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Warming temperatures and ectoparasitic sea lice impair internal organs in juvenile Atlantic salmon

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ABSTRACT: As a consequence of climate change and open net-pen salmon farming, wild Atlantic salmon *Salmo salar* are increasingly likely to encounter elevated temperatures and parasite abundances during their early marine migration. Such stressors can compromise fitness by diminishing liver energy stores and impairing cardiac muscle. To assess whether temperature and infestation by salmon lice *Lepeophtheirus salmonis* are important correlates of liver energy stores and cardiac muscle performance in juvenile salmon, we experimentally infested fish at 3 abundances of louse infestation (zero, low, and high) and 5 temperatures (10, 13, 16, 19, and 22°C). At the end of the experiment (i.e. when sea lice reached adulthood), we calculated the percent dry weight of the liver (%DWL; a proxy for liver energy stores) and cardiosomatic index (CSI; a proxy for cardiac muscle performance) of each fish and fitted 5 linear mixed-effects models to both of these responses. For both %DWL and CSI, the best-supported model included additive fixed effects for both infestation level and temperature. Our top models predicted that, relative to zero infestation, high infestation reduces %DWL by 5.7% (95% CI: 5.3–6.2%) and increases CSI by 15.9% (14.4–18.0%), and low infestation reduces %DWL by 2.6% (2.2–3.0%) and increases CSI by 7.8% (6.7–10.0%). Our work suggests that stressors associated with ocean warming and coastal salmon aquaculture can compromise wild salmon fitness through the impairment of vital organs.

KEY WORDS: Climate change · Aquaculture · Salmon farms · Liver · Heart · Cardiosomatic index · *Lepeophtheirus salmonis* · Hepatosomatic index

1. INTRODUCTION

The progression of climate change in the marine environment and the increasing global reliance on seafood-based protein necessitate assessment of their individual and combined implications for wild and farmed fish. Over the past 3 decades, the growing demand for seafood has resulted in a rapid global expansion of aquaculture operations (Thilsted et al. 2016), which have compensated for fisheries catches that plateaued in the late 20th century (Pauly & Zeller 2017). Of the numerous varieties of finfish aquaculture, marine net-pen salmon farming is by far the most profitable (FAO 2018). Consequently, salmon farming is now a major contributor to overall seafood production in coastal countries like Norway, the UK, Ireland, Chile, and Canada, with the sector's global production exceeding 2.4 million t and US $17.1 billion annually (FAO 2020). Despite the recent growth and profitability of the salmon-aquaculture industry, concerns remain over its ecological consequences, as declines in wild Pacific (*Oncorhynchus* spp.) and

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Atlantic salmon (*Salmo salar*) populations in several regions have been linked to genetic introgression and transmission of pathogens and parasites from farmed salmon (Ford & Myers 2008, Karlsson et al. 2016, Vollset et al. 2016, Susdorf et al. 2018). Simultaneously, global sea surface temperatures (SSTs) have been increasing due to anthropogenic climate change, especially in the nearshore marine waters in which salmon-aquaculture facilities operate (Wong et al. 2014). Since there is no barrier between the internal net-pen environment and the surrounding coastal marine ecosystem, salmon-aquaculture operations stand to be affected by ocean warming.

The salmon louse *Lepeophtheirus salmonis* is a notorious parasite in the aquaculture industry due to its considerable economic and ecological effects. Estimates from Norwegian salmon farms suggest that these salmonid-specialist sea lice can cost the industry roughly 9% of revenues (Abolofia et al. 2017), which would correspond to billions of dollars in losses globally. Financial losses incurred by salmon-aquaculture companies include not only the cost of anti-parasitic treatment but also the cost of reduced biomass, since sea-louse infestations influence growth and survival by compromising immune and osmoregulatory function (Pike & Wadsworth 1999, Wagner et al. 2003, Finstad et al. 2010) and reducing food-conversion efficiency (Costello 2009a, Abolofia et al. 2017). While sea lice naturally occur on marine salmonids globally, they are especially prevalent in areas where salmon farms are present because farms act as sea-louse reservoirs that provide year-round infestation pressure to juvenile salmon that does not otherwise exist (Krkošek et al. 2007). The high densities of fish in salmon-aquaculture facilities provide ideal conditions for the proliferation of pathogens and parasites, and open net pens allow free transmission between wild and farmed populations (Krkošek et al. 2005, Costello 2009b). Due to the spatial overlap of aquaculture operations and salmon migration routes (Costello 2006, Krkošek 2017), louse transmission between sympatric farmed and wild salmon is inevitable (Marty et al. 2010, Peacock et al. 2013) and may negatively impact wild salmon populations (Connors et al. 2010, Krkošek et al. 2011, 2013, Vollset et al. 2016).

