

The effect of sea lice (*Lepeophtheirus salmonis*) on juvenile pink salmon (*Oncorhynchus gorbuscha*) swimming endurance

Paul A. Mages and Lawrence M. Dill

Abstract: The swimming endurance of naturally and experimentally infected juvenile pink salmon (*Oncorhynchus gorbuscha*) was measured to determine the effects of sea lice (*Lepeophtheirus salmonis*). Salmon naturally infected with adult male and preadult stage lice did not appear to have a reduced swim performance, but when experimentally infected with adult female lice, juvenile salmon showed a reduced ability to swim compared with uninfected control fish, and this effect increased with lice load. A reduced swimming endurance is not only likely to influence predation risk for salmon, but may have other ecological implications, such as slower seaward migration.

Résumé : Nous avons mesuré l'endurance à la nage de jeunes saumons roses (*Oncorhynchus gorbuscha*) infectés naturellement et expérimentalement pour mesurer les effets des poux de mer (*Lepeophtheirus salmonis*). Les saumons infectés naturellement avec des stades adultes mâles et pré-adultes des poux ne semblent pas avoir une performance de nage réduite; par contre, une fois infectés expérimentalement avec des poux adultes femelles, les jeunes saumons affichent une capacité de nage réduite par comparaison aux poissons témoins non infectés et l'effet augmente en fonction de la charge de poux. Une endurance réduite à la nage risque non seulement d'affecter la probabilité de prédation chez les saumons, mais peut avoir d'autres conséquences écologiques, telles qu'une migration plus lente vers la mer.

[Traduit par la Rédaction]

Introduction

Parasites play an important role in the ecology and survival of their hosts and can affect the behaviour and abilities of their hosts to carry out their day-to-day activities. For example, if the parasites create an energy drain on the host, less energy may be available for locomotion, especially costly movements (e.g., foraging forays, migration, escaping predators; Barber et al. 2000; Münderle et al. 2004; Östlund-Nilsson et al. 2005). Hosts may attempt to mitigate this energy deficit by altering their behaviour to increase energy intake or reduce activity, which can increase their susceptibility to predation (Lima and Dill 1990).

Although many parasites are relatively benign, situations may occur where these same parasites reduce host condition to the point of death (e.g., if abnormally abundant or infecting juveniles). High numbers of ectoparasitic sea lice (*Lepeophtheirus salmonis*) have been reported on out-migrating juvenile salmon in areas near fish farms in the Broughton Archipelago, British Columbia, and these have been suggested to cause up to 95% mortality (Morton et al. 2004, 2005; Krkošek et al. 2006). This study system provides an unparalleled opportunity to look at the potentially negative

effects of a “novel” parasite (sensu Krkošek et al. 2007) on its host.

Many studies have examined the costs of *L. salmonis* infection to salmonid hosts (Pike and Wadsworth 1999; Tully and Nolan 2002; Wagner et al. 2008). For example, physiological damage and death in Atlantic salmon (*Salmo salar*) postsmolts was associated with infections by motile stage sea lice (Grimnes and Jakobsen 1996). Sustained swimming tests on adult *S. salar* found reduced swimming ability due to decreased cardiac output after exercise when infected with *L. salmonis* at 0.13 lice·g⁻¹ (Wagner et al. 2003). Webster et al. (2007) found that infected juvenile pink salmon (*Oncorhynchus gorbuscha*) prefer fresh water and incur higher energy costs when in salt water, suggesting there are osmotic challenges associated with *L. salmonis* infection. Similarly, Wagner et al. (2004) found that adult Atlantic salmon performed better in freshwater than in saltwater swimming tests. Some studies used Fulton's condition factor to assess the effects of lice on juvenile pink salmon but found no difference in the condition factor of infected and noninfected fish (Jones and Nemec 2004; Butterworth et al. 2008). However, Morton and Routledge (2006, 2008) argue that condition factor is not a valid assessment of the impact

Received 19 February 2010. Accepted 11 September 2010. Published on the NRC Research Press Web site at cjfas.nrc.ca on 22 November 2010.
J21675

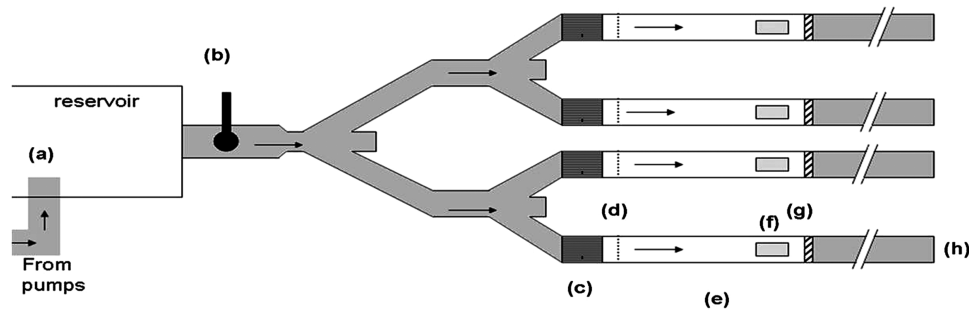
Paper handled by Associate Editor James Grant.

