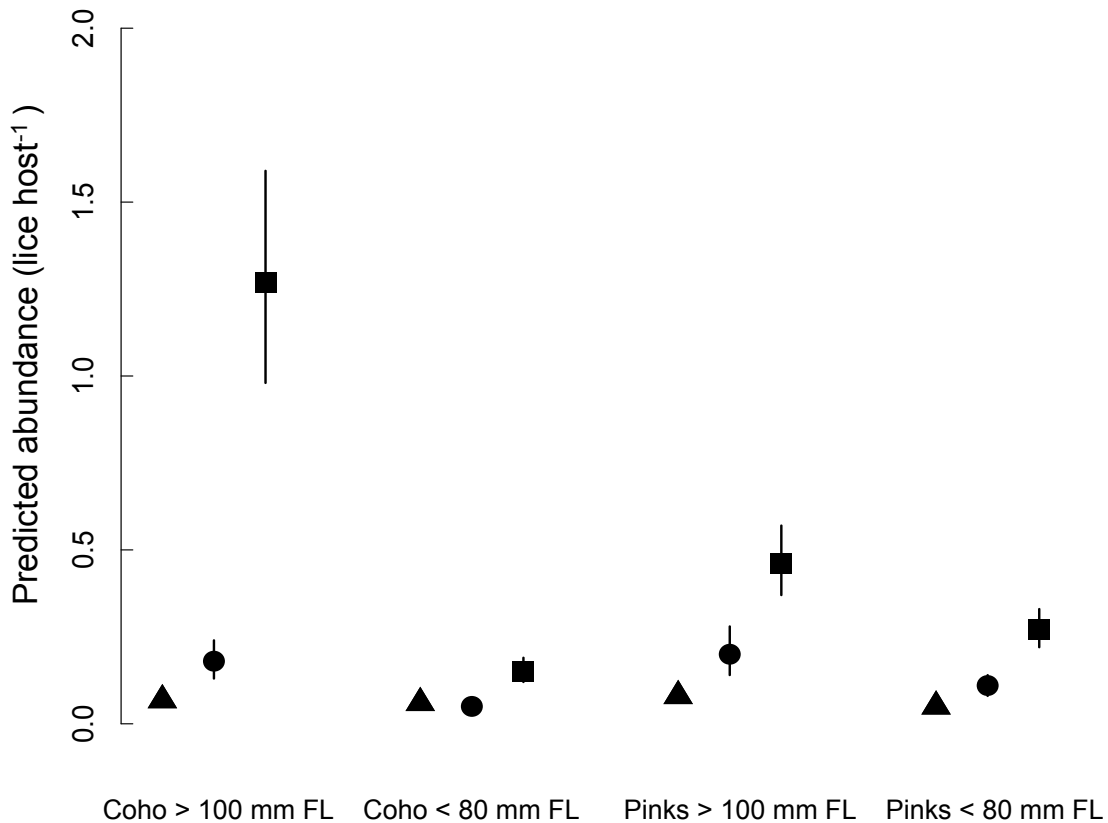
Figure 5.2. Predicted copepodid (triangle), chalimus (circle), and motile (square) abundance (+/- 95% CI) for each juvenile salmon size class. Values are transformed parameter estimates (i.e., $e^{(predicted\ abundance \pm CI)}$) from best fit GLMMs hence they are lower than observed abundance and conceptually represent relative differences in abundance between trophic groups once variation attributable to gear type, year, month, zone and sampling date is accounted for.

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 5.3 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 to the hypothesis that adult male-biased trophic transmission contributes to infection on predatory coho smolts.
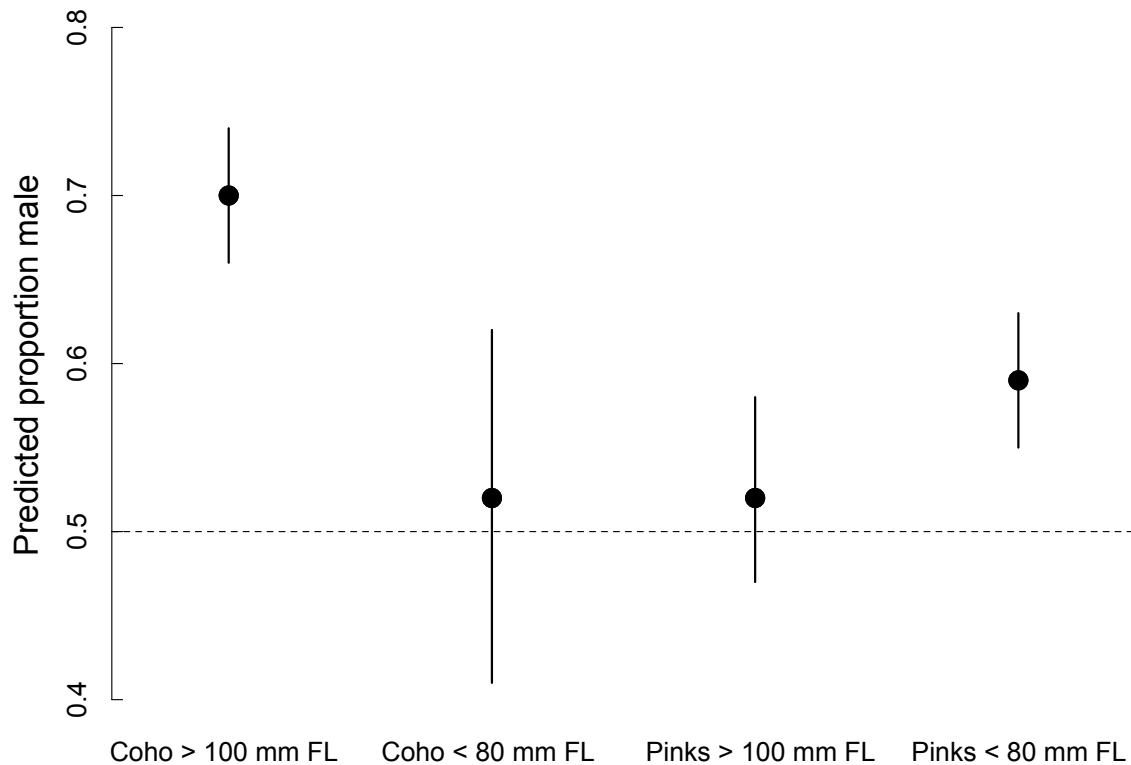
Figure 5.3. Predicted proportion of adult salmon lice that are male (+/- 95% CI) for each juvenile salmon size class.

