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Reduced growth in wild juvenile sockeye salmon *Oncorhynchus nerka* infected with sea lice

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Daily growth rings were examined in the otoliths of wild juvenile sockeye salmon *Oncorhynchus nerka* to determine whether infection by ectoparasitic sea lice *Caligus clemensi* and *Lepeophtheirus salmonis* was associated with reduced host body growth, an important determinant of survival. Over 98% of the sea lice proved to be *C. clemensi* and the fish that were highly infected grew more slowly than uninfected individuals. Larger fish also grew faster than smaller fish. Finally, there was evidence of an interaction between body size and infection status, indicating the potential for parasite-mediated growth divergence.

Key words: aquaculture; Fraser River; host–parasite; indirect effects; otolith; Pacific salmon.

INTRODUCTION

Pathogens are known to influence wildlife populations, especially when they interact with other stressors (Smith *et al.*, 2009; Pacioni *et al.*, 2015). Effects on biota resulting from the spread of pathogens are commonly associated with anthropogenic activities, such as through the introduction of non-native species (Dunn, 2009), climate change (Harvell *et al.*, 2009; Maynard *et al.*, 2015), and spill-over from domestic animal stocks (Daszak *et al.*, 2000). Indeed, nearly one quarter of the planet's most threatening invasive species cause disease in invaded systems (Hatcher *et al.*, 2012) and epizootics from the wildlife trade alone are responsible for large-scale economic and conservation consequences (Karesh *et al.*, 2005). Marine pathogens specifically can cause large population declines (Friedman *et al.*, 2000; Hewson *et al.*, 2014) and billions of pounds in losses for fisheries and aquaculture globally (Lafferty *et al.*, 2015), in part because the absence of dispersal barriers facilitates rapid disease spread (McCallum *et al.*, 2003).

Outbreaks of disease are often prominent and can lead directly to mass mortality events for host species (Lessios, 1988; Skerratt *et al.*, 2007), yet indirect effects on host survival through traits such as growth, behaviour, and competitive ability are

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much less understood despite their potential importance to host survival. Growth is a particularly important component of fitness for juvenile fishes, because it both expands their prey size range and it reduces predation risk (Parker, 1971; Hargreaves & LeBrasseur, 1986; Sogard, 1997). It has long been hypothesized that there is a critical period in the early life history of marine fishes that determines overall survival (Hjort, 1914). Evidence for the critical period hypothesis has been mixed (Elliott, 1989) and the concept is usually applied to larval mortality soon after yolk sack absorption (May, 1974), but Pacific salmon *Oncorhynchus* spp. may well be a group of fishes with differential survival within and among year-classes determined during their early marine life. The importance of early marine growth to overall survival has been demonstrated in coho *Oncorhynchus kisutch* (Walbaum 1792) (Beamish *et al.*, 2004), Chinook *Oncorhynchus tshawytscha* (Walbaum 1792) (Duffy & Beauchamp, 2011), pink *Oncorhynchus gorbuscha* (Walbaum 1792) (Moss *et al.*, 2005), and sockeye salmon *Oncorhynchus nerka* (Walbaum 1792) (Farley *et al.*, 2007).

For over a decade, conservation concerns have been raised about elevated levels of parasites, in particular sea lice, on *Oncorhynchus* spp. (Naylor *et al.*, 2003; Krkošek *et al.*, 2007). Two main species of sea lice infect *Oncorhynchus* spp.: *Lepeophtheirus salmonis*, a salmonid specialist (Pike & Wadsworth, 1999), and *Caligus clemensi*, a generalist that also parasitizes other near-shore marine fishes, including Pacific herring *Clupea pallasii* Valenciennes 1847 (Parker & Margolis, 1964). These ectoparasites feed on the epidermis and, in extreme cases, the musculature of host fishes, and *L. salmonis* has been shown to alter host physiology (Wagner *et al.*, 2003; Sutherland *et al.*, 2011), influence behaviour (Krkošek *et al.*, 2011), and increase mortality (Morton & Routledge, 2005; Krkošek *et al.*, 2007; Connors *et al.*, 2010).

Most research on *Oncorhynchus* spp. and sea lice has focused on *L. salmonis* and its effects on juvenile *O. gorbuscha* and chum salmon *Oncorhynchus keta* (Walbaum 1792) (Jones *et al.*, 2007; Brauner *et al.*, 2012). Juvenile *O. nerka* migrating northward along the south coast of British Columbia, however, are primarily infected by *C. clemensi* (Price *et al.*, 2011; Godwin *et al.*, 2015) and are post-smolts (having spent at least 1 year in fresh water before migrating to the sea) rather than young-of-the-year. While direct mortality from sea lice is probably very low for *O. nerka* (Jakob *et al.*, 2013), the indirect effects of louse parasitism on these fish are unknown apart from an association with reduced competitive ability in highly infected fish (Godwin *et al.*, 2015). *Oncorhynchus nerka* are of particular interest because of their iconic status, their importance to fisheries (FAO, 2015), and their complex multi-host dynamics with sea lice; *C. clemensi* infestations of wild juvenile *O. nerka* are linked to domestic Atlantic salmon *Salmo salar* L. 1758 (Price *et al.*, 2011) and *C. pallasii* are commonly infected as well (Morton *et al.*, 2008; Beamish *et al.*, 2009).

Investigations into the effects of pathogens on the growth of fishes are scarce, with little research having been performed on salmonids (Speare *et al.*, 1998) or outside of the laboratory (Sandell *et al.*, 2015). For salmonids and other teleosts, body growth can be inferred from their otoliths, the calcified structures in the inner ear whose incremental depositions are proportional to changes in fish length (Campana & Neilson, 1985; Campana, 1990). Here, otolith microstructure analysis was used to determine whether out-migrating wild juvenile *O. nerka* exhibit differential growth based on sea-louse infection status. Specifically, it was hypothesized that highly infected juvenile *O. nerka* grow more slowly than uninfected individuals, larger fish grow faster than smaller fish,

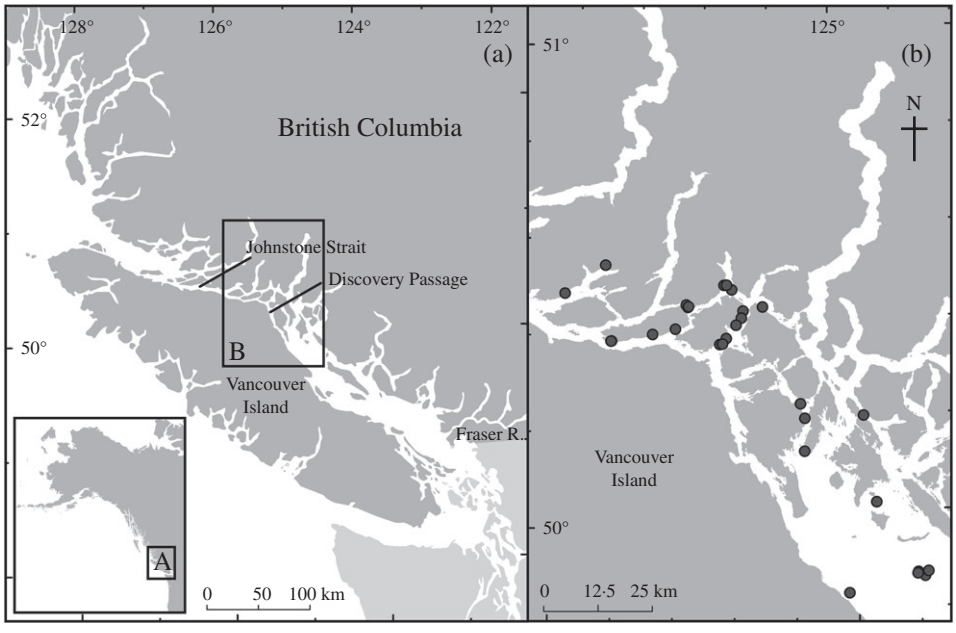

FIG. 1. (a) Area in British Columbia in which juvenile *Oncorhynchus nerka* were caught for the analysis of sea-louse infection on growth. (b) Collection locations (●) for out-migrating juvenile *O. nerka* used in the Discovery Passage.