P.A. Mages,¹ 1209 S. Mildred St., Philadelphia, PA 19147, USA.

L.M. Dill, Evolutionary and Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, BC V5A 1S6, Canada.

¹Corresponding author (e-mail: pmsalmon@gmail.com).

Fig. 1. Schematic drawing of swim tunnel seen from above. Water from pumps discharges into a 760 L plastic reservoir (a). Components are as follows: butterfly valve on 10.2 cm diameter polyvinyl chloride (PVC) pipe that is then reduced to 7.6 cm and split by Y-fittings (b), bundle of flow-straightening plastic drinking straws (c), 4 mm mesh screen (d), 7.6 cm × 76.2 cm clear PVC swim chambers (e), lid (f), electrified grid made of 0.5 mm diameter stainless steel wire mounted in a gate valve and connected to a variable transformer set to 2V AC (g), and outflow (h).



of sea lice on juvenile salmon, as their data suggest that condition factor is only reduced when the fish are moribund. Aside from the use (or misuse) of condition factor, there has not been any direct test of the effects of *L. salmonis* on juvenile pink salmon performance.

A prolonged swimming test was used to assess the impact of sea lice on the swimming endurance of naturally and experimentally infected salmon. Prolonged swimming tests, defined as high intensity swimming that lasts between 20 s and 120 min and ends in fatigue, are widely used to assess swimming performance (Beamish 1978; Hammer 1995). By measuring the point at which failure occurred, we tested the hypothesis that *L. salmonis* infection reduces juvenile pink salmon swimming endurance.

Materials and methods

Fish collection and maintenance

Natural infections

Wild juvenile pink salmon naturally infected with lice were collected with a beach seine (30.5 m × 2.5 m; 4 mm mesh) near Twin Lagoon, Broughton Archipelago, British Columbia. To be used in the experiment, all fish had to have a fork length of 53–57 mm, noninfected fish had to have zero lice (of any species) and no visual scarring (from either previous lice infections or predators), and infected fish had to have at least one motile *L. salmonis*, a chalimus scar (evidence of infection history), no other lice species, and no predator scars. Fish were visually assessed as in Krkošek et al. (2005), transferred to the Salmon Coast Research Station (Simoom Sound, British Columbia) in individual containers, and held overnight.

Experimental infections

Fish used in experimental infection trials were collected by seining in Spring Passage Channel and selected according to the same criteria as the noninfected fish above. Infected fish were held separately from test fish in flow-through floating tubs. Infection of previously noninfected fish with adult female lice gently removed from the infected fish occurred the following day.

Noninfected fish were selected haphazardly from holding tubs and placed into two buckets, randomly assigned as treatment or control groups. Treatment groups were manually in-

fectured with one, two, three, or four adult female lice, and the control group (no lice) was “sham infected” (i.e., all handling was the same except the placement of lice) at the same time. The fish to be infected was held in a small container partially filled with water, such that its dorsum was exposed; the louse was then manually placed on the fish. Because fish movement stimulated attachment, and to control for possible effects of anaesthetic on lice, fish were not anesthetized. Infections generally took less than 5 min, and fish were not out of water for more than 30 s. Handling times were kept consistent across treatment groups to ensure any difference between treatment levels were not due to increased emersion by repeating the procedure up to four times.

Swim tunnel design

Swim trials were conducted either the day following capture (naturally infected salmon) or approximately 38–46 h after experimental infection in a swim tunnel comprising four parallel chambers (Fig. 1). Fish were placed in the chambers through lids that sealed with a foam gasket and were secured by hose clamps. Stainless steel grids (mounted in gate valve housings in the rear of each swim chamber, allowing them to be raised to allow fish removal) remained electrified during trials but were switched off when the fish reached the endpoint (fatigue). The slight electrical current motivated the fish to continue swimming until complete exhaustion rather than resting against the grid. Water velocity in the chambers was regulated by adjusting the height differential between the water level in the reservoir and the outflow pipe; an adjustable overflow in the reservoir’s side allowed excess water to spill once the desired height differential was achieved. These levels were calibrated to specific flow velocities by measuring flow volume over time.

