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REGULAR PAPER

Oust the louse: leaping behaviour removes sea lice from wild juvenile sockeye salmon *Oncorhynchus nerka*

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We conducted a manipulative field experiment to determine whether the leaping behaviour of wild juvenile sockeye salmon *Oncorhynchus nerka* dislodges ectoparasitic sea lice *Caligus clemensi* and *Lepeophtheirus salmonis* by comparing sea-lice abundances between *O. nerka* juveniles prevented from leaping and juveniles allowed to leap at a natural frequency. Juvenile *O. nerka* allowed to leap had consistently fewer sea lice after the experiment than fish that were prevented from leaping. Combined with past research, these results imply potential costs due to parasitism and indicate that the leaping behaviour of juvenile *O. nerka* does, in fact, dislodge sea lice.

KEYWORDS

aquaculture, host–parasite, leaping, louse, sub-lethal effects, trade-offs

1 | INTRODUCTION

Why do fish leap? This question has captivated biologists and fishers alike for decades, giving rise to a multitude of hypotheses. Gudger (1944) wrote that "fishes are given to leaping for many reasons: in fear or panic, to escape their enemies, to ascend waterfalls, to capture food and sometimes in sheer exuberance – in plain English, in fun or play." He was preceded (and followed) by anglers noting the remarkable leaping powers of fish and bringing hypotheses of their own, for example that the leaping of whiprays (family Dasyatidae) is intended to remove remoras (family Echeneidae) attached to their bodies (Anon., 1912). While the question is an old one and speculation is abundant, there remain relatively few studies testing hypotheses associated with the leaping behaviour of fish.

Adult Pacific salmon *Oncorhynchus* spp. (Suckley 1861) leap over obstacles during upstream migration to their spawning grounds (Brönmark *et al*., 2014; Lauritzen *et al*., 2010), but no one knows why they frequently leap as juveniles in the coastal marine environment. In contrast to the hydrodynamically efficient leaping that improves swimming performance in many marine mammals (Fish *et al*., 2008),

the leaping behaviour of juvenile *Oncorhynchus* spp. does not appear to serve this role and often results in slapping contact with the water upon entry (Video S1 in Supporting information). Although some fish leap to catch airborne prey (Day *et al*., 2016) or avoid predators (Eklöv and Persson, 1996), the diet of sockeye salmon *Oncorhynchus nerka* (Walbaum 1792) is composed almost exclusively of zooplankton in the water column (Price *et al*., 2013) and in experimental settings juvenile *Oncorhynchus* spp. typically scatter rather than leap in response to predation threats (Krkošek *et al*., 2011). Parasite dislodgement, on the other hand, is a plausible reason for juvenile *Oncorhynchus* spp. to leap, as higher rates of leaping have been observed to occur in association with sea louse infestation in both aquaculture (Furevik *et al*., 1993; Stone *et al*., 2002; Wootten & Smith, 1982) and experimental settings (Grimnes & Jakobsen, 1996; Webster *et al*. 2007). Leaping is probably an energetically expensive behaviour (Krohn & Boisclair, 1994), so the fish presumably derive some benefit from the six- (Grimnes & Jakobsen, 1996) to fourteen-fold (Webster *et al*., 2007) increase in leaping rate associated with sea louse infestation.

Sea lice have been the subject of extensive research due to their adverse effects on both farmed and wild salmonids (reviewed in Costello 2006, 2009). These effects include direct mortality (Wooten & Smith, 1982; Krkošek *et al*., 2006), but mounting evidence suggests that sub-lethal effects, such as effects on host susceptibility (Peacock *et al*., 2015), competitive ability (Godwin *et al*., 2015) and growth (Godwin *et al*., 2017), may play an important role in determining survival of wild juvenile *Oncorhynchus* spp. infected with sea lice. Two primary species of sea lice *Lepeophtheirus salmonis* and *Caligus clemensi* parasitize *Oncorhynchus* spp. in the marine waters of coastal British Columbia (BC; Beamish *et al*., 2005; Johnson & Albright, 1991a). *Lepeophtheirus salmonis* has high host specificity for salmonids whereas *C. clemensi* has a broader host range that includes other nearshore marine fishes such as three-spine stickleback *Gasterosteus aculeatus* l. 1758, Pacific herring *Clupea pallasii* Valenciennes 1847 and greenling (*Hexagrammos* spp. Tilesius 1810) (Jones *et al*., 2006a; Morton *et al*., 2008; Parker & Margolis, 1964). The life cycle of both lice species begins with two free-living nauplius stages, followed by initial host attachment at the copepodid stage and development through several chalimus stages (two for *L. salmonis* and four for *C. clemensi*) attached by a frontal filament to their host (Hamre *et al*., 2013; Kabata, 1972). *Lepeophtheirus salmonis* chalimi moult into pre-adults then adults, both of which are characterized by their ability to move on and among hosts except for a brief period of attachment during moulting (Pike & Wadsworth, 1999). Adult *C. clemensi* are also mobile, but there is some uncertainty as to whether they have a pre-adult stage and associated attachment during moulting (Ho & Lin, 2004; Kabata, 1972). Hereafter, we collectively refer to pre-adult and adult *L. salmonis* and adult *C. clemensi* as motiles. For further life cycle details of *L. salmonis* and *C. clemensi*, see Johnson and Albright (1991b) and Kabata (1972) respectively.

It has long been hypothesized that fish may leap to remove ectoparasites (Gudger, 1944), but this has never been tested experimentally. We used a manipulative field experiment to test the hypothesis that sea lice are dislodged by the leaping behaviour of wild juvenile *O. nerka*. Our study used juvenile *O. nerka* (post-smolts) migrating from the Fraser River through Johnstone Strait, BC, where *C. clemensi* are more prevalent than *L. salmonis* (Godwin *et al*. 2015; Price *et al*., 2011). We focused on pre-adult and adult stages of sea lice, that are not attached by a frontal filament, for three reasons: they can be identified in the field quickly with minimal stress to the fish; they impose the greatest cost on their host (Jakob *et al*., 2013; Wootten & Smith, 1982); and they seem more likely than the attached stages to become dislodged when their host leaps, especially in the case of *Caligus* spp. which are attached during the copepod and chalimus stages (Kabata, 1972) but transfer frequently between hosts as adults (Hogans & Trudeau, 1989; Oines *et al*., 2006; Saksida, 2015). To test whether leaping behaviour dislodges motile sea lice on juvenile *O. nerka*, we held wild-caught *O. nerka* in ocean enclosures where we allowed one group of fish to leap freely and prevented a second group from leaping.

2 | MATERIALS AND METHODS

2.1 | Fish collection and transport

We conducted our field experiment in the Broughton Archipelago, BC, making six collections of *O. nerka* post-smolts in Bauza Cove, Johnstone Strait, BC (50.5437° N; 126.8171° W) between May 31 and June 23, 2016 (Figure 1). Based on the timing of the collections and previous genetic analyses, it is very likely that most of the collected fish originated from the Fraser River (Price *et al*., 2011; Hunt, 2016).