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. I 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.
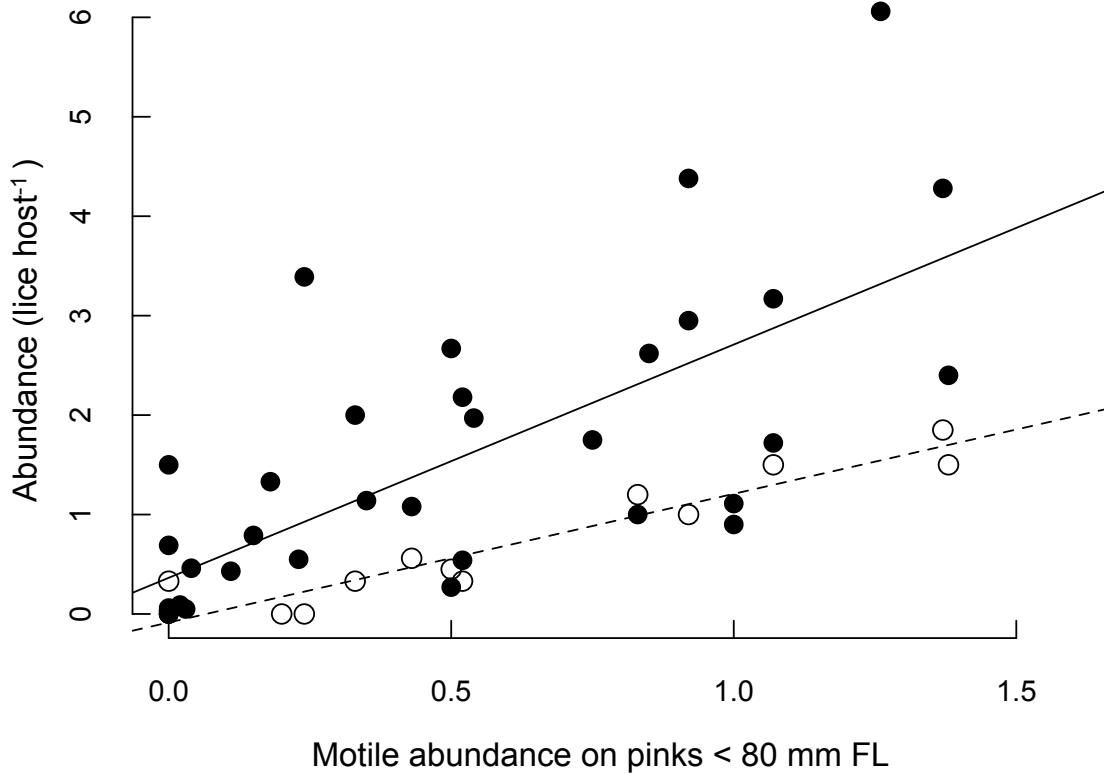
Figure 5.4. Relationship between mean motile abundance on juvenile pink salmon less than 80 mm FL and sympatric coho greater than 100 mm FL (solid circles) and pinks greater than 100 mm FL (open circles). Lines are best-fit regression lines for coho (solid line: y = 0.36 + 2.35x, $P < 0.001$) and pinks (dashed line: y = -0.08 + 1.29x, $P < 0.001$). The slope of the relationship is ~ 2 times greater on coho than on pinks (slope coefficient ± 1SE; coho: 2.35 ± 0.38, pinks: 1.29 ± 0.15).

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 and Celewycz 1994), shorter (Hartt and 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, I estimated that trophic transmission accounts for 53 to 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 my approach probably underestimates the true extent to which trophic transmission occurs. Despite these limitations the estimates suggest that trophic transmission contributes substantially to the louse burdens large coho experience during early marine life, increasing infection 2 to 3 fold.

Pacific salmon can 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 et al. 2008), louse burdens at much lower levels (e.g. as low as 0.1 lice gram^{-1}) can lead to changes in host physiology, biochemistry and immunology which may underlie observed changes in host behaviour with infection (Birkeland 1996, Wagner et al. 2003, Webster et al. 2007, Krkosek et al. In Press). However, I 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 (Johnson and Albright 1992a, b, Fast et al. 2002, Jones et al. 2007).

The 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. My findings strongly advocate for a shift in the management of lice on wild salmon to include (1) laboratory and field based studies of juvenile coho-salmon louse interactions, (2) quantitative examination of coho population dynamics in areas of recurrent salmon louse infestations, and (3) a more comprehensive ecosystem perspective to management and monitoring that includes the ecological interactions and productivity of all salmonid species.