Test protocol

Prior to each trial the reservoir and swim tunnel were flushed and filled with seawater. Four fish were chosen for each trial (when possible, two control and two treatment fish), placed randomly in a chamber and allowed to acclimate with no flow for 5 min. The swimming test was a constant acceleration test modified from Tierney et al. (2007), whereby water velocity was gradually increased to the initial velocity of 8.25 cm·s⁻¹ over 1 min and then increased by 2.75 cm·s⁻¹ every 5 min thereafter until the fish failed to

Table 1. Swimming and associated data for naturally and experimentally infected juvenile pink salmon.

Infection trial	Group	L_F (mm)	SD	N				Median dmax (m)	Median motscr
				Infected	Survived to testing	Failed	Censored		
Natural	NL	55.3	1.3	NA	42	27	15	719.56	NA
	L	54.9	1.3	NA	42	32	10	676.66	NA
Experimental	0	54.9	1.3	17	17	13	4	753.17	0
	1	54.9	0.9	14	13	12	1	590.70	2
	2	54.3	1.2	14	12	12	0	573.02	10
	3	55.4	1.6	16	9	8	1	439.89	12
	4	53.7	0.6	16	3	3	0	169.29	19

Note: Naturally infected fish ($N = 84$) were grouped by lice infection: no motile lice (NL) or motile lice (L). Experimentally infected fish ($N = 54$) were grouped by number of adult females (0–4). Juvenile pink salmon were experimentally infected for 40 h before testing. Censored data are the number of fish that did not fail. Median dmax is the distance at which 50% of fish failed, and motscr is the number of motile scars on juvenile pink salmon, counted after the trial. L_F , fork length; SD, standard deviation; NA, not applicable.

Table 2. Models representing competing hypotheses tested.

Model	Hypothesis
1. Lice + fork length + chamber	Lice effect
2. Lice + fork length + chamber + lice \times fork length	Lice effect
3. Fork length + chamber	No lice effect
4. Null	No lice effect

Note: For experimentally infected juvenile pink salmon, lice = the number of adult females (0–4); for naturally infected fish, lice = infected or noninfected group.

continue swimming against the flow and remained against the grid for >2 s. Because maximum velocity attainable ($37.75 \text{ cm}\cdot\text{s}^{-1}$) was reached before some fish failed, the final stage was extended an additional 30 min in those cases. Once the endpoint was reached, the grid was switched off for that chamber. At the end of the trial, all fish were flushed from the chambers into a net. Uninfected fish were later released near their collection point. Infected ones were sedated (clove oil) and euthanized so that motile louse scars could be counted as an indicator of lice damage. All protocols used in this research were approved by the Simon Fraser University Animal Care Committee (protocol #750B-05).

Eighty-four naturally infected fish (mean \pm standard deviation (SD) fork length = 55.1 ± 1.3 mm) were swum between 15 and 27 May 2007. Trials on experimentally infected fish ($n = 37$) and their uninfected controls ($n = 18$) were performed between 6 and 21 June 2007 (see Table 1 for fork lengths). Water temperature was 8.6 ± 0.2 °C and salinity was 28–32 ppt in both sets of trials.

Analysis

Critical swimming speed calculations could not always be performed because the final stage sometimes had a longer duration and some fish did not fail. Therefore, cumulative distance swum (dmax) was calculated for each fish as an ecologically relevant measure of performance: the time (s) swum at each stage multiplied by the stage velocity and summed for all stages swum. Time to event (survival) analysis was used to quantify the effect of lice infection on fish performance because both data sets (naturally and experimentally infected fish) included censored data (31% and

11%, respectively). Fish that did not fail before the trial was ended were assigned an “at least distance swum” without failure and were considered as censored data. Kaplan–Meier (KM) estimates of the probability of swimming a given distance were obtained using observed dmax values. Parametric survival models (Table 2) representing competing hypotheses were fit to the KM survival estimates by log-likelihood using three different error distributions, for a total of 12 models. All models (excluding the null) included the main effects of fork length and chamber to account for any effects of fish size and consistent velocity variation between chambers. Models testing for an effect of lice included a lice variable: presence or absence of lice for naturally infected fish and number of adult female lice for experimentally infected fish. The number of motile scars was not included in the models as it was highly correlated with number of lice present.

