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Hyper- and Hypo-Osmoregulatory Performance of Atlantic Salmon (*Salmo salar*) Smolts Infected With *Pomphorhynchus tereticollis* (Acanthocephala)

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Migratory species must cope with different parasite communities in different environments, but little is known about the ecophysiological effects of parasites on migratory performance. Some species/strains of acanthocephalan parasites in the genus *Pomphorhynchus* use anadromous salmonids as preferred definitive hosts, perforating the intestines, destroying mucosa and inducing inflammation–all of which might affect osmoregulatory function during transition between freshwater and marine environments. We used genetic barcoding to identify acanthocephalans in the intestines of wild Irish Atlantic salmon (*Salmo salar* L.) smolts as being the recently taxonomically resurrected species *Pomphorhynchus tereticollis*. We then investigated whether natural infection intensities of this parasite were associated with reduced osmoregulatory performance, as measured by plasma chloride concentrations, or potentially elevated stress, as measured by blood glucose, of hosts in freshwater or saltwater environments (24 or 72 h in ∼26PPT salt water, reflecting salinities of coastal waters through which smolts migrate). Although infection prevalence was high amongst sampled smolts, no associations were found within or across treatment groups between parasite abundance and plasma chloride concentrations or blood glucose levels. We found no intestinal perforations that would indicate *P. tereticollis* had recently vacated the intestines of smolts in either of the saltwater groups. Exploratory sampling in the 2 years preceding the experiment indicated that parasite prevalence and abundance are consistently high and comparable to the experimental individuals. Collectively, these results indicate that naturally occurring abundances of *P. tereticollis* do not reduce osmoregulatory function or affect blood glucose content in fresh water or within 72 h of entering coastal waters, although delayed pathologies affecting marine survival may occur. Future consideration of ecophysiological interactions between anadromous fish hosts and their parasites across different osmotic environments should provide general insights into coevolution between migratory hosts and their parasites.

Keywords: parasite, stress, osmoregulation, anadromy, salmonid, *Pomphorhynchus tereticollis*

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INTRODUCTION

Migration has evolved in a diverse array of animal taxa as a strategy for coping with, or exploiting, spatiotemporal environmental variation (Dingle, 2014). Physiological processes (e.g., metabolic and neuroendocrine pathways) drive how animals translate environmental cues into movement decisions (Goossens et al., 2020) and also mediate fitness costs of these decisions (Alerstam et al., 2003; Brownscombe et al., 2017) and consequent life-history trade-offs (Ricklefs and Wikelski, 2002). While the performance of migratory aquatic species has been clearly linked to a range of abiotic drivers such as temperature (e.g., Crossin et al., 2008; Gilbert and Tierney, 2018), oxygen limitation (e.g., Rosa and Seibel, 2010), water flow (e.g., Swanson et al., 2004), water chemistry (e.g., Borges et al., 2019), and pollution (e.g., Seewagen, 2020), the role of biotic factors in the ecophysiology of animal migration is arguably less well studied. In particular, parasites and pathogens have received relatively little attention, but are critical components of any ecosystem and are likely to exert a range of physiologically mediated influences on migration decisions and fitness outcomes (Piersma, 1997; Altizer et al., 2000; Gylfe et al., 2000; Norris and Evans, 2000; Møller and Szép, 2011).

Salmonid fishes (Family Salmonidae) are a group of broad ecological, economic, and cultural importance that exhibit a diversity of migratory strategies, ranging from residency, to potamodromy (migrations within freshwater) to anadromy (migration to sea for growth followed by return to freshwater for spawning). Their complex life cycles and amenability to experimental work and tracking studies has made salmonids the focus of much research in ecophysiology (see reviews by: McCormick et al., 1998; Poole et al., 2003; Hinch et al., 2005; Cooke et al., 2008, 2012; McCormick et al., 2009; Groot, 2010; Björnsson et al., 2011; Eliason and Farrell, 2016). The life histories of anadromous species such as Atlantic salmon (*Salmo salar* L.) necessitate the regulation of internal osmotic balance in hypoosmotic (freshwater) and hyperosmotic (saltwater) environments. In fresh water, osmoregulation requires excess water, which is passively absorbed through osmosis across the gills and skin, to be excreted as dilute urine (Genz et al., 2011). In contrast, osmoregulation in a marine environment requires salmon to continuously drink salt water and actively uptake H_20 through the intestinal epithelium into the body, while limiting intestinal absorption of ions in order to mitigate diffusive water losses through the gills and skin (Grosell, 2007; Whittamore, 2012).