Chapter 6

Coho salmon productivity in relation to salmon lice from infected prey and salmon farms[5]

Abstract

Pathogen transmission from open net pen aquaculture facilities can depress sympatric wild fish populations. However, little is known about the effects of pathogen transmission from farmed fish on species interactions or other ecosystem components. Coho salmon (*Oncorhynchus kisutch*) smolts are susceptible hosts to the parasitic salmon louse (*Lepeophtheirus salmonis*) as well as a primary predator of juvenile pink (*O. gorbuscha*) salmon, a major host species for lice. I used a hierarchical model of stock-recruit dynamics to compare coho salmon population dynamics across a region that varies in salmon louse infestation of juvenile coho and their pink salmon prey. During a period of recurring salmon louse infestations in a region of open net pen salmon farms, coho salmon productivity (recruits/spawner at low spawner abundance) was depressed ~ 7 fold relative to unexposed populations. Alternate hypotheses for the observed difference in productivity, such as declines in coho prey, perturbations to freshwater habitat or stochasticity, are less likely to explain this pattern. Lice parasitizing juvenile coho salmon were likely to be trophically transmitted during predation on parasitized juvenile pink salmon as well as directly transmitted from salmon farms. The finding that species interactions may cause the effects of pathogen transmission from farmed to wild fish to propagate up marine food webs has important conservation implications: (1) the management of salmon aquaculture should consider and account for species interactions and the potential for these interactions to intensify pathogen transmission from farmed to wild fish, (2) the ecosystem impact of louse transmission from farmed to wild salmon has likely been underestimated, and (3) comprehensive monitoring of wild salmon and their population dynamics in areas of intensive salmon aquaculture should be a priority to determine if open net pen salmon aquaculture is ecologically sustainable.

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[5] A version of this chapter appears as Connors, B.M., Krkosek, M. and L.M. Dill. 2010. Coho salmon productivity in relation to salmon lice from infected prey and salmon farms. Journal of Applied Ecology 47: 1372-1377.

Introduction

As a result of the extensive marine migrations of anadromous salmonids, juveniles are spatially and temporally separated from adults during early marine life. This serves as an allopatric barrier to pathogen transmission between age classes until they occur in sympatry either in the outer coastal environment or the open ocean (Krkosek et al. 2007b, Gottesfeld et al. 2009). A consequence of migratory allopatry is that during the first few months of marine life, when they are most vulnerable, juvenile salmonids are not subject to some pathogens common to older and larger salmonids. Intensive open net pen salmon aquaculture can undermine this natural barrier to transmission by providing a year-round host population in the nearshore marine environment whose pathogens can spill over to sympatric wild juvenile salmonids (Costello 2009). As global salmon aquaculture production continues to grow, many wild salmon populations in areas of intensive aquaculture are in decline as a result of pathogen transmission from farmed salmon to wild juvenile salmon as well as from competition and interbreeding (Ford and Myers 2008).

Pathogen transmission from farmed to wild salmon has been particularly well studied in the Broughton Archipelago of British Columbia, Canada, where salmon lice (*Lepeophtheirus salmonis*) from salmon farms can infect out-migrating juvenile pink salmon (*Oncorhynchus gorbuscha*) (Krkosek et al. 2005a) and elevate their early marine mortality (Krkosek et al. 2006). Coincident with louse exposure, pink salmon populations in the Broughton Archipelago have declined (Krkosek et al. 2007a). However, much debate surrounds the role that louse infection from salmon aquaculture has played in these declines (Costello 2009) as well as the broader consequences of louse transmission for the marine ecosystems in which it occurs.

Juvenile pink salmon are subject to predation from other larger juvenile salmonids, including coho salmon smolts (*O. kisutch*), during the first few months of marine life. Unlike pink salmon, which head to sea immediately after emergence from the gravel, coho spend one year or more in freshwater before entering the marine environment. In coastal marine environments coho smolts can be an important predator of pink salmon (Quinn 2005) and salmon lice have the potential to alter this natural predator-prey dynamic by increasing the susceptibility of pink salmon to predation (Krkosek et al. In Press), and through the trophic transmission of lice during predation events (Connors et al. 2008b). This latter process increases infection on coho smolts 2 to 3 fold in areas where they rear and interact with infected juvenile pink salmon prey (Connors et al. 2010a). Therefore louse transmission from salmon farms may indirectly influence the health of sympatric coho salmon smolts via the accumulation of lice from infected prey on coho. While the trophic accumulation of lice may

undermine the protection from ectoparasites conferred by the larger body size of coho, the effect of salmon louse infestation on coho at the population level has not been evaluated.

Here I examine time series data on coho salmon populations from the central coast of British Columbia (Figure 6.1) that have varied in their exposure to salmon louse infestations associated with salmon aquaculture. I compared coho productivity (recruits/spawner at low spawner abundance) between populations exposed and unexposed to salmon farms, both before and during louse infestations. These findings demonstrate that coho populations had depressed productivity when exposed to louse infestations associated with salmon farms, suggesting that parasite transmission from farmed to wild salmon can propagate up a salmonid food web with negative consequences for predatory salmon populations and the ecosystems in which they are embedded.

Methods

We compiled Fisheries and Oceans Canada escapement data (number of adult spawners) for 53 watersheds in 4 management areas from 1975 to 2007 (Figure 6.1). All records of "none-observed" and "adults present" as well as watersheds subject to coho enhancement programs (i.e., hatcheries) were removed. Because of temporal and spatial autocorrelation, commercial exploitation of coho ranging from 4-90% over the time series, and within- and among-year environmental stochasticity, I used a hierarchical model of stock-recruit dynamics with spatially covarying productivity. This allowed us to control for commercial exploitation, account for sources of environmental stochasticity, and test for an influence of recurrent louse infestations on coho population dynamics.