Akaike’s information criterion corrected for small sample sizes (AIC_c) was used to rank candidate models based on the relative differences (ΔAIC_c) between the model with the lowest AIC_c value and all other models in each set. AIC_c model weights (w ; the probability that a given model is truly “best” among the candidate models) were also calculated. Because all models contribute some information and there is uncertainty about which is actually “best”, all model w values were used to calculate estimated parameter likelihoods (importance of variable) and values, along with their unconditional standard error (SE). Only parameters with values ± 2 SE that did not encompass zero were considered to have an effect (Burnham and Anderson 2002). All analyses were performed in R version 2.6.1 (R Development Core Team 2007).

Results

Natural infections

Fish in the naturally infected group ($N_{NI} = 42$) had a mean (\pm SD) of 1.31 ± 0.60 motile lice, but a majority were pre-adult stages and adult males (Fig. 2). Some salmon were also infected with other juvenile stages of lice. Median distances swum (i.e., the distance at which 50% failed) were 676.7 and 719.6 m for infected and noninfected salmon, respectively (Table 1; Fig. 3). Despite this 6% difference, the null model with a lognormal distribution was eight times more

Fig. 2. Numbers of *Lepeophtheirus salmonis* stages on the naturally infected juvenile pink salmon ($N = 42$) used in this study. Lice stages are as follows: copepodid (CP), chalimus 1 and 2 (CalA), chalimus 3 and 4 (CalB), preadult 1 and 2 male (PAM), preadult 1 and 2 female (PAF), adult male (AM), and adult female (AF).

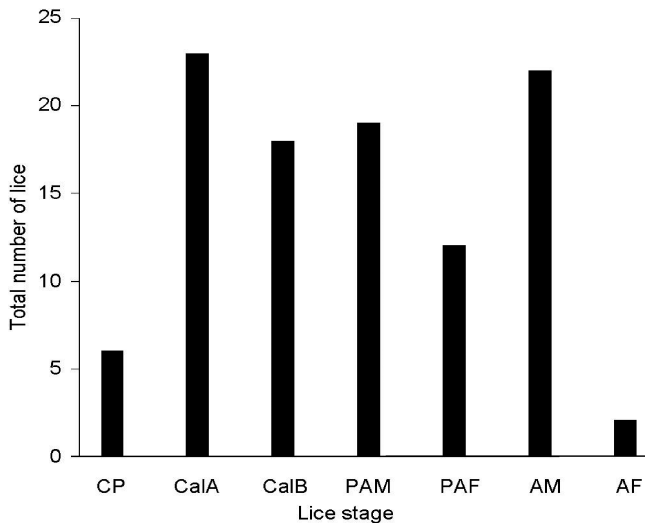
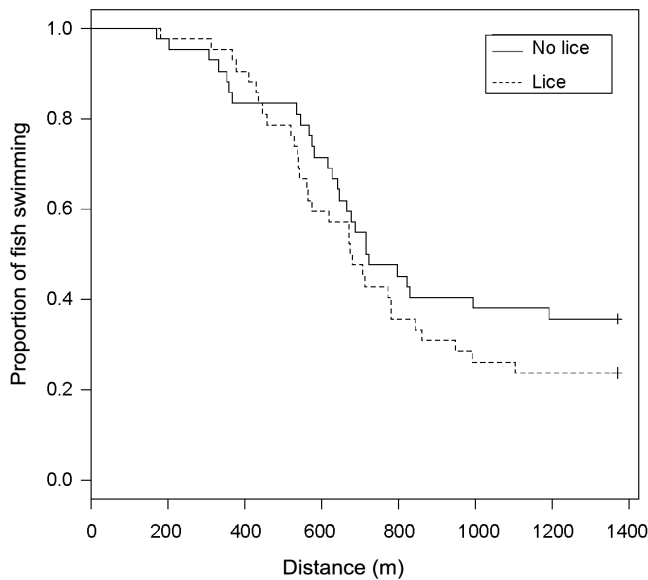


Fig. 3. Kaplan–Meier plot of the proportion of uninfected and naturally infected juvenile pink salmon still swimming after having swum a given distance. Each step indicates the distance where a swim failure event occurred; a plus symbol (+) indicates censored data (fish did not fail).



likely than the models incorporating an effect of lice to be the “best” model. Because of the superiority of the null model, no parameter estimates were calculated. These results suggest juvenile pink salmon swimming endurance is not reduced by natural infections of *L. salmonis* at the levels tested here.