and infection status and body size interact such that smaller fish experience a greater infection-associated reduction in growth compared with larger fish.

MATERIALS AND METHODS

SAMPLING DESIGN AND FISH SELECTION

The wild juvenile *O. nerka* used in this study were collected for a separate ecological investigation (Price *et al.*, 2011, 2013). Fish were collected from marine waters surrounding the Discovery Islands, between Vancouver Island and the mainland of British Columbia (BC), Canada (Fig. 1). Fish were caught from 28 May to 7 July 2009 and 4 June to 21 June 2010 using a modified purse seine (70 m × 10 m with 6 mm mesh). After pursing the net, the catch was concentrated in the bunt of the seine and fish were removed with a dip net and euthanized with a swift blow to the head. Fish were immediately frozen individually and labelled for subsequent laboratory analyses. Individual fish were thawed, weighed, measured for fork length (L_F), and assayed for sea lice using a dissecting microscope. Species of motile (*i.e.* pre-adult and adult) stages of sea lice were identified directly by morphology. Younger copepodid and chalimus stage lice were removed from the fish, mounted on slides and examined under a compound microscope for species determination based on detailed morphology (Kabata, 1972; Johnson & Albright, 1991). In the course of 79 collections, 2401 juvenile *O. nerka* were captured, 1420 in 2009 and 981 in 2010.

To select fish for otolith analyses, all collections were excluded that had fewer than two uninfected fish, or fewer than 10 total fish. From each of the remaining collections, the two most highly infected *O. nerka* were selected, giving priority to number of motile lice, followed by the total number of lice. All of these infected fish had motile infection intensities at or above the

TABLE I. Mean ± S.E. fork length (L_F) and sea-louse infection intensity of size-matched juvenile *Oncorhynchus nerka* examined for otolith analysis. Sea-louse infection intensities are presented as combined intensities for *Caligus clemensi* and *Lepeophtheirus salmonis*, but are dominated by *C. clemensi* (98·3%)

Year	Infection status	*n*	L_F (mm)	Motile lice	Total lice
2009	Highly infected	26	106·5 ± 2·9	2·38 ± 0·29	8·04 ± 0·96
2009	Uninfected	26	106·9 ± 2·1	–	–
2010	Highly infected	32	109·9 ± 1·9	1·56 ± 0·16	4·66 ± 0·41
2010	Uninfected	32	108·0 ± 2·0	–	–

90th percentile intensity from the 2401 *O. nerka* captured, so hereafter they are termed highly infected. For each collection, two uninfected fish were chosen by selecting those most similar in L_F to the two highly infected fish already selected. The mean ± S.E. difference in L_F between each pair of infected and uninfected fish was 5·1 ± 0·8 mm, which was *c*. 4·7% of overall mean L_F (Table I). The resulting dataset included 116 fish across 29 collections (Table I).

OTOLITH PREPARATION AND INTERPRETATION

Both sagittal otoliths were removed from the selected fish and placed in 2 cm^3 Eppendorf tubes pre-filled with 95% ethanol. For each fish, one of the otoliths was chosen randomly and carefully cleaned of soft tissue using distilled water and fine-tipped forceps under a dissecting microscope. Once clean, otoliths were mounted sulcus side up on a glass microscope slide using a clear thermoplastic adhesive (Crystalbond 509-3; Aremco Products Inc.; www.aremco.com). The mounted otoliths were polished with wetted 30 and 3 μm lapping film (Digikey Corporation; www.digikey.com) until the 10 outermost daily rings were visible on the pararostrum when viewed under a Leica DM1000 compound microscope (Leica Microsystems; www.leica-microsystems.com) at ×400 magnification (Fig. 2). The otolith polishing was finished using wet 0·3 μm lapping film to remove any scratches caused by the coarser grit film. During this process, otoliths were photographed frequently at ×400 magnification using a Leica ICC50 HD camera (Leica Microsystems) to ensure that an image was obtained before over-polishing. If, after polishing, damage prevented at least 10 successive peripheral rings to be discerned, the otolith was discarded and the second otolith was used in its place; this occurred six times. Comparable methods for mounting and polishing juvenile *O. nerka* otoliths were developed and validated independently by Stocks *et al.* (2014) and Freshwater *et al.* (2015) and have since been used successfully in multiple ecological studies (Freshwater *et al.*, 2016*a*, *b*).

Otolith growth was quantified for the 10 full days preceding capture by measuring the combined width of the 10 outermost daily increments. First, each prepared otolith was photographed with a scale bar in each image as a reference. ImageJ 1.48 (Rasband, 2015) was then used to measure the distance from the outermost ring on the pararostrum to the 10th ring inwards. Measurements were taken from the outermost ring rather than from the edge of the otolith to ensure that only full days of growth were considered. Finally, the radius (the distance from the otolith's core to the farthest point on the pararostrum) was measured at ×400 magnification for 30 otoliths using the same photographic and image processing software.

STATISTICAL ANALYSIS

To confirm that otolith growth was an acceptable proxy for body growth in this study's juvenile *O. nerka*, the Pearson correlation coefficient between L_F and otolith radius (R_O) was calculated for otoliths that had not been over-polished during preparation ($n = 30$). Body growth was then estimated for all 116 fish by multiplying their 10 day otolith growth by the slope of a linear regression between L_F (mm) and R_O (μm). Two-sample *t*-tests were used to determine whether L_F differed between infection categories, both within and across years. Linear