The compounding effects of climate change and coastal net-pen salmon farming may render sea-louse infestation increasingly harmful to wild and farmed fish. Higher temperatures accelerate sea-louse development (Johnson & Albright 1991, Hamre et al. 2019); thus, louse outbreaks are anticipated to become more frequent and severe as louse generation times shorten with climate warming (Bateman et al. 2016, Godwin et al. in press). Water temperature also regulates key physiological processes of salmonids, such as cardiorespiratory rate and metabolism (Jonsson & Jonsson 2004), meaning that there are many potential pathways for interactions between sea-louse infestation and temperature. One such pathway is through the heart. Salmonid hearts perform less effectively at high temperature (e.g. dysrhythmia and reduced maximum stroke volume and cardiac output; Eliason et al. 2013), and louse-infested salmon have slower heart rates and critical swimming speeds than their non-infested counterparts (Wagner et al. 2003). Although direct and indirect effects of parasites on cardiac physiology and morphology have garnered recent interest (see review by Powell & Yousaf 2017), nothing is known about such effects in the important social–ecological system of farmed and wild salmon. A second pathway through which the effects of sea-louse infestation and temperature may interact is depletions in energy reserves. Infestation by sea lice is likely to be energetically demanding for the host (Wagner et al. 2003, Wells et al. 2006). Elevated metabolic rates associated with higher temperatures can elicit rapid catabolism of energy reserves and induce greater nutritional requirements (Hevrøy et al. 2012), both of which can be reflected by the condition of the liver (Bruslé & Anadon 1996). Considering that sea-louse infestation and temperature can have similar effects on the physiology of salmon, and that metabolic distress and nutrient deficiency are suspected to work in concert with other extrinsic stressors (e.g. pathogens) to cause mortality of apparently healthy farm fish (Dessen et al. 2020), rising sea temperatures may well interact with sea-louse infestation to exacerbate the physiological stress of infestation and further imperil salmon health.

While the effects of sea lice on host immune response and osmoregulatory function are generally well understood, comparatively few attempts have been made to discern how sea lice affect the internal organs of the host, and nothing is known about whether these potential effects are mediated by temperature. We performed a manipulative experiment to determine whether salmon-louse infestation affects the liver and heart — and, therefore, the energetic or physiological state — of juvenile Atlantic salmon, and whether water temperature interacts with infestation to exacerbate the effects of parasitism. To address these questions, we evaluated metrics of liver energy stores and cardiac muscle performance of the experimental fish, using the proxies of percent dry weight

of the liver (%DWL; Wuenschel et al. 2019) and cardiosomatic index (CSI; Frisk et al. 2020). We predicted that the effects of the parasites on their hosts would be accentuated at higher temperatures.

2. MATERIALS AND METHODS

To determine the effect of multiple stressors on energy stores and heart muscle performance in juvenile salmon, we analyzed the proportional size of the livers and hearts of Atlantic salmon post-smolts that had been experimentally infested with sea lice at 3 abundance levels (zero, low [mean ± SE abundance = 1.43 ± 0.14 lice fish^{-1}], and high [6.76 ± 0.41 lice fish^{-1}]) in triplicate at 5 temperature treatments (10, 13, 16, 19, and 22°C).