The initial period of acclimation to the marine environment necessitates significant changes to the internal physiology of salmon smolts (Stefansson et al., 2012) and provides an acute physiological challenge (Handeland et al., 2014). Plasma cortisol levels rise during the parr-smolt transformation, and this natural stress response is thought to benefit smolts by mobilizing energy reserves and increasing saltwater tolerance (Bisbal and Specker, 1991; Strand and Finstad, 2007). However, further sources of acute or chronic stress can greatly impair osmoregulatory ability in salmonid smolts (Redding and Schreck, 1983; Iversen et al., 1998) as observed with infestations of ectoparasitic sea lice (*Lepeophtheirus salmonis*) (Poole et al., 2000) or *Gyrodactylus salaris* (Bakke and Harris, 1998). Parasite-induced damage to organs involved in osmoregulation such as the skin, gills or intestines can also directly impact the ability of salmonids to maintain osmotic homeostasis in salt water, leading to disruption of physiological processes, elevated stress, and ultimately mortality (Dawson et al., 1998; Wells et al., 2006; Finstad et al., 2012; Hvas et al., 2017). Through these pathological effects, increased sea lice infestations associated with fish farming are regarded as a significant factor contributing to declines in the marine survival of many Atlantic salmon and sea trout (anadromous *Salmo trutta* L.) stocks in recent decades (Poole et al., 2007; Krkošek et al., 2013; Thorstad et al., 2015; Shephard and Gargan, 2017).

Pomphorhynchus tereticollis is an acanthocephalan endoparasite of various freshwater and brackish fishes with a complex (heteroxenous) life cycle that requires infection of both intermediate and definitive host species. Previously regarded as a synonym for the phenotypically similar *Pomphorhynchus laevis*, recent genetic characterisation has led to the resurrection of *P. tereticollis* as a distinct species within the (former) *P. laevis* complex (Špakulová et al., 2011). Based on morphological and molecular examinations of new and archived material, recent studies provide convincing evidence that *P. tereticollis* is the only *Pomphorhynchus* species present in Ireland and Britain, and that all previous literature pertaining to *P. laevis* in this region represents misidentifications of *P. tereticollis* (Perrot-Minnot et al., 2018; Andreou et al., 2020; Tierney et al., 2020). To avoid confusion, we use the term *P. laevis s.l.* (*sensu lato*) when referring to older studies in which *P. tereticollis* may have been misidentified as *P. laevis*, or to more recent studies in which the taxonomy was uncertain. Such studies have shown that *P. laevis s.l.* infection rates of Irish brown trout peak in spring, coinciding with the annual smolt run (Molloy et al., 1995), and that parasite abundance and prevalence are highest in smolt-aged Atlantic salmon (i.e., 2+) (Fitzgerald and Mulcahy, 1983). Pippy (1969) found that the incidence of *P. laevis s.l.* in Atlantic salmon smolts in Ireland was 25 times higher than in Scotland, England and Wales. Thus anadromous salmonids in Ireland have a particularly high chance of entering salt water while infected by these acanthocephalan parasites.

Pomphorhynchus tereticollis uses gammarid species as intermediate hosts and trophic transmission to a definitive host requires the consumption of an infected gammarid by a suitable fish species (Perrot-Minnot et al., 2020). Upon consumption by a salmonid, *P. tereticollis* use their hooked proboscis to pierce all layers of the intestinal wall and anchor themselves in place. This process creates a perforation leading from the interior to the exterior of the intestinal wall, destroying intestinal mucosa, causing a localized inflammatory response and potentially altering the physiological performance of the intestine in controlling transepithelial ion transport (Wanstall et al., 1986, 1988; Dezfuli et al., 2002b, 2008). Previous studies have concluded that, despite causing such intestinal damage, infection with these acanthocephalans does not significantly reduce growth rates in salmonids and does not directly cause mortality of the host (Hine and Kennedy, 1974; Wanstall, 1984;

Wanstall et al., 1986). However, these studies have focused on the impact of acanthocephalan infection on salmonids in fresh water where osmoregulation does not require equivalent control of transepithelial ion transport or active H_20 uptake through the intestinal wall, as is necessary in saltwater environments.