To incorporate commercial exploitation I obtained estimated exploitation rates for the populations in each year of the time series from Fisheries and Oceans Canada. These estimates are based on coded-wire tags placed in out-migrating smolts and recovered by fisheries as adults return to their natal watersheds (Simpson et al. 2004). Average exploitation based on estimates from three indicator streams (Quinsam, Big Qualicum and Black Creek), when available, was used from 1975 to 1998 for all populations. In 1998 coho fisheries became selective for hatchery fish and so only estimates from Black Creek (a wild indicator stock) were used subsequently. Big Qualicum exploitation estimates from 1986-1989 were excluded because of concerns with smolt quality (J. Irvine, Fisheries and Oceans Canada, personal communication).
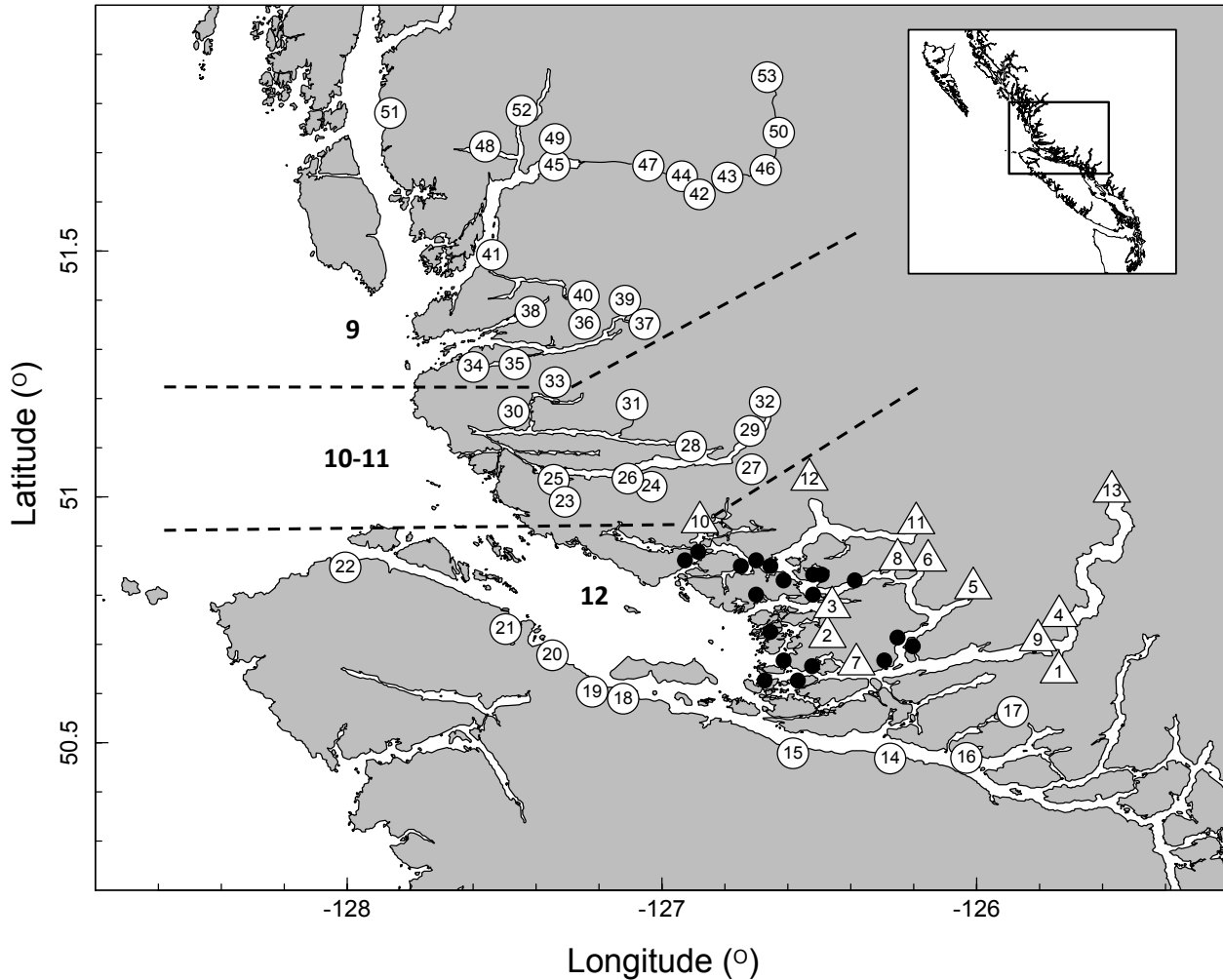
Figure 6.1. Coho salmon populations (see Connors et al. 2010b for corresponding names) from the midcoast of British Columbia used to examine population dynamics in exposed (open triangles, 1-13) and unexposed (open circles, 14-53) populations before and during recurrent salmon louse infestations associated with salmon farms (solid black circles). Dashed lines separate Fisheries and Oceans Canada management areas. Locations of watersheds and farms are approximate and farms outside of the region associated with recurrent salmon louse infestations are not plotted.

With the escapement records and exploitation estimates I calculated recruitment for each population in each year:

$$R_{i,t} = N_{i,t}[1 - \mu_t]^{-1} \tag{eqn. 1}$$

where R is the number of adult recruits, N is the coho escapement estimate and μ is the exploitation estimate for all populations in year t. The stock that produced the recruits in population i and year t is the escapement estimate for population i in year t-3 assuming a three year lifecycle for coho (Groot

and Margolis 1991). I then assumed stochastic Ricker population dynamics (Ricker 1954) and incorporated recruitment from equation 1 to build the stock recruit relationship:

$$R_{i,t} = N_{i,t-3} \exp[r - b_i N_{i,t-3} + \varepsilon_{i,t}]$$ (eqn. 2)

where r is productivity at low spawner abundance and b reflects density dependence in relation to the carrying capacity of population i. Equation 2 can be log transformed to obtain the linear equation:

$$\ln[R_{i,t}/ N_{i,t-3}] = r - b_i N_{i,t-3} + \varepsilon_{i,t}$$ (eqn. 3)

whose parameters can be estimated using linear mixed effects models.