Experimental infections

A total of 37 fish infected with 1, 2, 3, or 4 lice and 18 control fish were swum in this experiment (Table 1). The median distances infected salmon could swim before they

Fig. 4. Kaplan–Meier plot of the proportion of experimentally infected juvenile pink salmon still swimming after having swum a given distance. Each step indicates the distance where a swim failure event occurred; a plus symbol (+) indicates censored data (fish did not fail). Adult female (AF) group refers to the number of adult female lice per fish.



failed were less than that for control fish (Table 1), and as the number of adult female (AF) lice increased, the distances fish could swim declined in a continuous fashion (Table 1; Fig. 4). The top ranking models included lice and fork length (L_F)–AF interactions with a lognormal or Weibull error distribution and were two to three orders of magnitude more informative than the competing models (Table 3). The number of AFs had a large and significant negative effect on swimming endurance (Table 4). The interaction of L_F and AF had a significant positive effect on endurance, which can be interpreted as female lice having less of an effect on larger fish. Lice damage, as indicated by the number of motile scars, was highly correlated with the number of AF lice (Table 1; Spearman’s rho = 0.815, $P < 0.01$).

Discussion

When experimentally infected with adult female lice, juvenile pink salmon had reduced swimming endurance. This seems biologically reasonable, given the large size and energy needs of the female parasites, which were acquiring resources to produce eggs (supported by evidence of females having fed on the test fish, i.e., motile scars). While there was a large overall effect of lice load, it was most evident for higher lice loads, particularly given that the majority of these fish died before they could be tested. Since only fish capable of withstanding the challenge of three and four lice were swum, the estimated impact of adult female lice on swimming endurance must be considered a conservative one. Although the maximum loads are high, the results are ecologically relevant, as loads of these magnitudes are found on naturally infected fish (Morton et al. 2004; Krkošek et al. 2006). Our findings are similar to those from the swimming tests performed by Wagner et al. (2003) on large Atlantic

Table 3. Summary of models for experimentally infected juvenile pink salmon.

Model and variables	Distribution	<i>K</i>	LL	AIC _c	Δ	<i>w</i>
1. ^a Adult female + fork length + chamber + adult female \times fork length	Weibull	7	-556.7	1127.40	0.00	0.80
2. Adult female + fork length + chamber + adult female \times fork length	Lognormal	7	-558.1	1132.63	2.80	0.20

Note: Model is $\text{Log}(\text{dmax}) = \text{intercept} + \text{model variables} + \sigma \times e$, where σ is a scale parameter and e is an error term based on Weibull or lognormal distributions (exponential error distributions did not provide an adequate fit). For each model, $N = 54$, K = number of model parameters, LL = maximum log-likelihood estimate, AIC_c = Akaike's information criterion corrected for small sample size, Δ = the change in AIC_c between the model and the model with the lowest AIC_c, and w = Akaike weight (the likelihood of superiority over other models in the set). Only models with $w > 0.001$ are shown.

^aThe model with the lowest AIC_c.

Table 4. Model parameters for experimentally infected juvenile pink salmon, parameter likelihoods (importance of variables), and estimates with unconditional standard error (SE).

Parameter	Parameter likelihood	Parameter estimates	Unconditional SE
Intercept ^a	1.00	20.31	5.26
Adult female ^a	1.00	-11.17	2.43
Fork length	1.00	-0.16	0.09
Chamber	1.00	0.08	0.32
Adult female \times fork length ^a	1.00	0.20	0.04
Σ	1.00	-0.75	0.76
<i>E</i>	1.00	0.42	NA

Note: Parameters were calculated using w of both experimental swimming models in Table 3; other models, not shown, have $w = 0$ and thus do not influence parameter estimates. Values are rounded to the nearest 0.01.

^aParameter for which estimates ± 2 unconditional SEs do not overlap 0, and therefore are considered significant.

salmon and to those reported for other fish host-parasite systems; parasites reduce prolonged swimming ability in the European eel (*Anguilla anguilla*; Munderle et al. 2004), the cardinal fish (*Cheilodipterus quinquelineatus*; Östlund-Nilsson et al. 2005), and unfed Atlantic cod (*Gadus morhua*; Martinez et al. 2003, 2004).

A parasite-induced decline in swimming endurance suggests that lice infection is energetically costly to pink salmon. There are several possible reasons for this. For example, adult females feed on blood, and its removal can induce anaemia (Wagner and McKinley 2004). To obtain the blood meal, a louse punctures the skin (causing the motile scars), which likely increases the energy required to maintain osmotic homeostasis. Repairing this tissue damage and fighting off secondary infections from these wounds is an additional cost. Because lice infections cause an increase in energy requirements, they may lead to reduced swimming ability if fish cannot compensate for lost resources.