We caught fish from a 6 m motorized vessel at distances of *c*. 5–60 m from shore, using a small purse seine designed for manual retrieval (bunt: 27 × 9 m with 13 mm mesh; tow: 46 × 9 m with 76 mm mesh). Temperature and salinity were measured at the collection site 1 m below the surface of the water for three of the six collections (equipment was unavailable for the other three; Table 1), although measurements taken at the collection site for other ongoing research projects fluctuated little during the collection period (Hunt, 2016). Captured fish were initially held alongside the vessel in a submerged portion of the seine bunt end, allowing fish to swim without contacting the net and minimizing louse dislodgement. Individual fish were transferred from the net as in Godwin *et al*. (2015) by capturing them using a seawater-filled 3.79 l plastic milk jug with the base removed and allowing them to swim out of the re-submerged milk jug after transfer. This method prevented direct contact with the fish to minimize sea louse dislodgement and the same technique was used for all subsequent transfers of individual fish. Fish were first transferred to 13.2 l transparent plastic aquaria [0.36 m length (L) × 0.21 m width (W) × 0.21 m height (H)] where they could be visually inspected to confirm species identification of the fish and to confirm the presence of at least one motile sea louse per fish. To expedite the fish handling procedure and minimize stress to the fish, at this point sea louse abundances on each fish were not assessed beyond confirming their presence. Fish confirmed to have at least one motile sea louse were transferred into an insulated 300 l fish tote (0.97 m L × 0.55 m W × 0.58 m H) half-filled with seawater. To minimize pre-experiment holding time, collection ceased after the first fish had been in the tote for approximately 1 h. For each collection, we retained between 64 and 95 juvenile *O. nerka* with motile lice (Table 1).

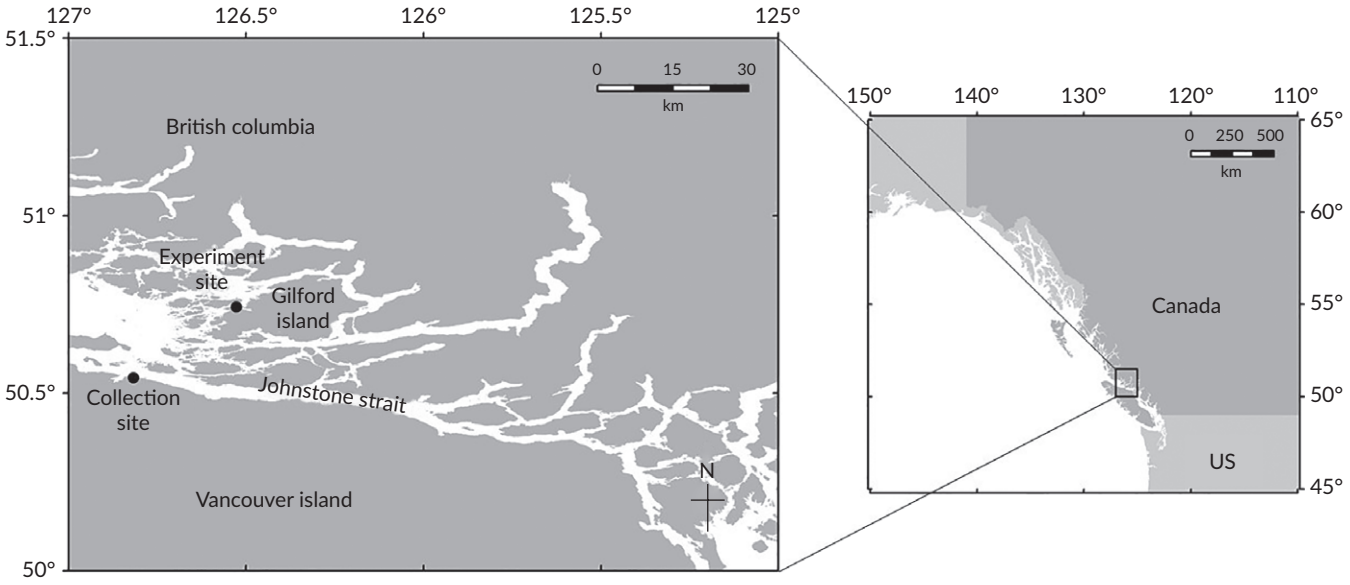

FIGURE 1 The study area, collection site, and experiment site for the *Oncorhynchus nerka* leaping experiment. All collections were made at Bauza Cove, BC, off the north-eastern coast of Vancouver Island, and the trials were conducted at a floating research facility off Gilford Island

We transported juvenile *O. nerka* by boat to Cramer Passage, BC (Figure 1; 50.74279° N; 126.52797° W), using ice packs and battery-powered aquarium bubblers in the insulated tote to maintain appropriate temperature and oxygenation during the 1 h journey. During transport, fish were monitored for behaviours indicating stress, including gasps at the surface, fins clamped against their bodies and unusual movement (Martins *et al*., 2012). All fish from the six collections survived transport and no characteristic stress behaviours were observed. Detached lice were sought but not observed in the aquaria or in the insulated tote before or during transport.

For each of the six collections, we transferred fish to one of four flow-through net pen enclosures [4.4 m L × 3.2 m W × 2.3 m depth (D), with 8 mm knotless mesh] at a research facility composed of multiple floating wooden docks in a location sheltered from wave action. Individual fish were collected haphazardly from the transport tote (capturing the first fish that swam into the milk jug) and transferred sequentially to one of the four enclosures (*i.e.* first fish to enclosure 1, second to enclosure 2, *etc*. and then starting again with the fifth fish in enclosure 1), thus avoiding one enclosure receiving all of the first or last fish. The four enclosures housed two treatments (leaping prevented) and two control (leaping allowed) trials that we describe below (Figure 2). We used a random number generator to select which two enclosures would house the covered treatments and repeated this randomisation for each collection to prevent any bias in pre-trial louse abundance that might have resulted from covering the same enclosures for each collection. In total, we had six collections, each of which consisted of two treatment and two control trials, resulting in 24 trials overall (Table S1 in Supporting information).

2.2 | Leaping experiment

For each of the six collections, we covered the two treatment enclosures to prevent leaping while leaving the two control enclosures uncovered, allowing the fish to leap freely. The covering consisted of pieces of netting (4.4 m L × 3.2 m W, with 3 mm knotless mesh) that were carefully secured across the top of the enclosures, approximately 10 cm below the surface of the water (Figure 2). The surface netting was raised on two sides of the enclosure, creating an area (approximately 30 cm wide) for the fish to surface for air to fill their swim bladder, while still not being able to leap (Figure 2). We began each trial once the surface netting was secured over the covered enclosure and the four concurrent trials for each collection lasted for *c.* 3 days.