Salmon louse infestations on juvenile pink salmon have been documented in the Broughton Archipelago in the spring of 2001, 2002 and from 2004-2006 (Morton and Williams 2003, Morton et al. 2004, Krkosek et al. 2005a, Morton et al. 2005, Krkosek et al. 2006, Jones and Hargreaves 2007), which correspond to adult coho that returned to spawn in 2002, 2003 and from 2005-2007. Juvenile coho have been examined for lice in two of these years (spring of 2004 and 2005) and in both years infestations on coho were positively correlated with infestation on pinks (Connors et al. 2010a). I extended equation 3, which became the null model, to include variation in productivity among populations exposed and unexposed to salmon farms before and during salmon louse infestations:

$$\ln[R_{i,t}/ N_{i,t-3}] = r_j - b_i N_{i,t-3} + \varepsilon_{i,t}$$ (eqn. 4)

where j is one of six groups: exposed and unexposed populations in years preceding salmon louse infestations (1975-2000), during recurrent salmon louse infestations (2001-2002, 2004-2006) and during a non-random fallowing management action (i.e., emptying of salmon farms during the spring of 2003).

We also extended the null and stratified models to include synchronous environmental variation at two spatial scales:

$$\ln[R_{i,t}/ N_{i,t-3}] = (r_j + \theta_t + \theta_{t,a})- b_i N_{i,t-3} + \varepsilon_{i,t}$$ (eqn. 5)

resulting in three components of environmental stochasticity: variation among years synchronously for all populations (θ_t), variation among years synchronously for populations within each Fisheries and Oceans management area nested within θ_t ($\theta_{t,a}$; Figure 6.1) and variation within populations that is independent among years ($\varepsilon_{i,t}$). Each of these components were normally distributed random

variables with a mean of zero and variance that is estimated. The null and stratified models as well as the components of environmental stochasticity were fit using maximum likelihood and compared using AIC (Burnham and Anderson 2002) and likelihood ratio tests (Hilborn and Mangel 1997) in R (R Development Core Team 2010).

In order to statistically compare parameter estimates (i.e., productivity among exposed and unexposed populations before and during infestations) I constructed 95% confidence intervals for r_j by modifying the bootstrapping algorithm of Dennis and Taper (1994) to account for the hierarchical nature of the data, commercial exploitation and changes in productivity. In each iteration of the algorithm I forecasted recruitment for each $N_{i,t}$ observation where there was a $N_{i,t}$ and $N_{i,t-3}$ data pair using the r_j corresponding to the estimate from exposed and unexposed populations before and during infestations. Stochasticity was included in the simulation by drawing a random deviate from θ_t for each year, $\theta_{t,a}$ for each management area in each year and $\varepsilon_{i,t}$ for each population within each year. Once these stochastic elements were generated I used the untransformed version of equation 5 to simulate recruitment data for each $N_{i,t}$ observation where there was a $N_{i,t}$ and $N_{i,t-3}$ data pair. The same model (i.e., equation 5) was then fit to the simulated data, as described above with the original dataset, 1000 times and at each iteration values of r were recorded for each population group (before infestations, during infestations, and the fallow year for exposed and unexposed populations). Confidence intervals were then calculated as the 2.5 and 97.5 percentiles of the 1000 bootstrap estimates of r.

To examine the likelihood that the observed difference in population growth rates between exposed and unexposed populations during salmon louse infestations was spurious, I built on an approach first described by Carpenter et al. (1989) to detect changes in a manipulated ecosystem relative to an undisturbed reference system when opportunities for randomization and replication are not available. This involved fitting equation 5 retaining the same exposed/unexposed before/during infestation grouping structure (i.e., 2 years exposed to sea lice followed by a fallow year and then 3 exposed years with the remaining years of the time series as pre-exposed) in one-year increments starting in 1975. At each of the 27 iterations I calculated the difference in productivity between "exposed" and "unexposed" populations during "infestations". This approach allowed us to compare the observed difference in productivity between exposed and unexposed populations during the true infestations to the difference I would expect to see based on chance alone given the natural variability in productivity among populations and years in the dataset. A normal distribution was fit to the distribution of simulated differences in r and the probability of observing a difference as great as or greater than the one observed was calculated.

Results

Excluding populations with years without escapement estimates resulted in 636 stock-recruit data pairs. The best-supported model included group-specific productivity and variation among years synchronously for all populations and populations within each management area (Table 6.1). During recurrent salmon louse infestations exposed populations were characterized by generally negative survival (Table 6.2) and had significantly lower productivity than (a) unexposed populations during the recurrent infestations, and (b) exposed and unexposed populations prior to salmon louse infestations (Figure 6.2). Exposed and unexposed productivity during the fallow year was not significantly different from pre-salmon louse infestation productivity. However, given the paucity of stock recruit pairs for coho that went to sea during the fallow (i.e., 2003 and returned to spawn in 2004), the power to detect a difference was weak. The point estimates of productivity translate into ~ seven fold decline in productivity for coho salmon populations in the exposed region relative to those not exposed to salmon aquaculture (i.e., e^r for exposed populations was ~0.75 recruits/spawner at low spawner abundance while for control populations it was ~5.75 recruits/spawner at low spawner abundance). The next best-supported model (ΔAIC of 5.5; Table 6.1) did not include variation among years synchronously for populations within each management area. Productivity estimates based on the next best-supported model did not differ substantially from the best-supported model (i.e., Δ in productivity between control and exposed populations during louse infestations changes by 0.03 [from -1.99 to -1.96]).

The observed difference in productivity between exposed and control groups during louse infestations was unprecedented in the time series (Figure 6.3). The probability of observing a difference in productivity as great as or greater than the one observed, given the distribution of differences in the rest of the time-series, was 0.000017 ($\mu = -0.12$, $\sigma = 0.45$; Z-score = -4.14).