Exposure to sub-optimal conditions or stressors in fresh water has been shown to reduce osmoregulatory performance and increase the susceptibility of salmonids to parasitic infection and associated mortality in the marine environment (Finstad et al., 2012, 2007). In the present study, we first used genetic barcoding techniques to confirm that Atlantic salmon smolts in our Irish study system are infected by *P. tereticollis*. We then investigated whether natural infection intensities of *P. tereticollis* in wild-caught smolts affect their osmoregulatory performance in saltwater or freshwater environments, and whether such osmoregulatory impacts might also be associated with potentially increased stress. We hypothesized that perforations made by *P. tereticollis* in the intestinal wall would allow uncontrolled ingress of water into the peritoneum, while parasite-induced damage to mucosa, and the associated inflammatory response, would further reduce the ability of salmonids to control ion uptake or water absorption through the intestines. Through these processes, *P. tereticollis* infection was predicted to compromise the osmoregulatory performance of Atlantic salmon in salt water (i.e., hypo-osmoregulation), leading to elevated stress and increased ion concentrations in the blood within marine environments. While we regarded a strong reduction in hyper-osmoregulatory performance as less likely, we predicted that pathological effects of *P. tereticollis* infection (including reduced control of transepithelial ion transport) could also lead to elevated stress and, potentially, reduced blood ion concentrations in freshwater environments.

We characterized *P. tereticollis* infection prevalences and intensities in wild smolts captured from the Burrishoole catchment, Co. Mayo, over a 3-year period and investigated whether infection patterns were associated with smolt size, sex or condition. Smolts captured on the third year were held in fresh (n = 66) or salt (n = 132) water prior to sampling and blood samples were extracted shortly after euthanasia. We then tested whether higher parasite abundance (higher numbers of *P. tereticollis* per individual) was associated with reduced osmoregulatory performance of smolts within each osmotic environment (fresh or salt water) as indicated by plasma chloride concentrations, which provide a direct measure of internal osmotic balance (Strand and Finstad, 2007; McCormick, 2012; Archer et al., 2019). We also measured blood glucose levels as one potential indicator of physiological stress (McGeer et al., 1991) that might accompany impaired osmoregulatory performance in fresh or salt water environments.

MATERIALS AND METHODS

Exploratory Sampling

Wild Atlantic salmon smolts were captured for stock assessment purposes at the tidal limit of the Burrishoole river system (NW Ireland; 53° 55′ 13 N, 9° 35′03 W) in May 2016 (n = 136) and May 2017 (n = 39). The Burrishoole system is comprised of over 45 km of small rivers and streams that link two main freshwater lakes, Bunaveela Lough (46 ha) and Lough Feeagh (410 ha), and ultimately flow into Lough Furnace (141 ha), a brackish, partially tidal lake opening into Clew Bay (Matthews et al., 1997; Whelan et al., 1998). The majority (∼89%) of salmon from the Burrishoole catchment smoltify and migrate to sea as 2 year old fish (Fealy et al., 2014; de Eyto et al., 2016). Captured smolts were dissected and their digestive tracts inspected for the presence of acanthocephalan parasites. Attached and unattached acanthocephalans in each smolt were recorded and stored in ethanol for subsequent DNA barcoding work. Smolt weight (to 0.1 g) and fork length (to 1 mm) were recorded before dissection and sex was determined by inspection of gonads during removal of the digestive tract. Chi-square and Mann-Whitney U tests were used to investigate whether there was a significant relationship between acanthocephalan prevalence or infection intensity, respectively, and sex amongst the smolts sampled in 2016, 2017 or amongst the experimental 2018 samples.

Experimental Setup

On two occasions during 2018, emigrating wild smolts (mean fork length = 138.9 mm, SD = 9.5 mm, range = 121–168 mm) were captured at the Salmon Leap fish trap located at the confluence between the freshwater component of the Burrishoole river system and the saline environment of Lough Furnace and Clew Bay (de Eyto et al., 2020). On each occasion, captured smolts were transported <100 m to an indoor Marine Institute research facility where they were transferred in an *ad hoc* fashion to evenly populate four 500 L aerated experimental tanks. On the first capture occasion (02 May), 66 smolts were distributed evenly amongst four tanks that had each been filled with 300 L of fresh water (i.e., 16–17 smolts per tank). After 24 h all 66 smolts were terminally sampled (see next section), at which point the experiment finished for this freshwater treatment group (24FW) and the four tanks were emptied of water.

On the second capture occasion (05 May), 132 smolts were distributed evenly amongst the same four tanks, each now pre-filled again with 50 L of fresh water (i.e., 33 smolts per tank). During the 2 h after the 132 smolts were transferred, 300 L of locally sourced sea water were gradually added to each tank, raising the salinity in each tank to 26.1–26.3 PPT at a rate that reflects the natural salinity increase experienced by wild smolts moving from the Burrishoole system to coastal waters. Twenty-four hours after the salinity had reached this peak, 66 smolts (16–17 smolts per tank) were terminally sampled and this group then comprised the 24 h in saltwater (24SW) treatment group. The remaining 66 smolts were then terminally sampled 48 h later, i.e., after a total of 72 h in saltwater (72SW). Water temperatures ranged between 8.4 and 13.9°C and dissolved oxygen was maintained at >8.5 mg/L during all phases of the experiment. The tanks were covered throughout the experiment in order to reduce exposure to potential external sources of stress.