In contrast with the results for experimentally infected salmon, naturally infected salmon showed no diminution of endurance. There are at least two possible explanations for this inconsistency. First, males (preadult and adult) comprised 83% of the lice on these fish. *Lepeophtheirus salmonis* males are smaller than females and likely have lower energy requirements. Since they are seeking out mating opportunities, they may not feed as often or as much as females and thus may be less detrimental. Studies of the effects of sea lice on Atlantic (Dawson et al. 1999; Wagner et al. 2003; Wells et al. 2006) and Pacific (Morton and

Routledge 2005; Krkošek et al. 2006) salmonids found that the onset of pathogenicity began with the preadult stages, but did not look at gender-specific effects.

A second possibility is that the current level of motile lice on a host fish is not a good indicator of past lice intensity on that fish or the duration of that infection and thus is only weakly correlated with the host's current swimming ability. To account for this, tests were performed on fish that had a chalimus scar as evidence of prior infection; however, given the transient nature of motile lice and the fact that juvenile pink salmon are able to rid themselves of lice (Jones et al. 2007; M. Krkošek, University of Washington, School of Fishery and Aquatic Sciences, Seattle, WA 98195, USA, personal communication, 2007), this may have been insufficient to account for their infection history. It would thus be premature to conclude that there is no effect of the lice stages represented on the naturally infected salmon, but rather that snapshot tests such as these are insufficient to determine effects on swimming ability. Future studies should use experimental infections or track infections over time.

Reduced swimming endurance could have ecological consequences for salmon. Because juvenile salmon migrate in large shoals, a fish with reduced swimming endurance may be less able to compete for food, maintain its position within the shoal, or remain with the shoal at all, thereby losing the benefits that the shoal provides, such as protection from predators. Reduced swimming endurance may also increase predation susceptibility if it makes infected individuals less likely to escape from a courting predator, such as a coho

salmon (*Oncorhynchus kisutch*) or cutthroat trout (*Oncorhynchus clarkii*). The costs incurred from infections may also increase infected salmon susceptibility to predation if, in an attempt to mitigate these costs, they increase their foraging effort and thus their exposure to predators (see Mages 2008).

This study is the first to use swimming tests on wild juvenile pink salmon performed in a field lab in close proximity (<5 km) to collection sites and demonstrates that experimental infection is essential when testing for the effects of lice on swimming performance and perhaps other measures of condition. As suggested by the two control groups having very similar median swimming distances, fish were not placed under additional stress because of the experimental infection methodology, suggesting that the infection protocol used in this study is a valid method with which to assess the effects of motile lice on fish swimming performance.

Overall, the findings illustrate the need for further work using swimming tests, both on fish naturally infected with varying (and higher) numbers of adult lice and on those experimentally infected, to investigate the effects of other lice stages and infection durations. These tests should be run concurrently with physiological measurements to understand the mechanisms underlying any effects observed. Information gained from such studies will shed light on the impact of *L. salmonis* infections on wild juvenile pink salmon. This is the first study to show an effect of sea lice on juvenile salmon swimming endurance, and while direct mortality may be an important driver of population declines, reductions in swimming performance may contribute to the impact of sea lice on pink salmon populations.

Acknowledgements

We are thankful to the Kwakwaka'walw First Nations, in whose territorial waters this research took place. We thank K. Swoboda for his assistance in field collections and swimming fish and D. Stabel, M. Casselman, C. Curry, H. Ford, C. Lagasse, M. Krkošek, C. Losos, and B. Connors for their assistance in swim tunnel construction and collection and infections of fish. Thanks also go to A. Morton and S. Rogers at Salmon Coast Research Station for field facilities and support; A.P. Farrell for his assistance and comments on the swimming chamber design and swimming tests; and B. Connors, E. Juarez-Colunga, and I. Côté for statistical help. Research was funded by Natural Sciences and Engineering Research Council of Canada grant A6869 to LMD and private donors: D. Bradshaw, B. and J. Hager, R. North, B. Wheeler, and D. Jennings.