TABLE 1 Collection data for juvenile *Oncorhynchus nerka* used in the leaping experiment

Collection	Date	Temperature (°C)	Salinity	Number of *O. nerka* transported	Covered enclosures		Uncovered enclosures	
					Number of fish	Number of fish	Number of fish	Number of fish
1	May 31, 2016	–	–	95	23	22	23	22
2	June 5, 2016	–	–	91	19	24	21	22
3	June 9, 2016	9.9	31.8	88	22	23	21	22
4	June 13, 2016	–	–	75	18	18	18	18
5	June 18, 2016	10.3	31.8	66	17	16	17	16
6	June 23, 2016	10	30.9	79	19	19	19	19

Note. Temperature and salinity measurements were taken 1 m below the surface of the water for three of the six collections.

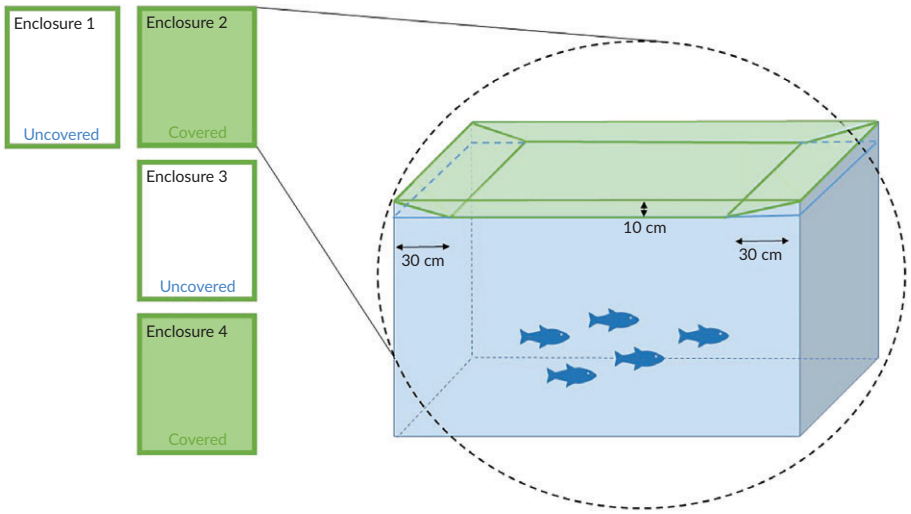

FIGURE 2 An example set-up of the *Oncorhynchus nerka* leaping experiment for one collection (four trials). Four flow-through net pen enclosures were housed at a floating research facility in the orientation shown. The surface netting for the covered enclosures was secured approximately 10 cm below the water, and was raised at two ends of the enclosure to create 30 cm gaps in which the fish could surface for air for their swim bladders

At the end of each trial, after retracting any coverings, each net-pen enclosure was pulled up to form a shallow pool and fish were carefully captured using the aforementioned milk jug method. For each set of trials, we used a random number generator to determine the order in which we pulled enclosures. Fish were transferred to individual 532 mL sterile sample bags (Whirl-Pak Write-On Bags; Nasco; www.enasco.com) and euthanized with 240 mg l^{-1} MS-222. Experienced individuals assessed the post-trial louse abundance of each fish using 16× (where × refers to the magnification) hand lenses to identify louse life stage and sex (for pre-adult and adult *L. salmonis* but not *C. clemensi*) as in Krkošek *et al.* (2005). We also measured the fork length (L_F) and body maximum dorso-ventral depth (D_{DV})of each fish.

2.3 | Behavioural observations

Throughout the 3 day trials, we conducted three 40 min observations each day to address two potential concerns: first, that the fish in the covered enclosures might be brushing against the surface covering, which could dislodge lice; second, that the fish in the uncovered enclosures might not leap at a sufficient rate to test for an effect of leaping on louse abundance. Observation periods occurred in the morning (*c.* 1 h after sunrise), midday (*c.* halfway between dawn and dusk) and evening (*c.* 2 h before sunset), during which an observer monitored one covered enclosure and one adjacent uncovered enclosure from a position with a clear view of each enclosure. Observers recorded the number of leaps in the uncovered enclosure as well as the number of contacts of any part of a fish body with the surface netting of the covered enclosure. We characterized leaps as surface behaviours in which most or all of the body left the water with distinct entry and exit points.

Fish were fed micropellet salmon feed (micro #1; EWOS; www.ewos.com) twice each day. Feeding took place midway through the dawn and evening observation periods so that any changes in leaping frequency due to feeding could be observed and to ensure that feeding did not induce fish contact with the surface netting. The fish were fed to satiation with approximately 2.1 g per fish day^{-1}, depositing the food using the same method and in the same corner of each enclosure. Salinity and temperature measurements were recorded at 0 and 1 m depths after most dawn observation periods, depending on equipment availability.

2.4 | Statistical analysis

As is often the case with count data (Manté *et al.*, 2016; Sellers *et al.*, 2017), the post-trial louse abundance data from the leaping experiment were over-dispersed (Figure 3), demonstrating greater than expected variation relative to a Poisson distribution (mean motile abundance = 1.87, variance = 2.46).

To describe the post-trial louse abundance on juvenile *O. nerka* from the experiment while accounting for the non-normal distribution of those data, we used hierarchical bootstrapping to estimate the 95% C.I. for the average abundances across the entire experiment of *C. clemensi* and *L. salmonis* motiles and chalimus-stage lice (Dicicco & Efron, 1996). We used 10,000 bootstrap samples, first resampling from the 24 actual trials and then resampling from individuals within each of those trials. We also estimated the 95% C.I. for per-trial average louse abundances via standard bootstrapping.

To determine whether juvenile *O. nerka* leaping behaviour was an important predictor of post-trial motile louse abundance, we used generalized linear mixed-effects models (GLMM) to accommodate the hierarchical structure of our experiment, with a negative binomial error structure allowing for over-dispersed counts. We built a set of five candidate models around our a priori hypothesis that fish allowed to leap (*i.e.* fish in uncovered enclosures) would have lower post-trial motile abundances due to louse dislodgement caused by leaping. Our models included combinations of two fixed effects and their interaction: treatment (covered or uncovered) and enclosure (Table 2). We included enclosure to test whether the position of the experimental enclosure (one of four in each collection) influenced post-trial motile abundance due to factors such as variation in water movement,

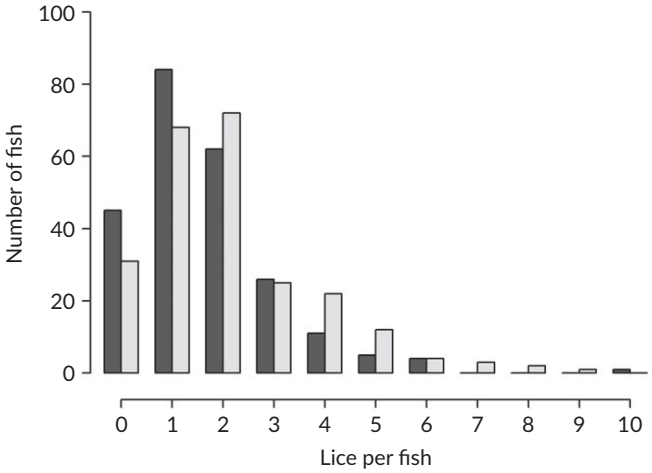

FIGURE 3 Combined total frequency distributions of post-trial abundance of motile sea lice (*L. salmonis* and *C. clemensi*) on juvenile *Oncorhynchus nerka* held either in uncovered pens that allowed leaping or covered nets that prevented leaping (■) Uncovered (Leaping), and (□) Covered (No leaping)

differences in the movement of motile lice into or out of the enclosures, or disturbance by researchers during the trial. We did not include data from the behavioural observations as predictors in the models because only two of the four enclosures were observed for each collection.