2.1. Experimental design

We conducted our experiment at the Aquatron Research Facility of Dalhousie University in Halifax, Nova Scotia, Canada, as part of a larger study that used the same animals to investigate the temperature-dependent effects of sea lice on Atlantic salmon (Godwin et al. 2020). We held Saint John River strain Atlantic salmon post-smolts, sourced from Cape d'Or Aquaculture (Nova Scotia, Canada), in 8 recirculating seawater tanks (1750 l capacity, radius = 92 cm, height of water line = 66 cm) at 12°C for 12 d. We anesthetized the fish in a 100 mg l^{-1} tricaine methanesulfonate (MS-222) seawater bath and inserted PIT tags (7 × 1.35 mm; FDX-B Loligo Systems) into their abdominal cavities, following a standard protocol (Columbia Basin Fish and Wildlife Authority PIT Tag Steering Committee 1999). After a 10 d recovery period, we transferred the fish to a 300 l tote (length = 97 cm, width = 55 cm, height = 58 cm) in batches using a dip net. From the tote, we transferred each fish sequentially into 45 × 70 l flow-through experimental tanks (radius = 21 cm, height of water line = 46 cm) equipped with an adjustable air bubbler at the base of the standpipe and a weighted temperature logger (HOBO® Pendant® MX2201, Onset Computer) situated 5 cm below the surface. The water temperature in each tank was recorded every 3 min for the duration of the experiment. We administered feed (3 mm pellets; Nutra RC, Skretting) daily at 1% of the average body weight. We monitored mortalities, air input, and water inflow (mean ± SE = 1.40 ± 0.14 l min^{-1}) daily, measured dissolved oxygen saturation (89.5 ± 0.3%) every 1–2 d, and checked pH (range: 7.2–7.7) and salinity (range: 28–32 ppt) intermittently. We calibrated the pH measurements to account for the effect of temperature and salinity.

We maintained the tanks at ambient seawater temperature (approximately 13°C) for 25 d before adjusting the tank temperatures by a maximum of 1.5°C d^{-1} to attain their randomly assigned temperatures (10, 13, 16, 19, and 22°C). We maintained these new temperatures for 10 d. Due to delays in obtaining sea lice, we returned the tanks to ambient temperature to prevent differential size and condition from temperature-related growth prior to infestation. Once lice had been successfully hatched at the Huntsman Marine Science Centre (HMSC; St. Andrews, New Brunswick, Canada) 14 d later, we adjusted the tanks back to their assigned temperatures, again at a maximum of 1.5°C d^{-1}. We permitted the fish to re-acclimate to the assigned temperatures for 10 d before anesthetizing them in a 100 mg l^{-1} MS-222 seawater bath to collect body weight and fork length measurements.

We infested the fish with sea lice 3 d after weighing them. The infective sea-louse copepodites (i.e. larvae) were cultured at HMSC from egg strings collected in August 2019 from sea-cage sites in the Bay of Fundy (New Brunswick, Canada). We introduced the copepodites to each tank according to our randomly assigned louse infestation treatments. Low- and high-infestation tanks received dilutions of a stock mixture with a known concentration of copepodites such that 150 ml of liquid were added to each tank with a concentration of 0, 15, or 70 lice fish^{-1}. The water inflow, which had been shut off prior to the addition of lice to facilitate louse settlement, was restored after 70 min. Dissolved oxygen levels were unchanged during the 70 min infestation period, and temperatures shifted by a maximum of 1.5°C. We infested the 45 experimental tanks in 3 stages separated by 20 min intervals, with each stage containing one of each possible unique temperature and infestation combination.

Less than 24 h following infestation, Hurricane Dorian swept through Halifax, Canada. The dramatic change in ambient seawater temperature in conjunction with equipment malfunction due to a power outage caused our lowest 3 temperatures (10, 13, and 16°C), which were maintained manually by technicians, to be warmer and more variable than planned for the first 10 d of the experiment (Fig. 1). The temperature groups remained distinct throughout this period, however, and the mean temperatures observed over the entire experiment (10.50, 13.63, 16.25, 19.03, and 22.04°C) remained within 0.63°C of the targeted temperatures (10, 13, 16, 19, and 22°C).