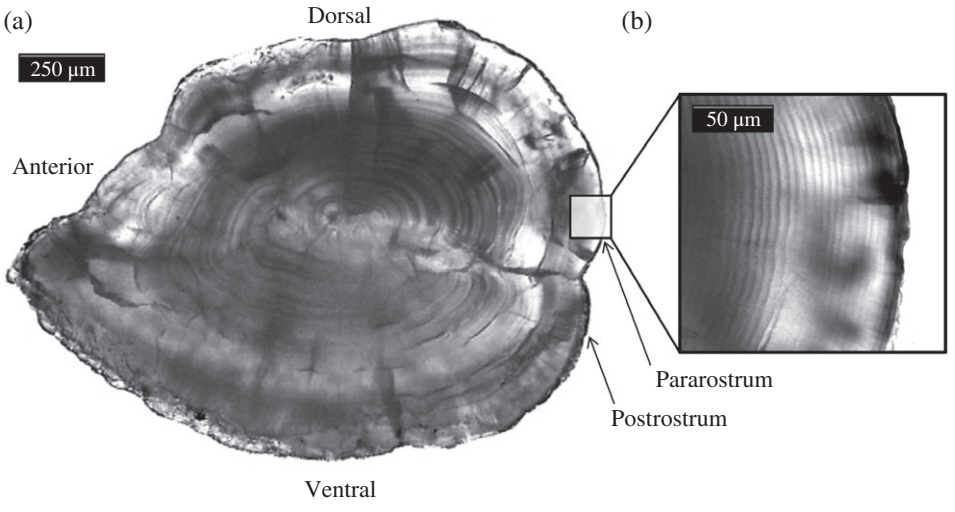

FIG. 2. (a) Photograph of a whole otolith from juvenile *Oncorhynchus neka* after polishing and (b) higher magnification of its daily growth increments.

regression was used to assess whether louse abundance increased with body size. Two-sample Wilcoxon–Mann–Whitney non-parametric tests were used to determine whether motile abundance and total louse abundance differed between years on highly infected fish.

The three main hypotheses were tested by competing mixed-effects models with different combinations of infection status, L_F and their two-way interaction as model variables. Because sea-louse abundance was higher in 2009 than in 2010 for the highly infected fish (Table I), a year variable was also included to determine whether growth was reduced in 2009. For the same reason, the three-way interaction between infection status, L_F, and year was included to assess whether the size-mediated effect of infection status differed with year. All 11 combinations of these fixed effects were fit because all were considered biologically plausible. Each mixed-effects model had a random-effect structure describing how the intercept varied according to collection number, which was determined *a priori*, as well as a power variance function structure needed to account for heteroscedasticity in the residual variation. Model selection was performed using Akaike information criterion corrected for small sample sizes (AICc; Hurvich & Tsai, 1989). Otolith growth was predicted to be higher in uninfected fish and larger fish, that the effect of infection on otolith growth would decrease with fish length, and that models including fish length, infection status and their two-way interaction (but not year or the three-way interaction) would have the most support.

Differences in body growth were estimated between highly infected and uninfected fish by generating model-averaged predictions for otolith growth and multiplying these by the rate of L_F growth μm^{-1} of otolith growth (*i.e.* the slope; Fig. 3). These body-growth estimates were used to calculate growth reductions for highly infected fish relative to uninfected fish of the same length by dividing the growth divergence between infection categories (the difference between the growth of uninfected and highly infected fish) by the growth of uninfected fish. All analyses were completed using the nlme, MuMIn, and AICcmodavg packages in R 3.1.1 (R Core Team, 2014).

GENETIC ANALYSES

As part of the broader study from which these fish were obtained (Price *et al.*, 2013), a subset of samples was genetically analysed to determine the population to which fish belonged. Forty-three of the 116 fish examined for otoliths had corresponding tissue samples extracted for genetic analysis. Tissue samples were analysed at the Fisheries and Oceans Canada (DFO) molecular genetics laboratory in Nanaimo, BC [see Price *et al.* (2011) for details on genetic

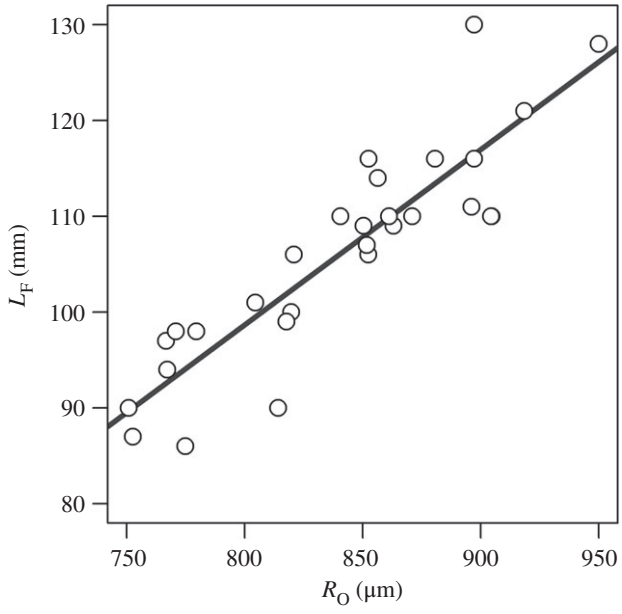

FIG. 3. *Oncorhynchus nerka* smolt fork length (L_F) in relation to otolith radius (R_O): $y = -47{\cdot}74 + 0{\cdot}18x$, $r = 0{\cdot}89$, $P < 0{\cdot}001$.

analyses]. Briefly, the 43 tissue samples had DNA extracted (Withler *et al.*, 2000) and amplified using PCR; samples were assigned to source populations using a Bayesian mixed-stock analysis (Pella & Masuda, 2001) and a baseline of 85 *O. nerka* populations when at least seven of 14 microsatellite loci amplified (Beacham *et al.*, 2004).

RESULTS

The majority (98·3%) of the sea lice in this study were *C. clemensi* rather than *L. salmonis*, which is consistent with previous reports (Price *et al.*, 2011; Godwin *et al.*, 2015). As only six of the 369 lice were *L. salmonis*, sea-louse infection intensities were analysed and are presented as the combined *C. clemensi* and *L. salmonis* infection intensities.

Fork length was strongly correlated with otolith radius ($r = 0{\cdot}89$; Fig. 3), indicating that otolith growth is a reasonable proxy for body growth during this period of the *O. nerka* life cycle. The L_F of the size-matched fish did not differ between the two infection categories in 2009 ($t = 0{\cdot}098$, d.f. = 50, $P > 0{\cdot}05$) or 2010 ($t = -0{\cdot}712$, d.f. = 62, $P > 0{\cdot}05$), nor across the 2 years ($t = -0{\cdot}424$, d.f. = 114, $P > 0{\cdot}05$; Table I). Louse abundance did not increase with body size ($r^2 = 0{\cdot}006$, d.f. = 114, $P > 0{\cdot}05$). The abundance of motile lice on the highly infected fish was higher in 2009 than in 2010 ($U = 546$, $P < 0{\cdot}05$; Table I), as was total louse abundance ($U = 594$, $P < 0{\cdot}01$; Table I).

Otolith growth was best explained by L_F and infection status (Table II). As predicted, larger fish grew faster than smaller fish and uninfected fish grew faster than highly infected fish (Fig. 4). No single model had overwhelming support; instead, the top three models were all within 1·27 AICc units of each other and the third-ranked model

TABLE II. Mixed-effects model selection results for otolith growth in juvenile *Oncorhynchus nerka*. Only the six models with >1% model support are shown

Rank	Model*	ΔAICc†	w_i
1	Infection + length	0	0·310
2	Infection × length	0·48	0·244
3	Length	1·27	0·164
4	Infection + length + year	1·97	0·115
5	Infection × length + year	2·17	0·105
6	Length + year	3·39	0·057

w_i, Akaike model weight.

*Models had a random intercept for collection number. The fixed effects used were infection category (infection), fork length (length), their two-way interaction, year and the three-way interaction.