Discussion

These results indicate that relative to unexposed populations coho salmon productivity in an area of intensive salmon aquaculture was depressed approximately seven fold during a period of salmon louse infestations. These declines are consistent with known louse exposure. Declines in productivity coincide with the first documented salmon louse epizootics in the Broughton Archipelago (Morton and Williams 2003). When farms were fallowed, lice abundance on out-migrating salmonids declined (Morton et al. 2005) and coho productivity appeared to rebound to pre-infestation levels, although I had low power to detect a difference if one did exist. Estimated productivity for populations in years

Table 6.1. Relative fit of models predicting productivity of coho salmon populations. Models relate survival (S; ln[recruits/spawner]) to productivity of all populations (P) or populations within each louse exposure group (subscript m) while accounting for population specific (subscript i) density dependence (D) and residual variation (ε). Variation among years synchronously for all populations (1|Y) and variation among years synchronously for populations within each management area nested within year (1|Y/A) are also included. ΔAIC is the AIC difference between the model in question and the best-supported model in bold.

Model	ΔAIC	Number of parameters
$S \sim P + D_i + \varepsilon$	724.1	55
$S \sim P_m + D_i + \varepsilon$	687.1	60
$S \sim P + D_i + (1|Y) + \varepsilon$	34.7	56
$S \sim P_m + D_i + (1|Y) + \varepsilon$	5.5	61
$S \sim P + D_i + (1|Y/A) + \varepsilon$	28.4	56
$S \sim P_m + D_i + (1|Y/A) + \varepsilon$	**0**	**62**

Table 6.2. Observed survival ($\ln[R_t /N_{t-3}]$) for exposed coho salmon populations in the Broughton Archipelago during salmon lice infestation years and the fallow treatment (i.e., the cohort that went to sea in 2003 and returned in 2004). Exposed watersheds without stock-recruit pairs from 2002-2007 (i.e., Ahta Valley, Embley, Gilford and Glendale) are not presented.

Population	2002	2003	2004	2005	2006	2007
Ahnuhati	0.52	-0.90	-	-1.14	-1.18	-3.46
Ahta	-1.22	-2.69	-	1.45	0.34	-3.22
Kakweiken	1.30	-1.32	-	-3.3	0.36	0.24
Kingcome	-0.54	-	-	-0.24	-	-1.92
Klinaklini	0.77	0.17	-	-	-	-
Kwlate	-1.21	-0.70	-	1.68	-	-
Shoal Harbour	-	-1.57	-0.01	-	0.42	-
Viner	0.19	-1.64	3.41	-	-	-
Wakeman	-	-1.34	-	1.27	0.42	-3.74
Average	**-0.03**	**-1.25**	**1.7**	**-0.05**	**0.07**	**-2.42**
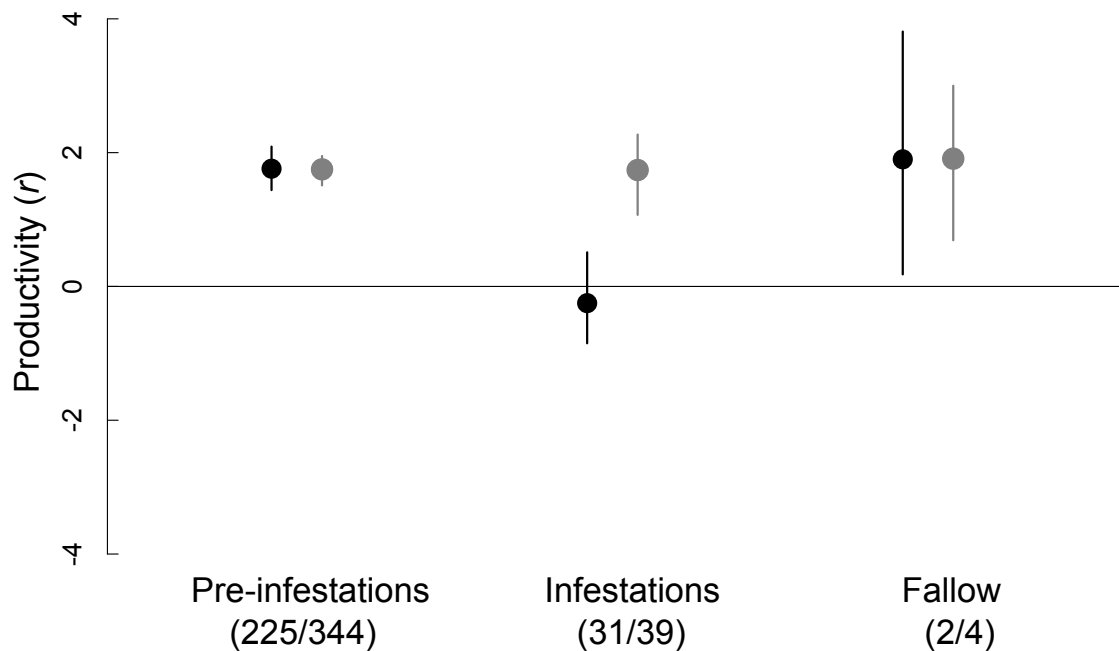
Figure 6.2. Productivity (+/- 95% bootstrapped confidence intervals) of coho salmon populations from exposed (black circles) and unexposed regions (grey circles) prior to and during years when salmon lice epizootics were observed in exposed populations as well as during the fallow treatment year. Values in parentheses below groups represent the number of stock recruit pairs used to estimate productivity for exposed and unexposed populations respectively.

and regions not exposed to lice are consistent with those estimated for salmonids elsewhere (Myers et al. 1999).