Experimental Sampling Procedure

At each sampling time (i.e., 24FW, 24SW, and 72SW), dip nets were used to transfer 16–17 smolts from each of the four tanks

into a pH buffered solution of tricaine methanesulfonate (450 mg L^{-1}) while minimizing disturbance to the remaining smolts. Smolts were monitored until opercular movement ceased and death was confirmed by severing the spinal cord with a scalpel (completing the killing of the animal in accordance with Annex IV of EU Directive 2010/63/EU and Irish Statutory Instrument 5432 of 2012). Blood samples were extracted from the caudal vein (along midline just posterior of the anal fin) with 1 ml 21G lithium-heparinised syringes (containing ∼6 USP units of lithium-heparin and providing ∼15 USP units per ml of blood) immediately after cervical dislocation and transferred to 1 ml Eppendorf© tubes which were stored on ice. Mean duration between dip netting and blood sampling was 9 min and 24 s (SD = 261 s, max = 1110 s, min = 121 s).

Sample Processing

A commercially available meter (FreeStyle Lite: Abbott) was used to take a single measurement of the blood glucose level (mmol/L) of each smolt within 1 min of sacrifice, requiring one drop of blood from the needle of each syringe. This meter has been shown to accurately measure glucose levels in teleosts (Eames et al., 2010). Each smolt was then weighed (to 0.1 g), measured (fork length "FL" to 1 mm), and a ∼2 mm^2 clip of caudal tissue was stored in ethanol for genetic sex determination. The condition factor (Fulton's K) for each smolt was then calculated by the following formula (Ricker, 1975):

$$K = \frac{W}{FL^3} \times 100,$$

where K is condition factor, W is smolt weight (g) and FL is fork length (cm).

Carcasses were placed in individual sealable plastic bags and stored on ice until dissection. All smolts were dissected within 8 h of mortality. An incision was made along the midventral line and the alimentary tract was removed after severing its junctures with the anus and the esophagus. The phenotypic sex of each smolt was determined by visual inspection of the gonads and in any case where the designation was uncertain genetic methods were used to verify sex (as per Finlay et al. (2020)).

Once removed from the body, the alimentary tract of each smolt was temporarily filled with water and pinched at each end to create water tight seals. The oesophageal end was then compressed to pressurize the internal water and the external wall was closely inspected for "pinprick" leaks that would indicate the presence of unplugged perforations left by previously attached acanthocephalans. The alimentary tract was then opened by mesial incision with a fine-point scissors and divided into four sections; (1) stomach (esophagus to pyloric caeca), (2) anterior intestine (33% of intestinal length from post-pyloric caeca to rectum); (3) intermediate intestine (middle 33% of intestine), and (4) posterior intestine (last 33% of intestine ending at anus). Each section was examined for the presence of parasites and the number of attached and unattached acanthocephalans in each section was recorded. On each sampling date, 30 acanthocephalans were examined under a microscope within 15 min of opening the digestive tract and their status as "alive" or "dead" was determined based on the presence or absence of observable movement in response to physical stimulus. A subset of acanthocephalans (n = 264) were also weighed in groups of 2–32 individuals (each group collected from a single smolt) and mean individual parasite weight per group and in total were calculated. Parasite abundance was measured as the number of acanthocephalans in an individual host, regardless of whether the host was infected or not. We calculated the prevalence of infection as the percentage of smolts containing acanthocephalans and infection intensity as the number of acanthocephalans in infected individuals.

Plasma was separated from all blood samples within 4 h of extraction by spinning in a centrifuge (ALC PK 421) at 3000 rpm for 10 min. Where possible, 0.07 ml of plasma was extracted from each sample (12 samples provided less than 0.07 ml of plasma) with an adjustable micropipette (Nichipet Ex) and stored in a 0.5 ml tube at −20°C for chloride analysis. Plasma chloride was measured by coulometric titration using a Jenway PCLM3 chloride meter (reproducibility ±1% or ±1 mmol/l for 100 µl sample at 100 mmol/l). Where plasma quantities were sufficient (98% of samples), chloride samples were tested in duplicate, and triplicates were run for any samples showing a difference greater than three units between the first two replicates. All blood assays were conducted within 3 weeks of freezing plasma.