All our models included a random intercept term to account for repeated trials within each collection and models that included treatment as a fixed effect also included an associated random term (a random slope) that again varied by collection.

During the chalimus life stages of both *C. clemensi* and *L. salmonis*, lice are attached by a frontal filament to their host and unable to detach and re-attach (Kabata, 1972; Johnson & Albright, 1991b). Assuming that attached lice are unlikely to be dislodged by leaping, the post-trial abundance of lice at this life stage can serve as a natural control for our experiment, with the expectation that their abundance would not differ between treatment groups after the experiment. To test whether the post-trial chalimus louse abundances differed between treatment groups, we fit the same set of five candidate models with chalimus abundance per fish as the response variable (Tables S2 and S3 in Supporting information). To prevent the potential influence of differential attachment between covered and uncovered enclosures of copepod lice that might moult into the chalimus stage within the 3 days trial period, we restricted the analysis to the final two of four *C. clemensi* chalimus stages (Kabata, 1972) and final one of two *L. salmonis* chalimus stages (Hamre *et al*., 2013), collectively referred to as large chalimus. We included the same random effects and again used a negative-binomial error structure to allow for over-dispersion (mean motile abundance = 2.48, variance = 5.94).

For both of the analyses, to determine which of our five models best explained motile or chalimus abundance, we conducted model selection using Akaike's information criterion (AIC; Akaike, 1998) as a measure of model parsimony. All the statistical analyses were performed in R 3.2.3 (www.r-project.org) using the glmmADMB package (Fournier *et al*., 2012).

TABLE 2 Statistics from generalized mixed-effects models fit to post-trial motile louse abundance from the *Oncorhynchus nerka* leaping experiment

Rank	Model	ΔAIC	w_i	Cumulative w_i
1	Treatment	0	0.740	0.740
2	Treatment + enclosure	2.54	0.208	0.948
3	Treatment × enclosure	6.64	0.027	0.975
4	Intercept only	7.68	0.016	0.991
5	Enclosure	8.82	0.009	1

Note. Models contained combinations of two fixed effects: Whether fish were in a covered or uncovered enclosure (treatment) and the enclosure in which the fish were held (enclosure). All models included a random effect on the intercept for collection number, and models including treatment as a fixed effect included an associated random effect for collection number. Models with interaction terms include all lower-order effects, and all models include an intercept term.
ΔAIC values are the differences in AIC from the top model; *w*: the Akaike model weight.

3 | RESULTS

On average, 9.71 ± 7.45 (mean ± S.D.) leaps were observed in an uncovered enclosure 40^{-1} min observation period. Only nine contacts with the surface netting were observed over the 38 observation periods (approximately 25 h in total). There was a higher frequency of leaps after feeding than before (paired *t*-test, $t = 2.2677$, d.f. = 95, $p < 0.05$). Fish L_F ranged from 8.3 to 14.1 cm with a mean of 10.01 ± 0.66 cm (Table S1 in Supporting information) and the mean D_{DV} = 17.38 ± 0.20 cm. Fork length did not differ significantly between covered and uncovered trials (two-sample *t*-test, $t = 0.0877$, d.f. = 469, $p > 0.05$), nor did D_{DV} (two-sample *t*-test, $t = -0.8734$, d.f. = 469, $p > 0.05$). Neither water temperature (two-sample *t*-test, $t = 0.0513$, d.f. = 50, $p > 0.05$) nor salinity (two-sample *t*-test, $t = 0.1040$, d.f. = 50, $p > 0.05$) differed significantly between covered and uncovered enclosures (Table S1 in Supporting information).

After the leaping experiment, the overall mean abundance of motile *C. clemensi* was 1.79 (bootstrapped 95% C.I. = 1.55–2.05), with 83.1% of fish having at least one *C. clemensi* motile. The maximum number of motile *C. clemensi* observed on a fish was 10 and 96% of the motile lice recorded on fish were *C. clemensi*. The mean abundance of motile *L. salmonis* was 0.08 (bootstrapped 95% C.I. = 0.05–0.12), with 6.9% of the fish having at least one motile *L. salmonis* and a maximum of two observed on a single fish. The mean abundance of *C. clemensi* and *L. salmonis* large chalimii was 2.48 (bootstrapped 95% C.I. = 1.81–3.11) with 77.4% of fish having at least one large chalimus louse.

The post-trial motile louse abundance on a fish (Figure 3 and Table S2 in Supporting information) was best explained by whether the fish was in a covered or uncovered enclosure. The most parsimonious model, which included treatment as the only fixed effect, accounted for 74% of model support, based on AIC weights (Table 2). Although there was no clear best-fit model based on AIC-difference guidelines (Burnham *et al*., 2011), all three top models included the treatment term and cumulatively accounted for 97.5% of model support.

Our treatment-only model predicted that fish in the uncovered enclosures (*i.e.* those allowed to leap) had fewer motile lice after the experiment (mean = 1.64, 95% C.I. = 1.32–2.03) than those in the covered enclosures (Figure 4; mean = 2.10, 95% C.I. = 1.82–2.45). There was no significant correlation between the number of leaps recorded over a 3 day trial and the difference in mean motile abundance between covered and uncovered enclosures (Pearson's $r = 0.58$, $p > 0.05$).

The post-trial abundance of large chalimus (attached) sea lice on fish did not differ between trials where we allowed fish to leap and those where we prevented fish from leaping (Table S2 in Supporting information). The abundance of this life stage was best explained by the intercept-only model, which accounted for 74% of the model support and had an AIC score 3.68 units lower than the next best model (Table S3 in Supporting information).

4 | DISCUSSION

Wild juvenile salmonids leap more frequently when infected with sea lice (Grimnes & Jakobsen, 1996; Webster *et al.* 2007) and our results indicate that the leaping behaviour of juvenile *O. nerka* dislodges motile stages of these ectoparasites. The vast majority of the sea lice infecting *O. nerka* in our study were *C. clemensi* (just 4% of motiles were *L. salmonis*) which is consistent with the emerging consensus that *C. clemensi* are the dominant louse species in the Inside Passage of BC (Godwin *et al.*, 2015, 2017; Price *et al.* 2011; Hunt, 2016) despite the current focus of sea louse research and management on *L. salmonis*.