†Difference from the top model AICc (ΔAICc).

still accounted for 16% of overall model support. The model in which otolith growth was affected both by fish size and infection status was 1·89 times more likely than the model in which otolith growth was only affected by fish size.

Daily growth divergence between infection categories was evident in the model-averaged predictions. These predictions indicated that 90 mm uninfected fish, *i.e.* those in the 10th percentile of L_F, grow at the same rate as 97·4 mm infected fish. The effect of infection, however, diminished slightly as body size increased, supporting the hypothesis for a size-mediated effect of infection. For example, the model-averaged predictions

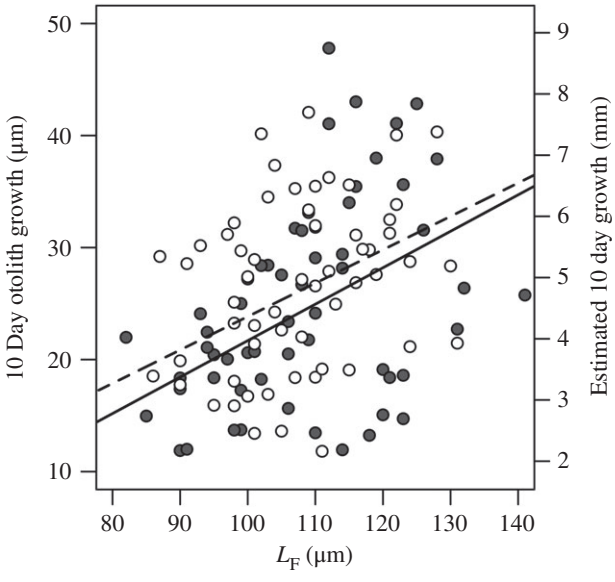

FIG. 4. Ten day otolith growth increases with fork length (L_F) for uninfected (- -○- -) and highly infected (—●—) juvenile *Oncorhynchus nerka*. Estimated 10 day growth is represented on the secondary *y* axis. Lines depict the model-averaged predictions.

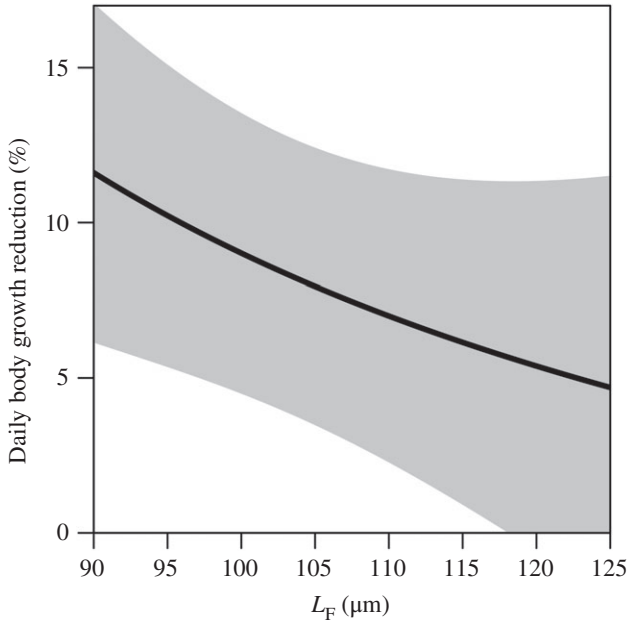

FIG. 5. Size-dependent reductions in daily body growth for highly infected juvenile *Oncorhynchus nerka* relative to uninfected fish. Growth estimates for each infection category were calculated by generating model-averaged predictions for otolith growth and multiplying these by the rate of fork length (L_F) growth μm^{-1} of otolith growth (*i.e.* the slope of Fig. 3). ■ denotes the 95% confidence region, which incorporates the unconditional S.E. of averaged predictions and the S.E. of *R*, the rate of L_F growth μm^{-1} of otolith growth.

suggested that 125 mm uninfected fish, *i.e.* those in the 90th percentile of L_F, grow at the same rate as 128·7 mm infected fish; thus, highly infected 90 mm *O. nerka* experience an 11·6% reduction in daily body growth relative to uninfected fish. In comparison, highly infected 125 mm fish only experience a 4·7% reduction and median-sized (105 mm) fish experience a 7·9% reduction (Fig. 5).

Genetic analyses indicated that the majority (91%) of the 43 fish examined were from 16 spawning systems within the Fraser River: Chilko (42%), Weaver (9%), Pitt (7%), Dolly Varden Creek (7%), Adams (2%), Birkenhead (2%), Bowron (2%), Cultus (2%), Nadina (2%), Nahatlatch (2%), North Thompson (2%), Raft (2%), Stellako (2%), Tachie (2%), and Taseko (2%). The remaining 9% were from the Phillips River system in the Discovery Islands region.

DISCUSSION

Oncorhynchus spp. may experience a critical period in their development where early marine growth determines overall survival and the results suggest that pathogens may play a role in modulating that growth. The analysis of otolith rings from juvenile *O. nerka* indicates that larger fish and those uninfected by sea lice grow faster than their smaller and highly infected counterparts.

Growth history of the fish was evaluated for the 10 days preceding capture. Ten days was chosen as the duration for three reasons: the 10 most recent daily rings could consistently be exposed on each of the otoliths; little to moderate turnover of sea lice would be expected from development alone in 10 days (Hogans & Trudeau, 1989; Johnson & Albright, 1991; Piasecki & MacKinnon, 1995); *C. clemensi* can disperse among hosts in its pre-adult and adult stages, so a longer time period would result in a higher chance that a host's infection status at the time of capture will not represent its infection status throughout the entire time period.

Juvenile *O. nerka* generate daily rings in their otoliths (Wilson & Larkin, 1980), but otolith formation stops when fish are reared below 5° C (Marshall & Parker, 1982), at least in fresh water. This cessation of daily-ring formation under the influence of low temperature is coupled with a greatly reduced rate of body growth. Since the fish captured were feeding actively (Price *et al.*, 2013) and travelling through waters well above 5° C (Price *et al.*, 2011), daily ring formation is not expected to have ceased prior to capture.

It cannot be known for certain that the relationship identified between sea-louse infection and growth rate is a causative one. Lice could differentially infect and survive on hosts that have lower initial body condition and could therefore be an indicator, rather than a cause, of condition differences among fish. While future laboratory research could come closer to identifying a causative relationship between sea-louse infection and fish growth (Tveiten *et al.*, 2010), the issue of condition differences among fish would still confound such studies and the effect in wild fish could be much different depending on how sea lice influence interacting factors that are absent in the laboratory. For example, juvenile *O. nerka* have lower competitive abilities with sea-louse infection (Godwin *et al.*, 2015), which should influence foraging outcomes and, ultimately, growth. Field studies are therefore necessary to place such host–pathogen relationships within an ecological context.