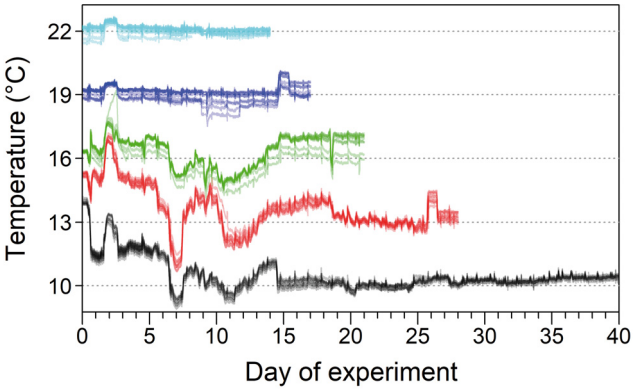

Fig. 1. Temperatures for experimental tanks from the time of infestation (Day 0) to the endpoint dissections. Each of the 45 tanks is represented by a semi-transparent line, and temperature groups (10, 13, 16, 19, and 22°C) are identified by colors. The duration from infestation to endpoint dissections differed among temperature groups due to the temperature-dependent rate of sea-louse development. The first 10 d following infestation depict the impact of Hurricane Dorian on the variation in ambient water temperature. The 3 lowest temperature groups, which were adjusted manually rather than electronically, exhibited the greatest variability. Reproduced from the supplementary information of Godwin et al. (2020)

We euthanized approximately 40% of the fish in each tank once the lice had reached the pre-adult stage (n = 286), then euthanized the remainder of the fish once the lice had reached the adult stage (i.e. 'endpoint dissections'; n = 400). The timing of these dissections varied with temperature group (e.g. 40 d for the 10°C group and 14 d for the 22°C group; see Table S1 in the Supplement at www.int-res.com/articles/suppl/m660p161_supp.pdf) because sea lice develop faster at higher temperatures (Johnson & Albright 1991). We used linear interpolation and extrapolation of the temperature-dependent development data presented by Hamre et al. (2019) to schedule sampling days for each of our temperature groups. To guarantee that all lice would have developed into adults by the endpoint dissection, we added an arbitrary 30% of the expected time to the predicted number of degree-days. On the prescribed sampling day, we euthanized the fish with a 250 mg l^{-1} overdose of MS-222 and recorded their body weight and fork length. We systematically excised and weighed the heart and liver of each fish; for consistency across dissections, we removed auxiliary heart structures as described by Johansen et al. (2017) and retained only the ventricle and bulbus arteriosus. We stored the liver samples separately at −20°C for subsequent processing.

2.2. Organ analyses

We used the livers and hearts from the endpoint dissections to calculate organosomatic indices for the 2 organs. Cardiosomatic index (CSI) and hepatosomatic index (HSI) are indicators of change in physiological and energy status (McPherson et al. 2011) frequently associated with stress response (Nilsson et al. 2018). In teleost fish, organosomatic liver indices positively correlate with liver energy density (Wuenschel et al. 2019), while CSI is a key indicator of cardiac muscle performance (Frisk et al. 2020, Waldrop et al. 2020). Since water can be incorporated into the liver in place of lipid, thereby confounding energy density estimation, we used percent dry weight of the liver (%DWL) in place of HSI (Johnson et al. 2017). We dried the livers at 60°C to a constant weight, as described by Wuenschel et al. (2019), and allowed them to cool before weighing (Pacific Northwest Laboratories 1993). We determined the optimal time for ensuring 'constant weight' by comparing the weights of liver samples (n = 20) dried for 16, 24, 40, and 48 h at 60°C (Fig. S1); the percent change in mass from 24 to 48 h was negligible (mean ± SE = −1.85 ± 0.25%), so we standardized sample drying time to 24 h.

We calculated %DWL in the same manner as Wuenschel et al. (2019):

$$\%\mathrm{DWL} = 100\% \times \left(\frac{W_{\mathrm{dry}}}{W_{\mathrm{wet}}}\right) \quad (1)$$

where W_{dry} and W_{wet} are liver dry and wet weight (g), respectively. We calculated CSI by modifying the ratio described by Johansen et al. (2017):

$$\mathrm{CSI} = 1000 \times \left(\frac{W_{\mathrm{heart}}}{W_{\mathrm{body}}}\right) \quad (2)$$

where W_{heart} is the wet weight (g) of the bulbus arteriosus and the ventricle, and W_{body} is the intact body wet weight (g). This ratio was multiplied by 1000 because the likelihood optimizer for mixed-effects modeling does not perform well with extremely small values. To prepare these data for model fitting, we identified and removed outlying observations indicative of data entry errors, using Tukey's fences and a conservative Tukey's constant of k = 4 (Fig. S2), which resulted in the removal of 3 observations from the %DWL data and 1 observation from the CSI data.