Molecular Species Identification

Twenty-two of the attached acanthocephalan parasites, representing two randomly selected acanthocephalans from each of eleven randomly selected experimental smolts, were selected for molecular confirmation of species identity. DNA extraction was performed on entire specimens using the DNeasy® Blood and Tissue Kit (Qiagen), following instructions provided in the kit handbook. A 558 bp region of the mitochondrial DNA COI gene was amplified using the PT/PL-COI primers described in Tierney et al. (2020). PCR was performed in a 20 µl total volume consisting of 10 µl of 2× Plain Combi PP Master Mix (Top-Bio), 1 µM each of forward and reverse primer and 10–50 ng of DNA. PCR cycling conditions were as follows; an initial denaturation step of 3 min at 95°C was followed by 35 cycles of 94°C for 30 s 51°C for 30 s and 72°C for 60 s, with final extension step of 72°C for 5 min. Electrophoresis of PCR products was performed on 1% agarose and products were excised and purified using a QIAquick™ Gel Extraction Kit (QIAGEN). Sequencing was performed from both directions using the BigDye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems). Sequencing reactions were purified using the EDTA-ethanol precipitation method described in the sequencing kit handbook and were run on an ABI3500XL DNA analyzer.

Ethics Statement

We adhered to the ASAB/ABS Guidelines for the Use of Animals in Research throughout this project. All actions relating to the capture and sampling of smolts as well as the manipulation of environmental salinity were carried out in accordance with S.I. No. 123/2014 Animal Health and Welfare (operations and procedures) Regulations 2014 and with approval of the Marine Institute animal welfare committee (MI Establishment Authorisation No: AE19121) and the Health Professionals

Regulatory Authority (HPRA Classification Request Number: 066). Procedures for euthanasia were appropriate for salmonids (Popovic et al., 2012). Sampling was carried out by personnel with appropriate training and Individual Authorisations under Scientific Animal Protection Legislation (HPRA).

Statistical Analyses

We conducted all analyses using the statistical computing software R v3.6.1 (R Core Team, 2019). We specified separate generalized least squares models (GLS) using the *gls* function in the *nlme* package (Pinheiro et al., 2019) to investigate the extent to which variation in blood parameters (blood glucose and plasma chloride) was associated with variation in two continuous (acanthocephalan count, i.e., parasite abundance, and smolt condition factor, measured as Fulton's K) and four categorical (treatment group, sex, operator, and tank) explanatory variables. Treatment group had three levels (24FW, 24SW, and 72SW) corresponding with the three sampling dates. Operator, with two levels designating the two operators who performed the blood sampling, was included to control for potential variation in response variables resulting from differences in sampling technique among personnel. Tank had four levels reflecting the four experimental water tanks and sex had two levels, male and female. GLS models were used in order to account for differences in the variance of each of the three response variables observed amongst the three treatment groups, i.e., to control for heteroscedasticity. Initial models included an interaction between parasite abundance and treatment group in order to test whether any effect of acanthocephalan infection on chloride or blood glucose depended on treatment group (i.e., whether parasite effects on these physiological parameters varied between hyper and hypo-osmotic environments, and whether effects increased with time spent in hyper-osmotic environments). Models excluding this interaction were then run in order to test whether parasite abundance was associated with variation in these blood parameters independently of treatment group. AIC values were used to compare models including and excluding the interaction between parasite abundance and treatment group.

We used the *glmmTMB* function (Brooks et al., 2017) to specify generalized linear models (GLMs) to explore the degree to which the variation in infection prevalence and individual infection intensity was associated with variation in the condition factor (Fulton's K), length, weight and sex of smolts sampled in 2016, 2017, and 2018 (n = 312, the subset for which sex and size were both recorded). The individual infection intensity model included only smolts that were infected (n = 257). We used negative binomial models with log link functions to investigate individual infection intensity, in order to account for residual overdispersion in the data, and binomial models with logit link functions to investigate infection prevalence. Due to high collinearity between fork length and weight (R^2 = 0.91), two models were specified for each response variable (i.e., infection prevalence and intensity), each including either fork length or weight, and AIC values were used to compare both models. As both the infection prevalence and infection intensity models containing fork length yielded marginally lower AIC values than the models containing weight (−0.4 and −0.6, respectively), only results from the models with fork-length are presented.