Sea lice can cause salmonids to reduce their feeding (Costello, 2006; Bravo *et al.*, 2008), which could cause reduced growth in their hosts. For *S. salar* infected with *L. salmonis*, this reduced feeding is only a temporary phenomenon when lice are at the pre-adult stage (the first motile stage) and host feeding recovers by the time lice moult into adults (Dawson *et al.*, 1999). The authors of this study are not aware of any similar studies involving *C. clemensi*. Nevertheless, if the infected fish experienced a temporary reduction in feeding due to a heavy infection of pre-adult lice, it is possible that the observed reduction in growth was also temporary. This is unlikely considering that 89% of the motile lice on this study's fish were adults, not pre-adults, but even if pre-adults were causing these fish to feed less, it would not be a temporary phenomenon. As 70% of the lice on the infected fish were non-motile (*i.e.* would later moult into pre-adults), these fish would probably not resume full feeding for several weeks under this scenario.

A growth difference was observed between infection categories of juvenile *O. nerka* despite a presumed lack of food limitation for these fish. Price *et al.* (2013) found empty stomachs in only 3·1% of juvenile *O. nerka* migrating through the Discovery Islands in 2009 and none in 2010. More recently, McKinnell *et al.* (2014) proposed a 'trophic gauntlet hypothesis' in which juvenile *O. nerka* migrating through Johnstone Strait, the body of water that they enter after migrating northward through the Discovery Islands, suffer an energy deficit due to a lack of prey. Although there is some overlap between the sampling area and the region described by McKinnell *et al.* (2014), growth differences would be expected to be accentuated further north where prey may be less

available if differential foraging success between uninfected and highly infected fish contributes to the differences observed.

It is not surprising that larger juvenile *O. nerka* grow faster than smaller individuals; larger fish are more likely to catch larger prey (Hargreaves & LeBrasseur, 1986) and hunt more efficiently due to higher visual acuity (Flamarique & Hawryshyn, 1996) and faster burst swimming speed (Hale, 1999). If this size-dependent growth is not a product of the fish being on different parts of a growth curve with an inflection point, in which case their body sizes could eventually converge, there may be growth divergence in this *O. nerka* life stage. Growth curves for younger *O. nerka* captured and reared in fresh water do not indicate an inflection point having already been reached (Brett *et al.*, 1969; Bilton & Robins, 1973; Brett & Shelbourn, 1975), but to the authors' knowledge, no high resolution size-at-age data exist for out-migrating juvenile *O. nerka* in marine waters. It may be that this relationship between age and increasing variance in body size is the incipient phase of what ultimately becomes differential survival among individuals.

The effects of infection status and body size were not independent, as infection interacted with heterogeneity in body size to amplify divergent growth in smaller fish and dampen it in larger individuals. Model-averaged predictions indicated that highly infected fish in the 10th percentile of L_F experience an 11·6% reduction in daily body growth relative to uninfected fish, but median-sized fish experience a 7·9% reduction and those in the 90th percentile only experience a 4·7% reduction. Since infection intensity did not increase with host body size, this diminished infection-associated growth reduction in larger *O. nerka* may be due to these fish hosting fewer parasites per unit mass. These results highlight one potential scenario in which small amounts of divergent growth due to parasitism may be subsequently reinforced and amplified by size-dependent divergent growth. Sea lice are associated with reduced competitive abilities in juvenile *O. nerka* (Godwin *et al.*, 2015) and this connection between sea lice and growth may demonstrate a second, delayed, effect of heavy sea-louse infection on survival.

The belief that bigger is better generally holds true with fishes (Sogard, 1997) and *Oncorhynchus* spp. are no exception (Beamish *et al.*, 2004; Moss *et al.*, 2005; Farley *et al.*, 2007). The growth reductions that were observed in highly infected fish (Fig. S1, Supporting Information) are comparable with those shown to influence survival in early marine *O. kisutch*. Calculations based on data in Beamish *et al.* (2004) indicate that early marine growth was 9·5% lower for the average *O. kisutch* soon after marine entry than for those that survived through their first marine winter. Juvenile *O. nerka* and *O. kisutch* have different early life histories, but both species usually enter the ocean after spending 1 year in fresh water. While the two species are not directly comparable, the growth reductions reported here in *O. nerka* are in the same range as those demonstrated to have survival consequences for their congener, which lends credence to the notion that these growth reductions could affect overall marine survival of *O. nerka* (Appendix SI). Furthermore, when projecting our results over 120 days, the resulting 6·2% difference in L_F for fish initially of median size (Fig. S2, Supporting Information) appears similar to the size difference reported by Farley *et al.* (2007) to be associated with a decrease in marine stage survival rate of a few per cent for juvenile *O. nerka*.

In light of the growing evidence that *C. clemensi* infection is correlated with components of fitness for wild juvenile salmonids and the fact that this species constitutes 98·3% of the lice observed on juvenile *O. nerka*, it is worth considering why there is

no management plan for this louse species on farmed *Oncorhynchus* spp. in BC. In contrast, *L. salmonis* are managed on BC *Oncorhynchus* spp. farms using an in-feed parasiticide [SLICE (emamectin benzoate); Intervet International B.V.; www.intervet.com; Saksida *et al.* (2010)]. As mandated by their licence for finfish aquaculture, marine farms perform a SLICE treatment when there is an average of at least three motile *L. salmonis* on a subset of their domestic fish, but there is no such threshold for *C. clemensi*. *Caligus clemensi* infestations of wild juvenile *O. nerka* are associated with open net-pen salmonid farms along their migration route (Price *et al.*, 2011) and infection prevalence in wild juvenile *O. nerka* continues to be extremely high (Godwin *et al.*, 2015). There seems no obvious reason for this discrepancy in treatment between the two louse species. Additional parasiticide treatments on farms for *C. clemensi* outbreaks could increase risk of louse resistance (Denholm *et al.*, 2002; Bravo *et al.*, 2008; Igboeli *et al.*, 2012), but at minimum, a combined threshold should be established in which *C. clemensi* and *L. salmonis* are considered together when determining when treatment should occur.

Fraser River *O. nerka* constitute a suite of populations under intense scientific and public scrutiny. After a two-decade decline in productivity, record low adult returns in 2009, and a federal judicial inquiry into the causes of the decline, Fraser River *O. nerka* briefly showed a modest rebound in productivity (DFO, 2015). Concern remains, however, as returns in 2016 were the lowest in over 100 years (PSC, 2016). Furthermore, while no single cause of the long-term decline in Fraser River *O. nerka* productivity was identified during the federal inquiry (Cohen, 2012), the decline was correlated with competition with *O. gorbuscha* and exposure to salmonid farms during early marine migration (Connors *et al.*, 2012). This has led to a call for research on the factors governing juvenile *O. nerka* survival, particularly in regard to pathogens (Cohen, 2012). As 91% of the 43 fish genetically tested in this study were from the Fraser River and 37% of these were from conservation units with amber (of concern) or red (threatened) statuses (Grant & Pestal, 2012), the results presented here provide insight into a potential pathogen-induced survival consequence for this *Oncorhynchus* spp. stock complex.

Any potential effect of sea lice on juvenile *O. nerka* is of particular concern given that *C. clemensi* is a generalist with multiple possible reservoir host populations. By infecting *C. pallasii* and domestic *S. salar*, *C. clemensi* can be maintained in the environment regardless of *O. nerka* abundance, thus sustaining infection pressure even at low *O. nerka* densities and creating the apparent competition structure that is most commonly associated with disease imperilment of wildlife (De Castro & Bolker, 2005). The results presented here highlight the need to consider the indirect effects of marine pathogens on host populations in addition to the traditional focus on direct mortality, as this may be vital for understanding wild-fish survival and, ultimately, for conserving at-risk populations.