References

- Barber, I., Hoare, D., and Krause, J. 2000. Effects of parasites on fish behaviour: a review and evolutionary perspective. *Rev. Fish Biol. Fish.* **10**(2): 131–165. doi:10.1023/A:1016658224470.
- Beamish, F.W.H. (Editor). 1978. *Swimming capacity*. Academic Press, New York.
- Burnham, K.P., and Anderson, D.R. 2002. *Model selection and multi-model inference: a practical information-theoretic approach*. Springer-Verlag, New York.
- Butterworth, K.G., Cubitt, K.F., and McKinley, R.S. 2008. The prevalence, density and impact of *Lepeophtheirus salmonis* (Krøyer) infestation on juvenile pink salmon (*Oncorhynchus gorbuscha*) from the central coast of British Columbia, Canada. *Fish. Res.* **91**(1): 35–41. doi:10.1016/j.fishres.2007.11.018.
- Dawson, L.H.J., Pike, A.W., Houlihan, D.F., and McVicar, A.H. 1999. Changes in physiological parameters and feeding behaviour of Atlantic salmon *Salmo salar* infected with sea lice *Lepeophtheirus salmonis*. *Dis. Aquat. Organ.* **35**(2): 89–99. doi:10.3354/dao035089. PMID:10092971.
- Grimnes, A., and Jakobsen, P.J. 1996. The physiological effects of salmon lice infection on post-smolt of Atlantic salmon. *J. Fish Biol.* **48**(6): 1179–1194. doi:10.1111/j.1095-8649.1996.tb01813.x.
- Hammer, C. 1995. Fatigue and exercise tests with fish. *Comp. Biochem. Physiol. A*, **112**(1): 1–20. doi:10.1016/0300-9629(95)00060-K.
- Jones, S.R.M., and Nemeč, A. 2004. Pink salmon action plan: sea lice on juvenile salmon and on some nonsalmonid species in the Broughton Archipelago in 2003. Canadian Science Advisory Secretariat, Res. Doc. 2004/105. Available from http://www.dfo-mpo.gc.ca/csas/Csas/DocREC/2004/RES2004_105_e.pdf [accessed June 2005].
- Jones, S.R.M., Fast, M.D., Johnson, S.C., and Groman, D.B. 2007. Differential rejection of salmon lice by pink and chum salmon: disease consequences and expression of proinflammatory genes. *Dis. Aquat. Organ.* **75**(3): 229–238. doi:10.3354/dao075229. PMID:17629118.
- Krkošek, M., Morton, A., and Volpe, J.P. 2005. Nonlethal assessment of juvenile pink and chum salmon for parasitic sea lice infections and fish health. *Trans. Am. Fish. Soc.* **134**(3): 711–716. doi:10.1577/T04-133.1.
- Krkošek, M., Lewis, M.A., Morton, A., Frazer, L.N., and Volpe, J.P. 2006. Epizootics of wild fish induced by farm fish. *Proc. Natl. Acad. Sci. U.S.A.* **103**(42): 15506–15510. doi:10.1073/pnas.0603525103. PMID:17021017.
- Krkošek, M., Gottesfeld, A., Proctor, B., Rolston, D., Carr-Harris, C., and Lewis, M.A. 2007. Effects of host migration, diversity and aquaculture on sea lice threats to Pacific salmon populations. *Proc. Biol. Sci. R. Soc. Lond. B*, **274**: 3141–3149. doi:10.1098/rspb.2007.1122.
- Lima, S.L., and Dill, L.M. 1990. Behavioural decisions made under the risk of predation — a review and prospectus. *Can. J. Zool.* **68**(4): 619–640. doi:10.1139/z90-092.
- Mages, P.A. 2008. The effects of sea lice on juvenile pink salmon predation susceptibility. M.Sc. thesis, Department of Biology, Simon Fraser University, Burnaby, B.C.
- Martinez, M., Guderley, H., Dutil, J.D., Winger, P.D., He, P., and Walsh, S.J. 2003. Condition, prolonged swimming performance and muscle metabolic capacities of cod *Gadus morhua*. *J. Exp. Bot.* **206**: 503–511. doi:10.1242/jeb.00098.
- Martinez, M., Bedard, M., Dutil, J.D., and Guderley, H. 2004. Does condition of Atlantic cod (*Gadus morhua*) have a greater impact upon swimming performance at U_{crit} or sprint speeds? *J. Exp. Bot.* **207**: 2979–2990. doi:10.1242/jeb.01142.
- Morton, A., and Routledge, R. 2005. Mortality rates for juvenile pink *Oncorhynchus gorbuscha* and chum *O. keta* salmon infected with sea lice *Lepeophtheirus salmonis* in the Broughton Archipelago. *Alaska Fishery Research Bulletin*, **11**: 146–152. Available from <http://www.adfg.state.ak.us/pubs/afrb/afrbhome.php> [accessed May 2005].
- Morton, A., and Routledge, R. 2006. Fulton's condition factor: Is it a valid measure of sea lice impact on juvenile salmon? *N. Am. J. Fish. Manage.* **26**(1): 56–62. doi:10.1577/M05-068.1.
- Morton, A., and Routledge, R. 2008. Comment on Butterworth, Cubitt, and McKinley (2008). *Fish. Res.* **92**: 345–346. doi:2008.02.015. 10.1016/j.fishres.