Prior to model fitting, collinearity between all continuous explanatory variables in each model was explored by Pearson's R with the *cor.test* function in the *stats* package and associations between continuous and categorical explanatory variables were examined visually. Variance inflation factors (VIFs) were calculated for all fixed effects in each GLM with the *check_collinearity* function in the *performance* package in R (Lüdecke et al., 2019). We tested for heteroscedasticity and violations of linearity amongst residuals from the GLMs by plotting fitted values against simulated (scaled) residuals with the *DHARMa* package (Hartig, 2019). We tested for temporal autocorrelation with the *acf* function in the *stats* package. The *qqnorm* and *plot* functions were used to investigate residual distributions from GLS models. Chi-square tests were used to investigate whether there were significant differences in acanthocephalan prevalence or abundance amongst experimental treatment groups or amongst tanks within each treatment group.

RESULTS

Molecular Identification of Acanthocephalan Parasite Species

All 22 acanthocephalan specimens examined were identified unambiguously as *P. tereticollis*, with 97–100% sequence match to voucher specimens. Sequence match with *P. laevis* was less than 90% in all cases.

Parasite Prevalence, Infection Intensity and Locations Within the Alimentary Tract

Acanthocephalan infection prevalences amongst smolts sampled in 2016, 2017, and 2018 were 74.2, 64.1, and 66.2%, respectively. Mean infection intensities amongst the 2016, 2017, and 2018 samples, respectively were 9.23, 7.28, and 6.9 acanthocephalans per infected smolt. Infection prevalence amongst male and female smolts, respectively was 76.2 and 75% in 2016 (χ^2 = 0.77, p = 0.68), 93.8 and 40.9% in 2017 (χ^2 = 11.82, p = 0.003), and 71.1 and 63.6% in 2018 (χ^2 = 0.84, p = 0.358). Mean infection intensity per infected smolt amongst males and females, respectively was 12.8 and 4.9 in 2016 (Mann-Whitney U test: W = 1171, p = 0.044), 7.9 and 7.0 in 2017 (W = 53.5, p = 0.416) and 6.0 and 7.6 in 2018 (W = 2063, p = 0.942). Ten of the 198 smolts sampled in 2018 contained unattached acanthocephalans with nine of these smolts also containing attached acanthocephalans. A total of 899 attached and 15 unattached acanthocephalans were recorded amongst the 2018 experimental samples and the number of attached worms per smolt ranged from 1 to 42 (**Figure 1**).

Almost all (93.64%) attached acanthocephalans were in the intermediate (central 33%) section of the intestine while 3.11 and 3.25% were located in the anterior and posterior sections, respectively. No attached or unattached acanthocephalans were found in the esophagus, stomach or pyloric caeca. A few (n = 7) acanthocephalans were attached to the muscle along the

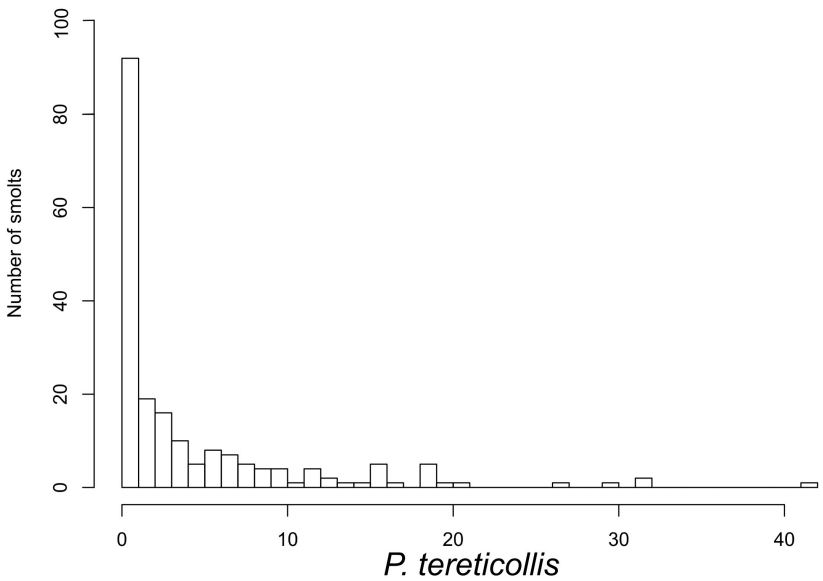

FIGURE 1 | Histogram of *P. tereticollis* abundance for all smolts used in experiment (n = 198).