We fitted 5 linear mixed-effects models to the %DWL and CSI data. Normality and homoscedasticity of the residuals were confirmed visually using Q-Q plots and plots of residuals against fitted values. The most complex model consisted of fixed effects for infestation level, temperature, and the multiplicative

interaction between the 2 factors. The remaining models comprised the other 4 combinations of these parameters, including an intercept-only model. We used the mean temperature observed in each temperature group as a continuous variable in our analysis. To account for the clustering of variance within tanks, every model included a random effect on the intercept for tank (Tables S2 & S3). We used Akaike's information criterion (AIC; Akaike 1974) to select the model which most appropriately described the %DWL and CSI data. We then determined the relative importance of each explanatory variable (RVI) by summing the weights of all models containing that variable. We conducted our analyses in R version 3.6.2 (R Core Team 2019), using the packages 'lme4' (Bates et al. 2015) and 'MuMIn' (Bartón 2019).

3. RESULTS

Sea-louse infestation and temperature affected the liver and heart of juvenile Atlantic salmon. For both %DWL and CSI, the best-supported model included additive effects of temperature and infestation level but no interaction between them. The top %DWL model was 3.40 AIC units lower than the second-ranked model and accounted for 84% of overall model support (i.e. AIC weight; Table S2). %DWL decreased with temperature and with increasing infestation level (Fig. 2). The model ranked second-best contained the additive and multiplicative effects of both temperature and infestation level and accounted for 15% of model support (Table S2). Infestation level had an RVI of 1.00, temperature had an RVI of 0.99, and their interaction had an RVI of 0.14 (Table S2). Our top model predicted that relative to zero infestation, high louse infestation reduced %DWL by 5.7% (95% CI: 5.3–6.2%) and low infestation reduced %DWL by 2.6% (2.2–3.0%), on average (Table S3).

The top CSI model was 3.06 AIC units lower than the second most supported model and accounted for 82% of overall model support (Table S4). CSI increased with temperature and infestation level (Fig. 3). As for %DWL, the model ranked second included the interaction between temperature and infestation level. Both of these correlates had an RVI of 1.00, and their interaction had an RVI of 0.17 (Table S4). Our top model predicted that high louse infestation increased CSI by 15.9% (95% CI: 14.4–18.0%) and low infestation increased CSI by 7.8% (6.7–10.0%), on average, relative to zero infestation (Table S5).

The louse abundances at the end of the experiment were 1.4 (95% CI: 1.2–1.7) lice per fish for the low-infestation treatment and 6.8 (6.2–7.4) lice per fish for the high-infestation treatment (Table S6).

4. DISCUSSION

With increasing temperature and louse abundance, we observed a decrease in %DWL and an increase in CSI. These findings suggest that liver energy stores and cardiac muscle performance are negatively impacted by elevated temperature and louse infestation. Contrary to our prediction and our

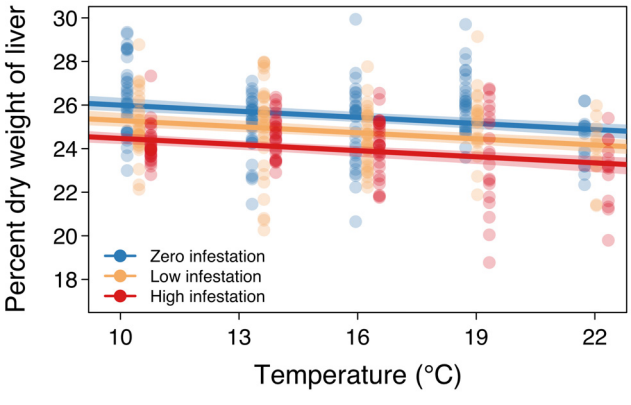

Fig. 2. Percent dry weight of the liver (%DWL) in Atlantic salmon post-smolts at each temperature and sea-louse infestation level. Points represent observed %DWL values (jittered by infestation level for visualization purposes), and the lines depict the mean predictions of the top %DWL model (with bootstrapped 95% CI) for each of the 3 infestation levels