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Supporting Information

Supporting Information may be found in the online version of this paper:
Appendix SI. Recursive growth model.

Fig. S1. Recursive growth models fit over 60 days using model-averaged predictions from the model set and initial lengths corresponding to the 10th, 50th, and 90th percentile lengths of captured *Oncorhynchus nerka*. Percentages represent the growth reductions for highly infected juvenile *O. nerka* relative to uninfected individuals after 60 days. The 95% C.I. were calculated using the unconditional S.E. of averaged predictions and the S.E. of R, the rate of fork length growth μm^{-1} of otolith growth.

Fig. S2. Recursive growth models fit over 120 days for the 10th, 50th, and 90th percentile of juvenile *Oncorhynchus nerka* fork length (L_F). Percentages represent the growth reductions for highly infected juvenile *O. nerka* relative to uninfected individuals after 120 days. The 95% C.I. were calculated using the unconditional S.E. of averaged predictions and the S.E. of R, the rate of L_F growth μm^{-1} of otolith growth.

References

Beacham, T. D., Lapointe, M., Candy, J. R., McIntosh, B., MacConnachie, C., Tabata, A., Kaukinen, K., Deng, L., Miller, K. M. & Withler, R. E. (2004). Stock identification of Fraser River sockeye salmon using microsatellites and major histocompatibility complex variation. *Transactions of the American Fisheries Society* **133,** 1117–1137. https://doi.org/10.1577/t04-001.1

Beamish, R., Mahnken, C. & Neville, C. (2004). Evidence that reduced early marine growth is associated with lower marine survival of coho salmon. *Transactions of the American Fisheries Society* **133,** 26–33. https://doi.org/10.1577/T03-028

Beamish, R., Wade, J., Pennell, W., Gordon, E., Jones, S., Neville, C., Lange, K. & Sweeting, R. (2009). A large, natural infection of sea lice on juvenile Pacific salmon in the Gulf Islands area of British Columbia, Canada. *Aquaculture* **297,** 31–37. https://doi.org/10.1016/j.aquaculture.2009.09.001

Bilton, H. & Robins, G. (1973). The effects of starvation and subsequent feeding on survival and growth of Fulton Channel sockeye salmon fry (*Oncorhynchus nerka*). *Journal of the Fisheries Research Board of Canada* **30,** 1–5. https://doi.org/10.1139/f73-001

Brauner, C., Sackville, M., Gallagher, Z., Tang, S., Nendick, L. & Farrell, A. (2012). Physiological consequences of the salmon louse (*Lepeophtheirus salmonis*) on juvenile pink salmon (*Oncorhynchus gorbuscha*): implications for wild salmon ecology and management and for salmon aquaculture. *Philosophical Transactions of the Royal Society B* **367,** 1770–1779. https://doi.org/10.1098/rstb.2011.0423

Bravo, S., Sevatdal, S. & Horsberg, T. E. (2008). Sensitivity assessment of *Caligus rogercresseyi* to emamectin benzoate in Chile. *Aquaculture* **282,** 7–12. https://doi.org/10.1016/j.aquaculture.2008.06.011

Brett, J. R. & Shelbourn, J. E. (1975). Growth rate of young sockeye salmon, *Oncorhynchus nerka*, in relation to fish size and ration level. *Journal of the Fisheries Research Board of Canada* **32,** 2103–2110. https://doi.org/10.1139/f75-248

Brett, J., Shelbourn, J. E. & Shoop, C. T. (1969). Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. *Journal of the Fisheries Research Board of Canada* **26,** 2363–2394. https://doi.org/10.1139/f69-230

Campana, S. E. (1990). How reliable are growth back-calculations based on otoliths? *Canadian Journal of Fisheries and Aquatic Sciences* **47,** 2219–2227. https://doi.org/10.1139/f90-246

Campana, S. E. & Neilson, J. D. (1985). Microstructure of fish otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* **42,** 1014–1032. https://doi.org/10.1139/f85-127

Connors, B. M., Krkošek, M., Ford, J. & Dill, L. M. (2010). Coho salmon productivity in relation to salmon lice from infected prey and salmon farms. *Journal of Applied Ecology* **47,** 1372–1377. https://doi.org/10.1111/j.1365-2664.2010.01889.x

Connors, B. M., Braun, D. C., Peterman, R. M., Cooper, A. B., Reynolds, J. D., Dill, L. M., Ruggerone, G. T. & Krkošek, M. (2012). Migration links ocean-scale competition and local ocean conditions with exposure to farmed salmon to shape wild salmon dynamics. *Conservation Letters* **5,** 304–312. https://doi.org/10.1111/j.1755-263X.2012.00244.x

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

Daszak, P., Cunningham, A. A. & Hyatt, A. D. (2000). Emerging infectious diseases of wildlife: threats to biodiversity and human health. *Science* **287,** 443–449. https://doi.org/10.1126/science.287.5452.443

Dawson, L. H., Pike, A. W., Houlihan, D. F. & McVicar, A. H. (1999). Changes in physiological parameters and feeding behaviour of Atlantic salmon *Salmo salar* infected with sea lice *Lepeophtheirus salmonis*. *Diseases of Aquatic Organisms* **35,** 89–99. https://doi.org/10.3354/dao035089

De Castro, F. & Bolker, B. (2005). Mechanisms of disease-induced extinction. *Ecology Letters* **8,** 117–126. https://doi.org/10.1111/j.1461-0248.2004.00693.x

Denholm, I., Devine, G. J., Horsberg, T. E., Sevatdal, S., Fallang, A., Nolan, D. V. & Powell, R. (2002). Analysis and management of resistance to chemotherapeutants in salmon lice, *Lepeophtheirus salmonis* (Copepoda: Caligidae). *Pest Management Science* **58,** 528–536. https://doi.org/10.1002/ps.482

Duffy, E. J. & Beauchamp, D. A. (2011). Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. *Canadian Journal of Fisheries and Aquatic Sciences* **68,** 232–240. https://doi.org/10.1139/F10-144

Dunn, A. M. (2009). Parasites and biological invasions. *Advances in Parasitology* **68,** 161–184. https://doi.org/10.1016/s0065-308x(08)00607-6

Elliott, J. M. (1989). The critical-period concept for juvenile survival and its relevance for population regulation in young sea trout, *Salmo trutta*. *Journal of Fish Biology* **35,** 91–98. https://doi.org/10.1111/j.1095-8649.1989.tb03049.x

Farley, E. V., Murphy, J. M., Adkison, M. D., Eisner, L. B., Helle, J. H., Moss, J. H. & Nielsen, J. (2007). Early marine growth in relation to marine-stage survival rates for Alaska sockeye salmon (*Oncorhynchus nerka*). *Fishery Bulletin* **105,** 121–130.

Flamarique, I. & Hawryshyn, C. (1996). Retinal development and visual sensitivity of young Pacific sockeye salmon (*Oncorhynchus nerka*). *Journal of Experimental Biology* **199,** 869–882.