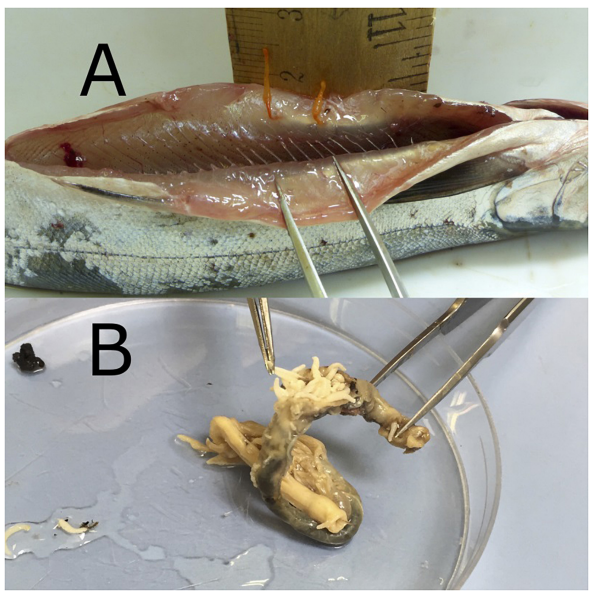

FIGURE 2 | (A) Photograph of *P. tereticollis* outside the alimentary tract of salmon smolt and attached to the peritoneum and muscle wall. **(B)** Salmon smolt intestine, heavily infected by *P. tereticollis*.

inside wall of the peritoneal cavity, having presumably passed completely through the wall of the digestive tract (**Figure 2A**). The mean weight of individual attached worms was 3.1 mg (SD of mean individual weight per smolt = 1.5 mg, max = 7 mg, min = 1.5 mg). All worms from all treatment groups that were observed under a microscope directly after removal from the intestines were found to be alive. Infection prevalence in the 24FW, 24SW, and 72SW treatment groups were 63.1, 56.9, and 77.6%, respectively (χ^2 = 6.7, p = 0.036). Mean acanthocephalan counts per smolt in the 24FW, 24SW, and 72SW treatment groups were 4.29, 3.48, and 5.88, respectively (χ^2 = 40.5, p = 0.769). Acanthocephalan prevalence did not differ significantly amongst the four tanks in the 24FW (χ^2 = 4.9, p = 0.183), 24SW (χ^2 = 6.7, p = 0.084), or 72SW (χ^2 = 0.8, p = 0.841) treatment groups. Acanthocephalan count did not differ significantly amongst the four tanks in the 24FW (χ^2 = 53.2, p = 0.507), 24SW (χ^2 = 43.9, p = 0.390), or 72SW (χ^2 = 49.3, p = 0.657) treatment groups.

No evidence of damage to intestine walls (i.e., pinprick leaks or visible perforations) from recently expelled acanthocephalans was observed in sampled smolts. Additionally, no leakage was observed through intestinal perforations that were plugged by the probosces of acanthocephalans. No mortality of smolts occurred in any treatment group prior to sampling. The binomial model revealed a significant positive association between infection prevalence and Fulton's K (p = 0.012) (**Figure 3A**) but no evidence of significant associations with sex or fork length (**Table 1**). The negative binomial model (**Table 2**) revealed a significant association between individual infection intensity and sex, with infected males having higher infection intensities than infected females (p = 0.043). This model also revealed a non-significant positive association between Fulton's K and infection intensity (p = 0.091) (**Figure 3B**).

Blood Parameters

The mean blood parameters in each treatment group fell within reported ranges for Atlantic salmon (**Table 3**; Bowers et al., 2000; Finstad et al., 2012; Kolarevic et al., 2014). Our initial chloride model revealed no significant interaction between acanthocephalan count and treatment group (p = 0.447). When this interaction was excluded, the model AIC value decreased