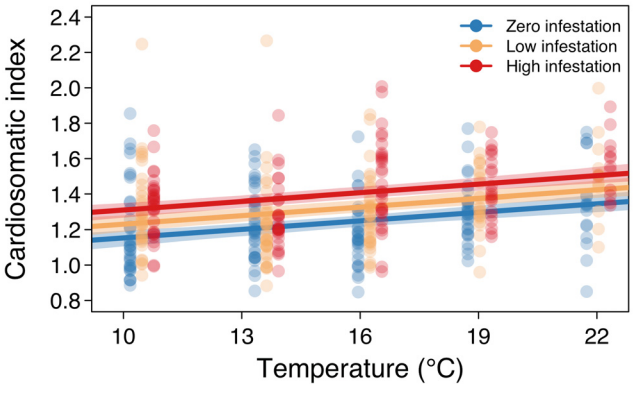

Fig. 3. Cardiosomatic index (CSI) of Atlantic salmon post-smolts at each temperature and sea-louse infestation level. Points represent observed CSI values (jittered by infestation level for visualization purposes), and the lines depict the mean predictions of the top CSI model (with bootstrapped 95% CI) for each of the 3 infestation levels

recent work, which found that the effects of sea lice on salmon survival, growth, and body condition all worsened at higher temperatures (Godwin et al. 2020), the impacts of louse infestation on salmon livers and hearts were not exacerbated at higher temperatures. Our findings, contextualized as repercussions of the innate stress response, indicate that stressors associated with climate change and coastal salmon aquaculture may be detrimental to the fitness of farmed and wild Atlantic salmon.

Depletion of liver energy stores due to the effects of temperature and sea-louse infestation could have major implications for Atlantic salmon. Liver energy content and %DWL exhibit a tight, positive correlation in teleost fish (Wuenschel et al. 2019), so the observed decreases in %DWL indicate that liver energy stores would also likely be depleted in response to high temperatures and louse infestation. In carnivorous teleosts such as salmonids, liver energy stores predominantly comprise proteins and lipids (Hendry & Beall 2004). Whereas protein content is governed by intrinsic factors, lipid levels are determined by both extrinsic and intrinsic factors (Shearer 1994), making these energy-dense and highly labile (McPherson et al. 2011) lipid stores vulnerable to depletion by pathogens and environment quality. Reproductive investment is believed to be contingent upon lipid-derived energy (Thorpe et al. 1998) and, in Atlantic salmon, low lipid stores are suggested to cause the postponement of maturation (Thorpe 2007). The quantity of stored energy has important consequences for the life history of salmon (Thorpe et al. 1998), which is punctuated by large energetic expenditures associated with migration and spawning, for which adequate energy reserves are crucial (Jonsson et al. 1991, Persson et al. 2018). The mechanism by which temperature and louse abundance may influence liver energy content may be through the effects of the stress hormone cortisol, which can cause macroscopic changes in salmonid liver tissue and depletions of energy stores (Harper & Wolf 2009).

The fitness of Atlantic salmon could also be reduced by the impairment of cardiac muscle associated with temperature and parasite stress. Although heart growth is often adaptive in salmonids (e.g. for spawning and cold acclimatization), cortisol-induced heart growth is maladaptive because it is associated with reduced cardiac efficiency and swimming performance (Johansen et al. 2017). Since elevated blood cortisol concentration is one of the primary physiological responses of salmonids to high temperatures (Chadwick & McCormick 2017, Madaro et al. 2018) and sea-louse infestation (Bowers et al. 2000, Tveiten et al. 2010), our findings suggest that juvenile Atlantic salmon experience maladaptive heart growth as a consequence of these 2 stressors. Fish in warmer conditions or that are infested by sea lice may therefore be at higher risk of mortality, as abnormal heart morphology decreases resilience to environmental or aquaculture-related stress (Poppe et al. 2003).