Freshwater, C., Trudel, M., Beacham, T. D., Neville, C.-E., Tucker, S. & Juanes, F. (2015). Validation of daily increments and a marine-entry check in the otoliths of sockeye salmon *Oncorhynchus nerka* post-smolts. *Journal of Fish Biology* **87,** 169–178. https://doi.org/10.1111/jfb.12688

Freshwater, C., Trudel, M., Beacham, T. D., Godbout, L., Neville, C.-E. M., Tucker, S. & Juanes, F. (2016*a*). Disentangling individual and population-scale processes within a latitudinal size gradient in sockeye salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **73,** 1–12. https://doi.org/10.1139/cjfas-2015-0344

Freshwater, C., Trudel, M., Beacham, T. D., Godbout, L., Neville, C.-E. M., Tucker, S. & Juanes, F. (2016*b*). Divergent migratory behaviours associated with body size and ocean entry phenology in juvenile sockeye salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **73,** 1723–1732. https://doi.org/10.1139/cjfas-2015-0425

Friedman, C. S., Andree, K. B., Beauchamp, K., Moore, J. D., Robbins, T. T., Shields, J. D. & Hedrick, R. P. (2000). '*Candidatus Xenohaliotis californiensis*', a newly described pathogen of abalone, *Haliotis* spp., along the west coast of North America. *International*

Journal of Systematic and Evolutionary Microbiology **50,** 847–855. https://doi.org/10.1099/00207713-50-2-847

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

Hale, M. E. (1999). Locomotor mechanics during early life history: effects of size and ontogeny on fast-start performance of salmonid fishes. *Journal of Experimental Biology* **202,** 1465–1479. https://doi.org/10.1007/978-94-010-9258-6_1

Hargreaves, N. B. & LeBrasseur, R. J. (1986). Size selectivity of coho (*Oncorhynchus kisutch*) preying on juvenile chum salmon (*O. keta*). *Canadian Journal of Fisheries and Aquatic Sciences* **43,** 581–586. https://doi.org/10.1139/f86-069

Harvell, D., Altizer, S., Cattadori, I. M., Harrington, L. & Weil, E. (2009). Climate change and wildlife diseases: when does the host matter the most? *Ecology* **90,** 912–920. https://doi.org/10.1890/08-0616.1

Hatcher, M. J., Dick, J. T. & Dunn, A. M. (2012). Disease emergence and invasions. *Functional Ecology* **26,** 1275–1287. https://doi.org/10.1111/j.1365-2435.2012.02031.x

Hewson, I., Button, J. B., Gudenkauf, B. M., Miner, B., Newton, A. L., Gaydos, J. K., Wynne, J., Groves, C. L., Hendler, G. & Murray, M. (2014). Densovirus associated with sea-star wasting disease and mass mortality. *Proceedings of the National Academy of Sciences* **111,** 17278–17283. https://doi.org/10.1073/pnas.1416625111

Hjort, J. (1914). Fluctuations in the great fisheries of northern Europe, viewed in the light of biological research. *Rapport et Proces-verbaux des Reunions*. *Conseil International pour L'exploration de la Mer* **20**.

Hogans, W. & Trudeau, D. (1989). Preliminary studies on the biology of sea lice, *Caligus elongatus*, *Caligus curtus* and *Lepeophtheirus salmonis* (Copepoda: Caligoida) parasitic on cage-cultured salmonids in the lower Bay of Fundy. *Canadian Technical Report of Fisheries and Aquatic Sciences* **1715,** 1–14.

Hurvich, C. M. & Tsai, C.-L. (1989). Regression and time series model selection in small samples. *Biometrika* **76,** 297–307. https://doi.org/10.1093/biomet/76.2.297

Igboeli, O. O., Fast, M. D., Heumann, J. & Burka, J. F. (2012). Role of P-glycoprotein in emamectin benzoate (SLICE®) resistance in sea lice, *Lepeophtheirus salmonis*. *Aquaculture* **344,** 40–47. https://doi.org/10.1016/j.aquaculture.2012.03.026

Jakob, E., Sweeten, T., Bennett, W. & Jones, S. (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. & Albright, L. (1991). 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. https://doi.org/10.1017/s0025315400051687

Jones, S. R., Fast, M. D., Johnson, S. C. & Groman, D. B. (2007). Differential rejection of salmon lice by pink and chum salmon. *Diseases of Aquatic Organisms* **75,** 229. https://doi.org/10.3354/dao075229

Kabata, Z. (1972). Developmental stages of *Caligus clemensi* (Copepoda: Caligidae). *Journal of the Fisheries Research Board of Canada* **29,** 1571–1593. https://doi.org/10.1139/f72-245

Karesh, W. B., Cook, R. A., Bennett, E. L. & Newcomb, J. (2005). Wildlife trade and global disease emergence. *Emerging Infectious Diseases* **11,** 1000–1002. https://doi.org/10.3201/eid1107.020194

Krkošek, M., Ford, J. S., Morton, A., Lele, S., Myers, R. A. & Lewis, M. A. (2007). Declining wild salmon populations in relation to parasites from farm salmon. *Science* **318,** 1772–1775. https://doi.org/10.1126/science.1148744

Krkošek, M., Connors, B. M., Ford, H., Peacock, S., Mages, P., Ford, J. S., Morton, A., Volpe, J. P., Hilborn, R., Dill, L. M. & 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

Lafferty, K. D., Harvell, C. D., Conrad, J. M., Friedman, C. S., Kent, M. L., Kuris, A. M., Powell, E. N., Rondeau, D. & Saksida, S. M. (2015). Infectious diseases affect marine fisheries

and aquaculture economics. *Annual Review of Marine Science* **7,** 471–496. https://doi.org/10.1146/annurev-marine-010814-015646

Lessios, H. (1988). Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? *Annual Review of Ecology and Systematics* **19,** 371–393. https://doi.org/10.1146/annurev.ecolsys.19.1.371

Marshall, S. L. & Parker, S. S. (1982). Pattern identification in the microstructure of sockeye salmon (*Oncorhynchus nerka*) otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* **39,** 542–547. https://doi.org/10.1139/f82-077

May, R. C. (1974). Larval mortality in marine fishes and the critical period concept. In *The Early Life History of Fish* (Blaxter, J. H. S., ed), pp. 3–19. Berlin: Springer-Verlag. https://doi.org/10.1007/978-3-642-65852-5_1

Maynard, J., van Hooidonk, R., Eakin, C. M., Puotinen, M., Garren, M., Williams, G., Heron, S. F., Lamb, J., Weil, E., Willis, B. & Harvell, C. D. (2015). Projections of climate conditions that increase coral disease susceptibility and pathogen abundance and virulence. *Nature Climate Change* **5,** 688–694. https://doi.org/10.1038/nclimate2625

McCallum, H., Harvell, D. & Dobson, A. (2003). Rates of spread of marine pathogens. *Ecology Letters* **6,** 1062–1067. https://doi.org/10.1046/j.1461-0248.2003.00545.x

McKinnell, S., Curchitser, E., Groot, K., Kaeriyama, 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

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

Moss, J. H., Beauchamp, D. A., Cross, A. D., Myers, K. W., Farley, E. V., Murphy, J. M. & Helle, J. H. (2005). Evidence for size-selective mortality after the first summer of ocean growth by pink salmon. *Transactions of the American Fisheries Society* **134,** 1313–1322. https://doi.org/10.1577/t05-054.1