Coho from the unexposed rivers were unlikely to interact with farmed salmon and infected pink salmon during early marine life because of the assumed direction of their migration. However, some unexposed populations may pass by salmon farms at a considerable distance later in marine life, and are therefore only relatively unexposed compared to exposed populations. Nonetheless, this would tend towards conservative estimates of an influence of farms because the analysis would then be trying to detect a localized effect in addition to any broader effects.
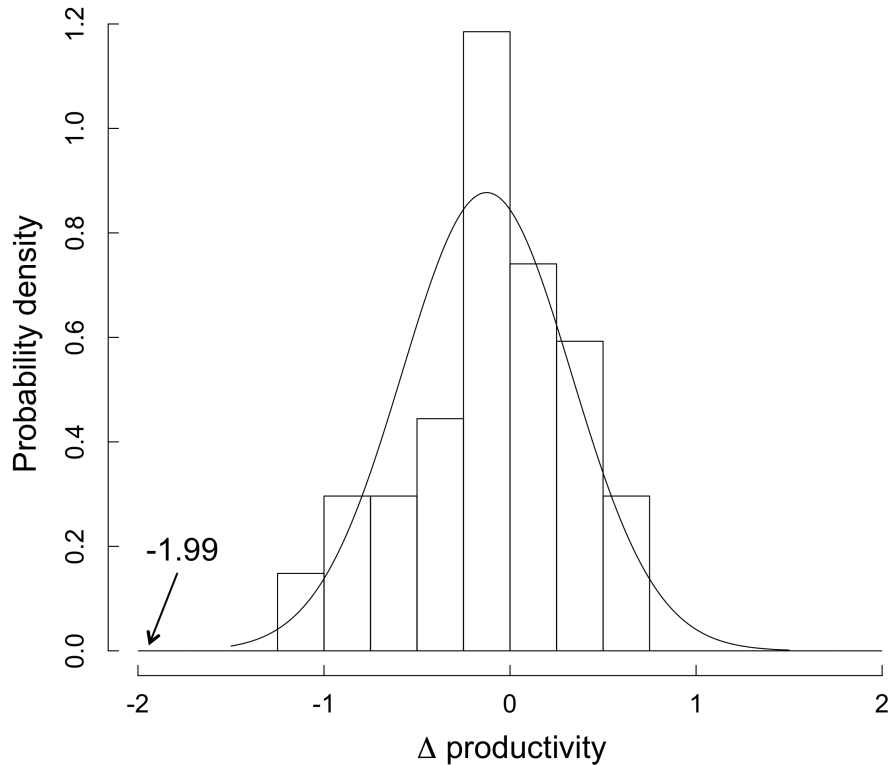
Figure 6.3. Histogram of difference in productivity between group of "exposed" and group of "unexposed" coho populations (Figure 6.1) during infestations if the year louse infestations began is arbitrarily assigned to a year between 1975 and 2000. The curve is the normal probability density distribution ($\mu = -0.12$, $\sigma = 0.45$) of the differences given the natural variability in productivity among populations and years. The arrow at -1.99 is the true difference in productivity between populations exposed and unexposed to recurrent salmon louse infestations beginning in the spring of 2001. The probability of this observed difference in productivity between exposed and unexposed populations is less than 0.0001.

Pink salmon populations in the Broughton Archipelago have also declined over the same time period (Krkosek et al. 2007a). As juvenile pink salmon can be an important early marine resource for coho smolts, declines in pink salmon could in theory contribute to, or even drive, the observed decline in coho productivity. However, evidence of a relationship between pink and coho salmon abundance in areas not exposed to aquaculture is equivocal (e.g., Briscoe et al. 2005, Beamish et al. 2008) suggesting that coho populations are not limited by the abundance of pink salmon fry during early marine life. I also cannot rule out the possibility that another factor specific to the Broughton Archipelago, such as a sudden coincident change in early marine productivity or degradation of freshwater habitat, drives both pink and coho productivity during exposed years. However, despite millions of dollars invested in government, industry and academic research programmes a non-louse factor has yet to be identified (Fraser et al. 2009).

Salmon louse transmission from farmed to wild pink salmon compromises the ability of juvenile pink salmon to escape predation, resulting in selective predation of infected pinks by coho (Krkosek et al. In Press) and the accumulation of motile (pre-adult and adult) lice on coho from their prey (Connors, Krkosek and Dill 2008; Connors et al. 2010a). These findings suggest that coho populations are depressed, at least in part, because of this indirect transmission of lice from salmon aquaculture. While the direct transmission of infective stage lice from farmed salmon to sympatric coho salmon undoubtedly contributes to salmon louse abundance on coho, the indirect accumulation of motile stage lice as a result of consuming infected prey may increase motile louse infection on coho by 2 to 3 times (Connors et al. 2010a). As motile stage sea lice are the most pathogenic to host fish (Costello 2006, Wagner et al. 2008), the role of trophic transmission in the observed declines in coho productivity may be considerable.

High abundance of motile stage lice can cause host morbidity, and mortality and louse burdens at lower levels can lead to changes in host physiology (reviewed by Wagner et al. 2008), which may underlie observed changes in host behaviour and fitness with infection (Webster et al. 2007, Wagner et al. 2008, Krkosek et al. In Press). Our understanding of the influence of salmon louse infection on coho smolts is limited to the latter's physiology, immunology and histopathology following a single exposure of infective stage sea lice (Johnson and Albright 1992a, Fast et al. 2002) at abundances lower than those observed in the field (Connors et al. 2010a). Small changes in early marine growth in coho can strongly influence early marine survival and resulting spawner abundance (Beamish et al. 2004) suggesting that if sub-lethal exposure to lice during the critical early marine period reduces coho smolt growth there could be consequences for coho population dynamics. The lack of data on salmon louse-coho interactions under controlled conditions precludes drawing definitive links between louse abundance in the field and coho health, and highlights the need for future work on coho-salmon louse interactions. Demonstrating causal linkages would require an ecosystem-scale experiment with randomization and replication of coho salmon populations exposed to manipulated abundances of sea lice on salmon farms. Such a study would be expensive, logistically difficult, socially contentious and may raise ethical issues. However, it is important to note a coordinated management plan has recently been implemented in the Broughton Archipelago, the success of which for salmon population dynamics has yet to be evaluated.