Preferential attachment of motile lice from outside the pens is unlikely to have generated the post-trial differences in motile abundance. While it could be argued that the surface netting of the covered enclosures induced a stress response in the fish due to reduced light levels, evidence for light levels triggering stress responses in fish is equivocal (Biswas *et al.*, 2006; Leonardi & Klempau, 2003) as is the evidence for the effect of stress on louse susceptibility (Haond *et al.*, 2003; Johnson & Albright, 1992). Similarly, there is mixed evidence for the effect of light intensity on the attachment and host-finding behaviour of sea lice. Experiments on *L. salmonis* have shown no light effect (Browman *et al.*, 2004; Hamoutene *et al.*, 2016) as well as both higher (Genna *et al.*, 2005) and lower copepodid settlement (Hevrøy *et al.*, 2003; Mordue & Birkett, 2009) under low light conditions. We could find no studies testing this with *C. clemensi* specifically although some studies on *L. salmonis* in Pacific Canada conduct infestation trials under dimmed-light conditions (Jones *et al.*, 2006b). There was no difference in salinity, temperature, or fish L_F between treatments and it is therefore unlikely that any of these factors drove differences in post-trial motile louse abundance. As predicted, the abundance of large chalimus lice (*C. clemensi* and *L. salmonis*) did not differ between covered and uncovered enclosures, supporting the assumption of equivalent pre-trial louse distributions on fish and the conclusion that the observed difference in motile louse abundance was due to leaping by the fish. Finally, *L. salmonis* (Pike & Wadsworth, 1999) and possibly *C. clemensi* motiles (Kabata, 1972; Ho & Lin, 2004) experience brief periods of attachment between the pre-adult and adult life stages, during which dislodgment by leaping may be less likely. This may have resulted in a conservative estimate of the dislodging effect of leaping but would not influence the relative difference between treatments as there is no reason to suggest that the proportion of moulting motiles would differ between covered and uncovered enclosures.

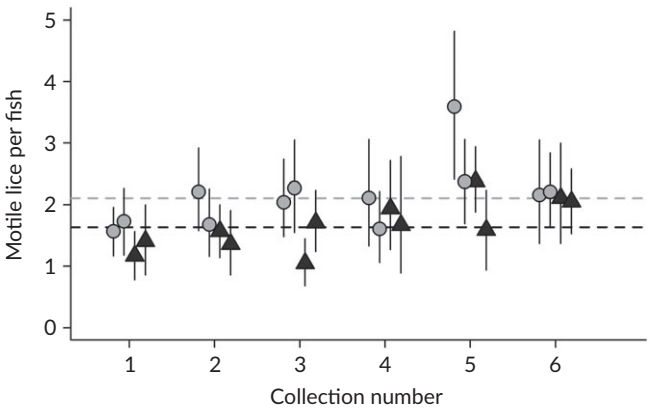

FIGURE 4 Mean (±95% C.I.) post-trial abundances of motile sea lice (*L. salmonis* and *C. clemensi*) on juvenile *Oncorhynchus nerka* in each of 24 trials with uncovered pens that allowed leaping or covered nets that prevented leaping. - - - (covered, 1.64 ± 95% C.I. Of 1.32–2.03) and - - - (uncovered, 2.10 ± 95% C.I. Of 1.82–2.45) estimated mean from the top model (Table 2) (▲) Uncovered (Leaping), and (●) Covered (No leaping)

The energetic costs associated with the leaping behaviour of juvenile *O. nerka* may be substantial. If the leaping frequency from the observation periods continued throughout the entire 3 day trial, then *O. nerka* hosts would have to dislodge approximately 0.018 lice per leap to generate the observed differences in post-trial motile abundance. This success rate of less than 2% would imply considerable energy expenditure for a fish to rid itself of even a single louse. The specific energetic costs associated with the leaping of juvenile *O. nerka* are unknown and represent an avenue for further study. Currently, only the metabolic costs of steady swimming have been measured for *O. nerka* (Brett, 1965), although spontaneous swimming (characterized by marked changes in speed and direction) has been associated with high energetic costs in juvenile brook trout *Salvelinus fontinalis* (Mitchill 1814) (Krohn & Boisclair, 1994) and leaping may incur similar energetic costs to spontaneous swimming. These costs may be particularly demanding for juvenile *O. nerka* migrating through prey-limited regions like Johnstone Strait (Mckinnell *et al.*, 2014). Furthermore, because our behavioural observations suggest that leaping frequency of juvenile *O. nerka* is associated with feeding, leaping behaviour may be reduced in prey-limited regions like Johnstone Strait, leading to higher louse burdens. While leaping may require substantial energy, these costs may be offset by multiple potential benefits of parasite removal.

By definition, parasites harm their hosts and behavioural changes of infected hosts that remove parasites can relieve this impairment (Hart, 1990). Several behavioural adaptations of hosts avoiding infection by pathogens and parasites have been demonstrated, including individual evasion behaviours and population migration patterns (Mikheev & Pasternak, 2006). For example, specific shoaling patterns of juvenile sticklebacks *Gasterosteus* spp. L. 1758 minimize the risk of

infestation by a crustacean ectoparasite, *Argulus canadensis* (Poulin & Fitzgerald, 1989) and rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) experience lower rates of eye-fluke establishment by avoiding an infestation source (Karvonen *et al*., 2004). There are many examples of behavioural patterns of terrestrial hosts that remove parasites once infested (Cotgreave & Clayton, 1994; Tanaka & Takefushi, 1993) and the leaping behaviour of juvenile *O. nerka* may be a marine example, akin to the reactive fly-repelling behaviour of terrestrial herbivores (e.g.,twitching, stamping, *etc*), which is an effective parasite removal strategy (Hillerton *et al*., 1986). The post-infestation behavioural removal of lice complements recent work showing that juvenile *Salmo salar* L. 1758 behaviour (including leaping) is associated with a 26–31% decrease in copepodid infestation (Bui *et al*., 2018), underlining the important role host behaviour plays both pre and post-infestation (Bui *et al*., 2017; Daly & Johnson, 2011). It is beyond the scope of this study to assess whether *O. nerka* leaping at the juvenile life stage is an evolutionary adaptation to ectoparasites, but if it were, the benefits of leaping would have to outweigh the costs.

The trade-offs underlying the leaping behaviour of juvenile salmonids imply that the costs of leaping yield a benefit of alleviating juvenile salmonids from the costs of sea-lice infestation. For example, heavy sea-louse infestation (primarily by *C. clemensi*) is correlated with reduced growth (Godwin *et al*., 2017) and competitive foraging ability (Godwin *et al*., 2015) in *O. nerka* and with decreased survival in other *Oncorhynchus* spp. (Ford & Myers, 2008; Krkošek & Hilborn, 2011; Morton & Routledge, 2005). Sea-lice removal may release hosts from future energetic costs associated with impaired swimming performance due to infestation (Mages & Dill 2010; Nendick *et al*. 2011; Wagner *et al*. 2003). In exchange for those benefits of dislodging lice, juvenile salmonids pay the energetic cost of leaping as well as non-energetic costs such as increased predation risk from spending more time at the water's surface (Collis *et al*., 2001). Accordingly, the costs associated with leaping may represent another example of a sub-lethal effect of sea lice (primarily *C. clemensi*) on *Oncorhynchus* spp. When combined with other studies showing that sea-lice infestation is associated with increased leaping frequency of juvenile *Oncorhynchus* spp. (Grimnes & Jakobsen, 1996; Webster *et al*., 2007), our results suggest that fish may use behavioural plasticity to balance costs and benefits of leaping and parasite dislodgement.