The temperatures and sea-louse infestation levels used in our experiment were good representations of predicted coastal ocean temperatures and the range of louse abundances observed on salmon farms. The experimental temperatures are similar to average summer near-surface temperatures in Atlantic Canada, which typically lie between 10 and 17°C but have been recorded to exceed 22°C (i.e. our highest experimental temperature) (Brewer-Dalton et al. 2015). Since average summer SSTs for coastal regions in eastern Canada are predicted to be approximately 4°C higher by mid-century than they were at the turn of the 21st century (Greenan et al. 2018), the range of our experimental temperatures are relevant for future coastal marine conditions. The experimental infestation levels fall within — and, in fact, below — the sea-louse abundances observed in Atlantic salmon farming operations in recent years (Atlantic Canada Fish Farmers Association 2020). Salmon farms in Atlantic Canada have much higher louse abundances than those in Pacific Canada or Europe, so we selected sea-louse infestation levels that are reflective of farm conditions in Atlantic Canada yet globally relevant. The paucity of publicly available data on louse abundances on wild juvenile Atlantic salmon prevents comparison between wild infestations and our experimental abundances.

Atlantic salmon aquaculture may benefit from a greater understanding of the effects of temperature and louse abundance on the condition of young fish. Our findings indicate that, as coastal temperatures inevitably increase, efforts to suppress louse outbreaks will be essential to minimize the effects of sea lice on farmed fish. These mitigation efforts may be even more crucial moving forward, given the capacity of temperature and louse effects to create a positive feedback mechanism that could exacerbate stress in salmonids. Thermal stress causes immune suppression in fish (Pickering & Pottinger 1995), rendering them more vulnerable to parasitism (Bailey et al. 2017) and, potentially, increasing deleterious effects associated with higher parasite loads (Tørud & Håstein 2008, Britton et al. 2011). Elevated temperatures also lead to higher rates of louse development and, therefore, accelerated louse generation time

and population growth (Stien et al. 2005, Costello 2006, Groner et al. 2014). Indeed, at the highest temperature in our experiment (22°C), salmonid hosts experience 2 generations of sea-louse infestation for every one generation at our lowest temperature (10°C). It is also possible that the effects of the first louse generation may make hosts more vulnerable to the effects of subsequent generations. Our experiment isolated the effects of one louse generation, but there is ample opportunity for meaningful investigation into the relative impacts of lice integrated over multiple generations, either through a modeling or laboratory-based approach.

Recognizing how temperature and sea lice influence liver energy stores and heart muscle condition of juvenile Atlantic salmon could provide opportunities to enhance stewardship of wild populations. While the response of wild fish may differ from that of the fish in our experiment, which were sourced from a commercial hatchery, the effect of these stressors on the liver and heart was clear. Depleted liver energy stores or impaired heart muscle performance may be detrimental to the fitness of wild salmon whose life histories include massive migrations that demand substantial energy expenditure (Jonsson et al. 1991, Persson et al. 2018). Since smoltification depletes energy stores (Sheridan 1989), juvenile salmon undertaking a coastal migration from their natal freshwater systems to the open ocean (Thorstad et al. 2012) may be disproportionately impacted by stressors such as parasitism and temperature that further exhaust energy stores. Furthermore, juveniles with scarce energy reserves are less capable of surviving their migration and overwintering period (Finstad et al. 2004). Although energy may be re-allocated in a manner that enhances survival rather than growth or reproductive investment, such energetic trade-offs can alter life history traits (e.g. fecundity, size at maturity, age at maturity), and individual fitness may still decline (Roff 1992). Wild Atlantic salmon populations are in decline globally (Nehlsen et al. 1991, Chaput 2012), and sea-louse transmission from salmon farms may contribute to reductions in wild salmon recruitment (Connors et al. 2010, Krkošek et al. 2011, 2013, Vollset et al. 2016). From a conservation perspective, it is important to identify regions and populations at particular risk of the compounding effects of ocean warming and net-pen salmon aquaculture and consider whether current parasite management practices on farms are sufficient.

Both wild and farmed Atlantic salmon are increasingly exposed to stressors such as rising ocean temperatures and parasitism by sea lice. Our findings indicate that liver energy stores and heart muscle performance of juvenile Atlantic salmon are influenced by the additive effects of temperature and louse infestation, and thus indicate the need to consider how the consequences of sea-louse outbreaks may change as coastal oceans continue to warm. In an era where global food security is becoming increasingly reliant on aquaculture and the effects of climate change are manifesting at the ecosystem level, it is crucial to understand the potential ramifications of their combined impacts on key social–ecological systems like farmed and wild salmon.

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