Naylor, R. L., Eagle, J. & Smith, W. L. (2003). Salmon aquaculture in the Pacific Northwest a global industry with local impacts. *Environment: Science and Policy for Sustainable Development* **45,** 18–39. https://doi.org/10.1080/00139150309604562

Pacioni, C., Eden, P., Reiss, A., Ellis, T., Knowles, G. & Wayne, A. F. (2015). Disease hazard identification and assessment associated with wildlife population declines. *Ecological Management and Restoration* **16,** 142–152. https://doi.org/10.1111/emr.12155

Parker, R. R. (1971). Size selective predation among juvenile salmonid fishes in a British Columbia inlet. *Journal of the Fisheries Research Board of Canada* **28,** 1503–1510. https://doi.org/10.1139/f71-231

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

Pella, J. & Masuda, M. (2001). Bayesian methods for analysis of stock mixtures from genetic characters. *Fishery Bulletin* **99,** 151–167.

Piasecki, W. & MacKinnon, B. (1995). Life cycle of a sea louse, *Caligus elongatus* von Nordmann, 1832 (Copepoda, Siphonostomatoida, Caligidae). *Canadian Journal of Zoology* **73,** 74–82. https://doi.org/10.1139/z95-009

Pike, A. & Wadsworth, S. (1999). Sealice on salmonids: their biology and control. *Advances in Parasitology* **44,** 233–337. https://doi.org/10.1016/s0065-308x(08)60233-x

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

Rasband, W.S. (2015). ImageJ 1.48. National Institutes of Health: Bethesda, Maryland, USA. https://imagej.nih.gov/ij/.

Saksida, S. M., Morrison, D. & Revie, C. W. (2010). The efficacy of emamectin benzoate against infestations of sea lice, *Lepeophtheirus salmonis*, on farmed Atlantic salmon, *Salmo salar* L., in British Columbia. *Journal of Fish Diseases* **33,** 913–917. https://doi.org/10.1111/j.1365-2761.2010.01192.x

Sandell, T., Teel, D. J., Fisher, J., Beckman, B. & Jacobson, K. (2015). Infections by *Renibacterium salmoninarum* and *Nanophyetus salmincola* Chapin are associated with reduced growth of juvenile Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Northeast Pacific Ocean. *Journal of Fish Diseases* **38,** 365–378. https://doi.org/10.1111/jfd.12243

Skerratt, L. F., Berger, L., Speare, R., Cashins, S., McDonald, K. R., Phillott, A. D., Hines, H. B. & Kenyon, N. (2007). Spread of chytridiomycosis has caused the rapid global decline and extinction of frogs. *EcoHealth* **4,** 125–134. https://doi.org/10.1007/s10393-007-0093-5

Smith, K. F., Acevedo-Whitehouse, K. & Pedersen, A. B. (2009). The role of infectious diseases in biological conservation. *Animal Conservation* **12,** 1–12. https://doi.org/10.1111/j.1469-1795.2008.00228.x

Sogard, S. M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science* **60,** 1129–1157. https://doi.org/10.2307/2679928

Speare, D. J., Daley, J., Markham, R., Sheppard, J., Beaman, H. & Sanchez, J. (1998). *Loma salmonae*-associated growth rate suppression in rainbow trout, *Oncorhynchus mykiss* (Walbaum), occurs during early onset xenoma dissolution as determined by *in situ* hybridization and immunohistochemistry. *Journal of Fish Diseases* **21,** 345–354. https://doi.org/10.1046/j.1365-2761.1998.00112.x

Stocks, A. P., Pakhomov, E. A. & Hunt, B. P. V. (2014). A simple method to assess the marine environment residence duration of juvenile sockeye salmon (*Oncorhynchus nerka*) using laser ablation. *Canadian Journal of Fisheries and Aquatic Sciences* **71,** 1437–1446. https://doi.org/10.1139/cjfas-2014-0073

Sutherland, B. J., Jantzen, S. G., Sanderson, D. S., Koop, B. F. & Jones, S. R. (2011). Differentiating size-dependent responses of juvenile pink salmon (*Oncorhynchus gorbuscha*) to sea lice (*Lepeophtheirus salmonis*) infections. *Comparative Biochemistry and Physiology D* **6,** 213–223. https://doi.org/10.1016/j.cbd.2011.04.001

Tveiten, H., Bjorn, P. A., Johnsen, H. K., Finstad, B. & McKinley, R. S. (2010). Effects of the sea louse *Lepeophtheirus salmonis* on temporal changes in cortisol, sex steroids, growth and reproductive investment in Arctic charr *Salvelinus alpinus*. *Journal of Fish Biology* **76,** 2318–2341. https://doi.org/10.1111/j.1095-8649.2010.02636.x

Wagner, G., McKinley, R., Bjørn, P. & 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

Wilson, K. H. & Larkin, P. A. (1980). Daily growth rings in the otoliths of juvenile sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* **37,** 1495–1498. https://doi.org/10.1139/f80-193

Withler, R. E., Le, K. D., Nelson, R. J., Miller, K. M. & Beacham, T. D. (2000). Intact genetic structure and high levels of genetic diversity in bottlenecked sockeye salmon (*Oncorhynchus nerka*) populations of the Fraser River, British Columbia, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* **57,** 1985–1998. https://doi.org/10.1139/f00-149

Electronic References

Cohen, B. I. (2012). Cohen commission of inquiry into the decline of sockeye salmon in the Fraser River – final report. The uncertain future of Fraser River sockeye, Vol. 3: recommendations, summary, process. Ottawa: Minister of Public Works and Government Services Canada. Available at https://www.watershed-watch.org/wordpress/wp-content/

uploads/2013/02/CohenCommissionFinalReport_Vol03_Full.pdf/ (last accessed 17 December 2015).

DFO (2015). Pre-season run size forecasts for Fraser River sockeye (*Oncorhynchus nerka*) and pink (*O. gorbuscha*) salmon in 2015. Ottawa: Canadian Science Advisory Secretariat Science Response. Available at http://publications.gc.ca/site/eng/9.802931/publication.html/ (last accessed 17 December 2015).

FAO (2015). Global capture production 1950–2013. Rome: Food and Agriculture Organization of the United Nations, Fisheries and Aquaculture Information and Statistics Branch. Available at http://www.fao.org/figis/servlet/TabSelector/ (last accessed 17 December 2015).

Grant, S. C. H. & Pestal, G. (2012). Integrated biological status assessments under the wild salmon policy using standardized metrics and expert judgement: Fraser River sockeye salmon (*Oncorhynchus nerka*) case studies. Ottawa: Canadian Science Advisory Secretariat. Available at http://www.dfo-mpo.gc.ca/Csas-sccs/publications/resdocs-docrech/2012/2012_106-eng.pdf/ (last accessed 6 November 2016).

PSC (2016). Fraser River panel weekly report – 19 August 2016. *Report* **6**. Vancouver: Pacific Salmon Commission. Available at http://www.psc.org/download/71/2016/4572/weeklyreport06.pdf/ (last accessed 16 November 2016).