The question why do fish leap has stimulated (and continues to stimulate) hypotheses, many of which have yet to be tested. The common leaping behaviour of juvenile *Oncorhynchus* spp. may be driven by multiple factors, but the leaping experiment presented in this study indicates that one motivation may be to remove ectoparasites such as sea lice.

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Authors' contributions

The study was conceptualized and designed by all authors. Fieldwork and data analysis were conducted by E.M.A, A.W.B, S.C.G and all authors contributed to writing and revising the manuscript.

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REFERENCES

Akaike, H. (1998). Information theory and an extension of the maximum likelihood principle. In E. Parzen, K. Tanabe, & G. Kitagawa (Eds.), *Selected papers of Hirotugu Akaike* (pp. 199–213). New York, NY: Springer New York. https://doi.org/10.1007/978-1-4612-1694-0_15

Anon. (1912). *Forest and Stream*, *79*, 446–447. Retrieved from www.babel.hathitrust.org/cgi/pt?id=mdp.39015079983055;view=1up;seq=455

Beamish, R. J., Neville, C. M., Sweeting, R. M., & Ambers, N. (2005). Sea lice on adult Pacific salmon in the coastal waters of Central British Columbia, Canada. *Fisheries Research*, *76*, 198–208. https://doi.org/10.1016/j.fishres.2005.06.007

Biswas, A. K., Seoka, M., & Tanaka, Y. (2006). Effect of photoperiod manipulation on the growth performance and stress response of juvenile red sea bream (*Pagrus major*). *Aquaculture*, *258*, 350–356. https://doi.org/10.1016/j.aquaculture.2006.03.048

Brett, J. R. (1965). The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). *Journal of the Fisheries Research Board of Canada*, *22*, 1491–1501. https://doi.org/10.1139/f65-128

Brönmark, C., Hulthen, K., Nilsson, P. A., Skov, C., Hansson, L. A., Brodersen, J., & Chapman, B. B. (2014). There and back again: Migration in freshwater fishes. *Canadian Journal of Zoology*, *92*, 467–479. https://doi.org/10.1139/cjz-2012-0277

Browman, H. I., Boxaspen, K., & Kuhn, P. (2004). The effect of light on the settlement of the salmon louse, *Lepeophtheirus salmonis*, on Atlantic salmon, *Salmo salar* L. *Journal of Fish Diseases*, *27*, 701–708. https://doi.org/10.1111/j.1365-2761.2004.00592.x

Bui, S., Oppedal, F., Samsing, F., & Dempster, T. (2018). Behaviour in Atlantic salmon confers protection against an ectoparasite. *Journal of Zoology*, *304*, 1–8. https://doi.org/10.1111/jzo.12498

Bui, S., Oppedal, F., Sievers, M., & Dempster, T. (2017). Behaviour in the toolbox to outsmart parasites and improve fish welfare in aquaculture. *Reviews in Aquaculture*. https://doi.org/10.1111/raq.12232

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: Some background, observations and comparisons. *Behavioural Ecology & Sociobiology*, *65*, 23–35.

Collis, K., Roby, D. D., Craig, D. P., Ryan, B. A., & Ledgerwood, R. D. (2001). Colonial waterbird predation on juvenile salmonids tagged with passive integrated transponders in the Columbia river estuary: Vulnerability of different salmonid species, stocks and rearing types. *Transactions of the American Fisheries Society*, *130*, 385–396. https://doi.org/10.1577/1548-8659(2001)130<0385

Costello, M. J. (2006). Ecology of sea lice parasitic on farmed and wild fish. *Trends in Parasitology*, *22*, 475–483. https://doi.org/10.1016/j.pt.2006.08.006

Costello, M. J. (2009). How sea lice from salmon farms may cause wild salmonid declines in Europe and North America and be a threat to fishes elsewhere. *Proceedings of the Royal Society B*, *276*, 3385–3394. https://doi.org/10.1098/rspb.2009.0771

Cotgreave, P., & Clayton, D. H. (1994). Comparative analysis of time spent grooming by birds in relation to parasite load. *Behaviour*, *131*, 171–187.

Day, R. D., Mueller, F., Carseldine, L., Meyers-Cherry, N., & Tibbetts, I. R. (2016). Ballistic Beloniformes attacking through Snell's window. *Journal of Fish Biology*, *88*, 727–734. https://doi.org/10.1111/jfb.12799

Daly, E. W., & Johnson, P. T. J. (2011). Beyond immunity: Quantifying the effects of host anti-parasite behavior on parasite transmission. *Oecologia*, *165*, 1043–1050. https://doi.org/10.1007/s00442-010-1778-y

Diciccio, T. J., & Efron, B. (1996). Bootstrap confidence intervals. *Statistical Science*, *11*, 189–228. https://doi.org/10.1098/rsbl.2008.0276

Eklöv, P., & Persson, L. (1996). The response of prey to the risk of predation: Proximate cues for refuging juvenile fish. *Animal Behaviour*, *51*, 105–115.

Fish, F. E., Howle, L. E., & Murray, M. M. (2008). Hydrodynamic flow control in marine mammals. *Integrative and Comparative Biology*, *48*, 788–800. https://doi.org/10.1093/icb/icn029

Ford, J. S., & Myers, R. A. (2008). A global assessment of salmon aquaculture impacts on wild salmonids. *PLoS Biology*, *6*, 0411–0417. https://doi.org/10.1371/journal.pbio.0060033

Fournier, D. A., Skaug, H. J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M. N., … Sibert, J. (2012). AD model builder: Using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software*, *27*, 233–249.

Furevik, D. M., Bjordal, Å., Huse, I., & Fernö, A. (1993). Surface activity of Atlantic salmon (*Salmo salar*) in net pens. *Aquaculture*, *110*, 119–128. https://doi.org/10.1016/0044-8486(93)90266-2

Genna, R. L., Mordue, W., Pike, A. W., & (Luntz) Mordue, A. J. (2005). Light intensity, salinity and host velocity influence presettlement intensity and distribution on hosts by copepodids of sea lice, *Lepeophtheirus salmonis*. *Canadian Journal of Fisheries and Aquatic Sciences*, *62*, 2675–2682. https://doi.org/10.1139/f05-163

Godwin, S. C., Dill, L. M., Reynolds, J. D., & Krkošek, M. (2015). Sea lice, sockeye salmon and foraging competition: Lousy fish are lousy competitors. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*, 1113–1120. https://doi.org/10.1139/cjfas-2014-0284

Godwin, S. C., Dill, L. M., Krkošek, M., Price, M. H. H., & Reynolds, J. D. (2017). Reduced growth in wild juvenile sockeye salmon infected with sea lice. *Journal of Fish Biology*, *91*, 41–57. https://doi.org/10.1111/jfb.13325

Grimnes, A., & Jakobsen, P. J. (1996). The physiological effects of salmon lice infection on post-smolt of Atlantic salmon. *Journal of Fish Biology*, *48*, 1179–1194.