My findings provide evidence to suggest that the transmission of salmon lice, directly and indirectly, from farmed salmon to coho salmon can depress coho salmon productivity. This may have important consequences for the structure and function of the coastal ecosystems in which farmed and wild salmon occur. That coho salmon populations are depressed in concert with louse exposure from

salmon farms has a number of important implications for the management of intensive open net pen aquaculture in regions with wild salmon populations. The transmission of parasites from farmed to wild fish does not occur in an ecological vacuum; interactions among species may intensify or mitigate transmission and its consequences. I suggest there is an urgent need to consider the broader ecosystem consequences of pathogen transmission from farmed to wild salmon and to tailor monitoring and management accordingly. This should include monitoring the health of all salmonids during early marine life in areas of intensive salmon aquaculture in concert with management actions aimed at eliminating the transmission of lice from farmed to wild salmon. Only through careful monitoring and rigorous assessment of the health of salmon at both the individual and population levels can managers and conservationists hope to determine if wild and farmed salmon can co-exist in coastal marine environments.

Chapter 7

General Conclusions

Few studies have examined how parasite behaviour mediates emerging infections in wildlife, yet an understanding of the factors that shape the distribution and abundance of parasites among hosts is key to predicting and managing emerging disease (Daszak et al. 2000). In this thesis, I link an understanding of the drivers of individual parasite behaviour to the distribution and abundance of parasites among hosts and the dynamics of host populations. In Chapter 2, I show that as salmon lice approach sexual maturity they leave one host individual in search of another, first in response to competition for host resources and then in search of mates. This results in considerable movement among hosts; in Chapter 3 I estimate that more than 50% of the lice observed on juvenile pink and chum salmon during early marine life are likely to have developed on a different host. Movement of lice among hosts increases the probability that a louse interacts with multiple hosts, possibly mediating louse transmission among and between farmed and wild salmon as well as the spread of other pathogens, if lice act as vectors. While these findings highlight that the movement of motile lice among hosts has been previously underestimated, a key question that arises is to what extent (if at all) does the movement of lice result in the transmission of bacterial and viral pathogens among and between farmed and wild salmon? Viral and bacterial infections on farmed fish (Brocklebank et al. 1993, Saksida 2006) and louse transmission from farmed to wild salmon (Price et al. 2010, Price et al. 2011) is increasingly well documented in British Columbia. While lice can transmit viruses in the lab (Nylund et al. 1994) and bacteria and viruses have been isolated from motile lice in the field (Nese and Enger 1993, Barker et al. 2009) our current understanding of the role motile lice play as vectors is limited. Coupled with lab-based investigations, the broad scale assaying of motile lice and farmed and wild hosts for viral and bacterial pathogens would be an important step towards determining the extent to which lice vector disease in coastal British Columbia.

Coho salmon smolts are an important predator of juvenile pink salmon during early marine life (Quinn 2005), a period of time when exposure to lice is generally very low (Krkosek et al. 2007b). However, louse transmission from farmed salmon can alter this natural predator-prey dynamic by increasing pink salmon susceptibility to predation (Krkosek et al. In Press). In Chapter 4 I show that as pinks are consumed by coho, lice infecting pinks are able to transfer from predator to prey thereby

escaping the fate of their pink salmon host. I show in Chapter 5 that the selective predation of infected pinks leads to the accumulation of lice on coho, thereby increasing infection by 2 to 3 fold, and in Chapter 6 I show that these louse infestations are associated with coho salmon populations that are depressed ~ 7 fold relative to unexposed populations. The final 3 chapters highlight that species interactions may cause the effects of louse transmission from farmed to wild fish to propagate up marine food webs. While these observations are an important first step towards understanding both the extent and consequences of the trophic transmission of lice, further laboratory and field studies on the influence of louse infection on coho salmon behaviour, growth, physiology and survival are needed. It has often been assumed that only those salmonids that are very small at marine entry (i.e., pink and chum salmon) can be negatively affected by exposure to lice. The finding that coho salmon populations are depressed coincident with infection suggests that this may not always be the case. Instead, subtle changes in early marine growth (an important determinant of marine survival; Beamish et al. 2004) as a result of infection may reduce the productivity of wild salmon populations. The decline of other species of wild salmon coincident with exposure to lice from salmon farms (e.g. sockeye; Price et al. 2011) highlights that further work on louse infection and host growth in all Pacific salmonids would be an important step towards informing management and policy regarding acceptable levels of louse exposure for wild salmon.

This thesis argues that the transmission of lice from farmed to wild fish does not occur in an ecological vacuum; rather, louse behaviour and interactions among host species may play an important role in shaping louse transmission and its consequences. 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. The findings of this thesis argue for a more comprehensive ecosystem perspective to the management and monitoring of sea lice on wild salmon that includes parasite behaviour and the ecological interactions and productivity of all salmonid species. Myriad biotic and abiotic factors are likely to mediate louse impacts on wild fish and disentangling them all to definitively link population declines with louse exposure is not a trivial task. Ultimately large scale ecosystem manipulations (i.e., randomized, replicated exposure of wild salmon populations to manipulated abundances of lice on salmon farms), may be the only way to definitively test for population level impacts of lice from aquaculture on wild salmon populations.

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