- Morton, A., Routledge, R., Peet, C., and Ladwig, A. 2004. Sea lice (*Lepeophtheirus salmonis*) infection rates on juvenile pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon in the nearshore marine environment of British Columbia, Canada. *Can. J. Fish. Aquat. Sci.* **61**(2): 147–157. doi:10.1139/f04-016.
- Morton, A., Routledge, R.D., and Williams, R. 2005. Temporal patterns of sea louse infestation on wild Pacific salmon in relation to the fallowing of Atlantic salmon farms. *N. Am. J. Fish. Manage.* **25**(3): 811–821. doi:10.1577/M04-149.1.
- Münderle, M., Sures, B., and Taraschewski, H. 2004. Influence of *Anguillicola crassus* (Nematoda) and *Ichthyophthirius multifiliis* (Ciliophora) on swimming activity of European eel *Anguilla anguilla*. *Dis. Aquat. Organ.* **60**(2): 133–139. doi:10.3354/dao060133. PMID:15460857.
- Östlund-Nilsson, S., Curtis, L., Nilsson, G.E., and Grutter, A.S. 2005. Parasitic isopod *Anilocra apogonae*, a drag for the cardinal fish *Cheilodipterus quinquelineatus*. *Mar. Ecol. Prog. Ser.* **287**: 209–216. doi:10.3354/meps287209.
- Pike, A.W., and Wadsworth, S.L. 1999. Sealice on salmonids: their biology and control. *Adv. Parasitol.* **44**: 233–337. doi:10.1016/S0065-308X(08)60233-X. PMID:10563397.
- R Development Core Team. 2007. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Tierney, K., Casselman, M., Takeda, S., Farrell, T., and Kennedy, C. 2007. The relationship between cholinesterase inhibition and two types of swimming performance in chlorpyrifos-exposed coho salmon (*Oncorhynchus kisutch*). *Environ. Toxicol. Chem.* **26**(5): 998–1004. doi:10.1897/06-459R.1. PMID:17521148.
- Tully, O., and Nolan, D.T. 2002. A review of the population biology and host–parasite interactions of the sea louse *Lepeophtheirus salmonis* (Copepoda: Caligidae). *Parasitology*, **124**(7): S165–S182. doi:10.1017/S0031182002001889.
- Wagner, G.N., and McKinley, R.S. 2004. Anaemia and salmonid swimming performance: the potential effects of sub-lethal sea lice infection. *J. Fish Biol.* **64**(4): 1027–1038. doi:10.1111/j.1095-8649.2004.0368.x.
- Wagner, G.N., McKinley, R.S., Bjorn, P.A., and Finstad, B. 2003. Physiological impact of sea lice on swimming performance of Atlantic salmon. *J. Fish Biol.* **62**(5): 1000–1009. doi:10.1046/j.1095-8649.2003.00091.x.
- Wagner, G.N., McKinley, R.S., Bjorn, P.A., and Finstad, B. 2004. Short-term freshwater exposure benefits sea lice-infected Atlantic salmon. *J. Fish Biol.* **64**(6): 1593–1604. doi:10.1111/j.0022-1112.2004.00414.x.
- Wagner, G.N., Fast, M.D., and Johnson, S.C. 2008. Physiology and immunology of *Lepeophtheirus salmonis* infections of salmonids. *Trends Parasitol.* **24**(4): 176–183. doi:10.1016/j.pt.2007.12.010. PMID:18329341.
- Webster, S.J., Dill, L.M., and Butterworth, K. 2007. The effect of sea lice infestation on the salinity preference and energetic expenditure of juvenile pink salmon (*Oncorhynchus gorbuscha*). *Can. J. Fish. Aquat. Sci.* **64**(4): 672–680. doi:10.1139/F07-043.
- Wells, A., Grierson, C.E., MacKenzie, M., Russon, I.J., Reinardy, H., Middlemiss, C., Bjørn, P.A., Finstad, B., Bonga, S.E.W., Todd, C.D., and Hazon, N. 2006. Physiological effects of simultaneous, abrupt seawater entry and sea lice (*Lepeophtheirus salmonis*) infestation of wild, sea-run brown trout (*Salmo trutta*) smolts. *Can. J. Fish. Aquat. Sci.* **63**(12): 2809–2821. doi:10.1139/F06-160.