Gudger, E. W. (1944). Fishes that play "leapfrog.". *The American Naturalist*, *78*, 451–463.

Hamoutene, D., Mitchell, J. S., Murray, H. M., Eaves, A., Marshall, K., Belley, R., & George, S. (2016). The effect of light regimen on settlement patterns of sea lice, *Lepeophtheirus salmonis*, on Atlantic salmon, *Salmo salar*, post-smolts while taking into account fish size and fin erosion in a static tank system. *Aquaculture*, *465*, 1–6. https://doi.org/10.1016/j.aquaculture.2016.08.026

Hamre, L., Eichner, C., Caipang, C. M. A., Dalvin, S. T., Bron, J. E., Nilsen, F., … Skern-Mauritzen, R. (2013). The salmon louse *Lepeophtheirus salmonis* (Copepoda: Caligidae) life cycle has only two chalimus stages. *PLoS One*, *8*, 1–9. https://doi.org/10.1371/journal.pone.0073539

Haond, C., Nolan, D. T., Ruane, N. M., Rotllant, J., & Wendelaar Bonga, S. E. (2003). Cortisol influences the host-parasite interaction between the rainbow trout (*Oncorhynchus mykiss*) and the crustacean ectoparasite (*Argulus japonicus*). (2003). *Parasitology*, *127*, 551–560. https://doi.org/10.1017/S0031182003004116

Hart, B. L. (1990). Behavioral adaptations to pathogens and parasites: Five strategies. *Neuroscience & Biobehavioral Reviews*, *14*, 273–294.

Hevrøy, E. M., Boxaspen, K., & Oppedal, F. (2003). The effect of artificial light treatment and depth on the infestation of the sea louse (*Lepeophtheirus salmonis*) on Atlantic salmon (*Salmo salar*) culture. *Aquaculture*, *220*, 1–14. https://doi.org/10.1016/S0044-8486(02)00189-8

Hillerton, J. E., Morant, S. V., & Harris, J. A. (1986). Control of Muscidae on cattle by flucythrinate ear-tags, the behaviour of these flies on cattle and the effects on fly-dislodging behaviour. *Entomologia Experimentalis et Applicata*, *41*, 213–218. https://doi.org/10.1111/j.1570-7458.1986.tb00531.x

Ho, J.-S., & Lin, C.-L. (2004). *Sea lice of Taiwan: Copepoda, Siphonostomatoida, Caligidae*. Taiwan: Sueichan Press.

Hogans, W. E., & Trudeau, D. J. (1989). *Caligus elongatus* (Copepoda: Caligoida) from Atlantic salmon *(Salmo salar)* cultured in marine waters of the lower Bay of Fundy. *Canadian Journal of Zoology*, *67*, 1080–1082.

Jakob, E., Sweeten, T., Bennett, W., & Jones, S. R. M. (2013). Development of the salmon louse (*Lepeophtheirus salmonis*) and its effects on juvenile sockeye salmon (*Oncorhynchus nerka*). *Diseases of Aquatic Organisms*, *106*, 217–227. https://doi.org/10.3354/dao02642

Johnson, S. C., & Albright, L. J. (1991a). The developmental stages of *Lepeophtheirus salmonis* (Krøyer, 1837) (Copepoda: Caligidae). *Canadian Journal of Zoology*, *69*, 929–950. https://doi.org/10.1139/z91-138

Johnson, S. C., & Albright, L. J. (1991b). Development, growth and survival of *Lepeophtheirus salmonis* (Copepoda: Caligidae) under laboratory conditions. *Journal of the Marine Biological Association of the United Kingdom*, *71*, 425–436.

Johnson, S. C., & Albright, L. J. (1992). Effects of cortisol implants on the susceptibility and the histopathology of the responses of naïve coho salmon *Oncorhynchus kisutch* to experimental infection with *Lepeophtheirus salmonis* (Copepoda: Caligidae). *Diseases of Aquatic Organisms*, *14*, 195–205. https://doi.org/10.3354/dao014195

Jones, S. R., Prosperi-Porta, G., Kim, E., Callow, P., & Hargreaves, N. B. (2006a). The occurrence of *Lepeophtheirus salmonis* and *Caligus clemensi* (Copepoda: Caligidae) on three-spine stickleback *Gasterosteus aculeatus* in coastal British Columbia. *Journal of Parasitology*, *92*, 473–480.

Jones, S., Kim, E., & Dawe, S. (2006b). Experimental infections with *Lepeophtheirus salmonis* (Kroyer) on threespine sticklebacks, *Gasterosteus aculeatus* L. and juvenile Pacific salmon, *Oncorhynchus* spp. *Journal of Fish Diseases*, *29*, 489–495.

Kabata, Z. (1972). Developmental stages of *Caligus clemensi* (Copepoda: Caligidae). *Journal of the Fisheries Research Board of Canada*, *29*, 1571–1593.

Karvonen, A., Seppalla, O., & Valtonen, E. T. (2004). Parasite resistance and avoidance behaviour in preventing eye fluke infections in fish. *Parasitology*, *129*, 159–164. https://doi.org/10.1017/S0031182004005505

Krkošek, M., Morton, A., & Volpe, J. P. (2005). Nonlethal assessment of juvenile pink and chum salmon for parasitic sea lice infections and fish health. *Transactions of the American Fisheries Society*, *134*, 711–716. https://doi.org/10.1577/T04-133.1

Krkošek, M., Lewis, M. A., Morton, A., Frazer, L. N., & Volpe, J. P. (2006). Epizootics of wild fish induced by farm fish. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 15506–15510. https://doi.org/10.1073/pnas.0603525103

Krkošek, M., Connors, B. M., Ford, H., Peacock, S., Mages, P., Ford, J. S., … Lewis, M. A. (2011). Fish farms, parasites and predators: Implications for salmon population dynamics. *Ecological Applications*, *21*, 897–914. https://doi.org/10.1890/09-1861.1

Krkošek, M., & Hilborn, R. (2011). Sea lice (*Lepeophtheirus salmonis*) infestations and the productivity of pink salmon (*Oncorhynchus gorbuscha*) in the Broughton archipelago, British Columbia, Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, *68*, 17–29. https://doi.org/10.1139/F10-137

Krohn, M. M., & Boisclair, D. (1994). Use of stereo video system to stimate the energy expenditure of free-swimming fish. *Canadian Journal of Fish Aquatic Sci*, *51*, 1119–1127.

Lauritzen, D. V., Hertel, F. S., Jordan, L. K., & Gordon, M. S. (2010). Salmon jumping: Behavior, kinematics and optimal conditions, with possible implications for fish passageway design. *Bioinspiration & Biomimetics*, *5*, 1–11. https://doi.org/10.1088/1748-3182/5/3/035006

Leonardi, M. O., & Klempau, A. E. (2003). Artificial photoperiod influence on the immune system of juvenile rainbow trout (*Oncorhynchus mykiss*) in the Southern Hemisphere. *Aquaculture*, *221*, 581–591. https://doi.org/10.1016/S0044-8486(03)00032-2

Mages, P. A., & Dill, L. M. (2010). The effect of sea lice (*Lepeophtheirus salmonis*) on juvenile pink salmon (*Oncorhynchus gorbuscha*) swimming endurance. *Canadian Journal of Fisheries and Aquatic Sciences*, *67*, 2045–2051. https://doi.org/10.1139/F10-121

Manté, C., Kidé, S. O., Yao-Lafourcade, A.-F., & Mérigot, B. (2016). Fitting the truncated negative binomial distribtuion to count data.

Environmental and Ecological Statistics, *23*, 359–385. https://doi.org/10.1007/s10651-016-0343-1

Martins, C. I. M., Galhardo, L., Noble, C., Damsgård, B., Spedicato, M. T., Zupa, W., … Kristiansen, T. (2012). Behavioural indicators of welfare in farmed fish. *Fish Physiology and Biochemistry*, *38*, 17–41. https://doi.org/10.1007/s10695-011-9518-8

Mckinnell, S., Curchit, E., Groot, K., Kaeriy, M., & Trudel, M. (2014). Oceanic and atmospheric extremes motivate a new hypothesis for variable marine survival of Fraser River sockeye salmon. *Fisheries Oceanography*, *23*, 322–341. https://doi.org/10.1111/fog.12063

Mikheev, V. N., & Pasternak, A. F. (2006). Defense behavior of fish against predators and parasites. *Journal of Ichthyology*, *46*, S173–S179. https://doi.org/10.1134/S0032945206110063

Mordue, A. J., & Birkett, M. A. (2009). A review of host finding behaviour in the parasitic sea louse, *Lepeophtheirus salmonis* (Caligidae: Copepoda). *Journal of Fish Diseases*, *32*, 3–13. https://doi.org/10.1111/j.1365-2761.2008.01004.x

Morton, A., & Routledge, R. (2005). Mortality rates for juvenile pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon infested with sea lice (*Lepeophtheirus salmonis*) in the Broughton Archipelago. *Alaska Fishery Research Bulletin*, *11*, 146–152.

Morton, A., Routledge, R., & Krkošek, M. (2008). Sea louse infestation in wild juvenile salmon and Pacific herring associated with fish farms off the east-central coast of Vancouver Island, British Columbia. *North American Journal of Fisheries Management*, *28*, 523–532. https://doi.org/10.1577/M07-042.1

Nendick, L., Sackville, M., Tang, S., Brauner, C. J., & Farrell, A. P. (2011). Sea lice infection of juvenile pink salmon (*Oncorhynchus gorbuscha*): Effects on swimming performance and postexercise ion balance. *Canadian Journal of Fisheries and Aquatic Sciences*, *68*, 241–249. https://doi.org/10.1139/F10-150

Oines, O., Simonsen, J. H., Knutsen, J. A., & Heuch, P. A. (2006). Host preference of adult *Caligus elongatus* Nordmann in the laboratory and its implications for Atlantic cod aquaculture. *Journal of Fish Diseases*, *29*, 167–174. https://doi.org/10.1111/j.1365-2761.2006.00702.x

Parker, R. R., & Margolis, L. (1964). A new species of parasitic copepod, *Caligus clemensi* sp. nov. (Caligoida: Caligidae), from pelagic fishes in the coastal waters of British Columbia. *Journal of the Fisheries Research Board of Canada*, *21*, 873–889. https://doi.org/10.1139/f64-085

Peacock, S. J., Krkošek, M., Bateman, A. W., & Lewis, M. A. (2015). Parasitism and food web dynamics of juvenile Pacific salmon. *Ecosphere*, *6*, 1–16. https://doi.org/10.1890/ES15-00337.1

Pike, A. W., & Wadsworth, S. L. (1999). Sealice on salmonids: Their biology and control. *Advances in Parasitology*, *44*, 233–337. https://doi.org/10.1016/S0065-308X(08)60233-X

Poulin, R., & FitzGerald, G. J. (1989). Shoaling as an anti-ectoparasite mechanism in juvenile sticklebacks (*Gasterosteus* spp.). *Behavioral Ecology and Sociobiology*, *24*, 251–255. https://doi.org/10.1007/BF00295205

Price, M. H. H., Proboszcz, S. L., Routledge, R. D., Gottesfeld, A. S., Orr, C., & Reynolds, J. D. (2011). Sea louse infection of juvenile sockeye salmon in relation to marine salmon farms on Canada's west coast. *PLoS One*, *6*, e16851. https://doi.org/10.1371/journal.pone.0016851

Price, M. H. H., Glickman, B. W., & Reynolds, J. D. (2013). Prey selectivity of Fraser River sockeye salmon during early marine migration in British Columbia. *Transactions of the American Fisheries Society*, *142*, 1126–1133. https://doi.org/10.1080/00028487.2013.799517

Sellers, K. F., Swift, A. W., & Weems, K. S. (2017). A flexible distribution class for count data. *Journal of Statistical Distributions and Applications*, *4*, 1–22. https://doi.org/10.1186/s40488-017-0077-0

Stone, J., Roy, W. J., Sutherland, I. H., Ferguson, H. W., Sommerville, C., & Endris, R. (2002). Safety and efficacy of emamectin benzoate administered in-feed to Atlantic salmon, *Salmo salar* L., smolts in freshwater, as a preventative treatment against infestations of sea lice, *Lepeophtheirus salmonis* (Krøyer). *Aquaculture*, *210*, 21–34. https://doi.org/10.1016/S0044-8486(01)00822-5

Tanaka, I., & Takefushi, H. (1993). Elimination of external parasites (lice) is the primary function of grooming in free-ranging Japanese macaques. *Anthropological Science*, *101*, 187–193. https://doi.org/10.1537/ase.101.187

Wagner, G. N., McKinley, R. S., Bjørn, P. A., & Finstad, B. (2003). Physiological impact of sea lice on swimming performance of Atlantic salmon. *Journal of Fish Biology*, *62*, 1000–1009. https://doi.org/10.1046/j.1095-8649.2003.00091.x

Webster, S. J., Dill, L. M., & Butterworth, K. (2007). The effect of sea lice infestation on the salinity preference and energetic expenditure of juvenile pink salmon (*Oncorhynchus gorbuscha*). *Canadian Journal of Fisheries and Aquatic Sciences*, *64*, 672–680.

Wootten, R., & Smith, J. W. (1982). Aspects of the biology of the parasitic copepods *Lepeophtheirus salmonis* and *Caligus elongatus* on farmed salmonids and their treatment. *Proceedings of the Royal Society of Edinburgh*, *81B*, 185–197.

ELECTRONIC REFERENCES

Saksida, S. (2015). A summary of sea lice in BC–Wild and farmed monitoring and management. Victoria, BC: Sea to Sky Veterinary Services. Retrieved from www.docplayer.net/33230468-A-summary-of-sea-lice-in-bc-wild-and-farmed-monitoring-and-management.html

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