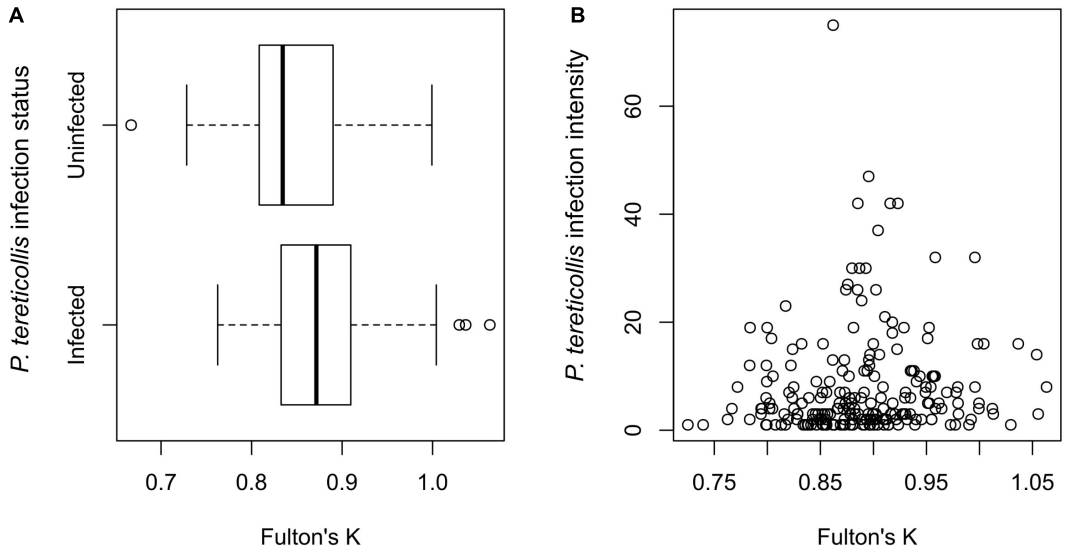

FIGURE 3 | (A) Boxplot of infection status (i.e., whether individual smolts contain *P. tereticollis* or not) vs. Fulton's K (condition factor) (n = 312) and **(B)** scatterplot of individual infection intensity (i.e., the number of *P. tereticollis* per infected smolt) vs. Fulton's K (n = 218). Data include smolts sampled in 2016, 2017, and 2018.

TABLE 1 | Parameter estimates for the binomial prevalence GLM where individual infection status (i.e., infected or uninfected) is the binary response variable.

	Estimate	Std. Error	*z* value	*p* value
(Intercept)	−3.212	2.793	−1.150	0.250
Fultons' K	5.339	2.113	2.527	0.012
Fork Length	−0.054	0.126	−0.426	0.670
Sex: Male	0.252	0.255	0.990	0.322

The intercept corresponds to the estimates (on the logit scale) for females.

TABLE 2 | Parameter estimates for the negative binomial GLM where individual infection intensity (i.e., the number of *P. tereticollis* per infected smolt) is the response variable.

	Estimate	Std. Error	*z* value	*p* value
(Intercept)	−1.338	1.497	−0.893	0.372
Fultons' K	2.030	1.201	1.690	0.091
Fork Length	0.104	0.063	1.640	0.101
Sex: Male	0.276	0.137	2.023	0.043

The intercept corresponds to the estimates (on the log scale) for females.

TABLE 3 | Mean and standard deviations for each blood parameter and physical measurements for each treatment group.

Treatment Group	24FW	24SW	72SW
Chloride	103.9 ± 10.1	117.7 ± 3.9	119.3 ± 4.8
Glucose	6.7 ± 2.6	4.0 ± 0.9	3.3 ± 0.7
Fork length (mm)	139.9 ± 9.1	138.1 ± 7.9	138.7 ± 8.5
Weight (g)	24.5 ± 5.1	22.8 ± 4.1	23.1 ± 4.7
Condition factor (K)	0.884 ± 0.063	0.858 ± 0.054	0.855 ± 0.058

by ∼7 and the main effect of acanthocephalan count was non-significant (p = 0.26) (**Figure 4**). The model without an interaction revealed significantly higher plasma chloride concentrations in the 24SW and 72SW treatment groups relative to the 24FW group (**Tables 3**, **4**). This model also revealed a significant negative relationship between Fulton's K and plasma chloride (**Table 4**). However, acanthocephalan count was not associated with variation in plasma chloride.

Our initial glucose model revealed no significant interaction between acanthocephalan count and treatment group (p = 0.391). Removal of the acanthocephalan count by treatment group interaction term lowered the model AIC value by ∼12.1. No significant association was found between blood glucose and acanthocephalan count in this model (**Table 5** and **Figure 4**). Glucose levels in the 24SW and 72SW groups were significantly lower than in the 24FW group (**Tables 3**, **5**). This model also revealed that blood glucose was significantly negatively related to Fulton's K (**Table 5**).

DISCUSSION

We found little evidence that natural infection by acanthocephalan parasites affected the osmoregulatory performance of Atlantic salmon smolts immediately prior to, or within the first 72 h of, entry into salt water. Moreover, there was no evidence of physiological stress associated with acanthocephalan infection–at least as captured by blood glucose levels, which is one of several possible secondary physiological responses linked to general stress in fishes (Barton, 2002). Infection prevalence amongst experimental smolts was 66.2% and parasite abundance exhibited greater-than-Poisson variance (raw variance 10.3 times greater than raw mean), with few smolts containing many parasites (**Figure 2B**) and many individuals containing zero parasites: a common finding in parasitology in general (Poulin, 2007). The acanthocephalan

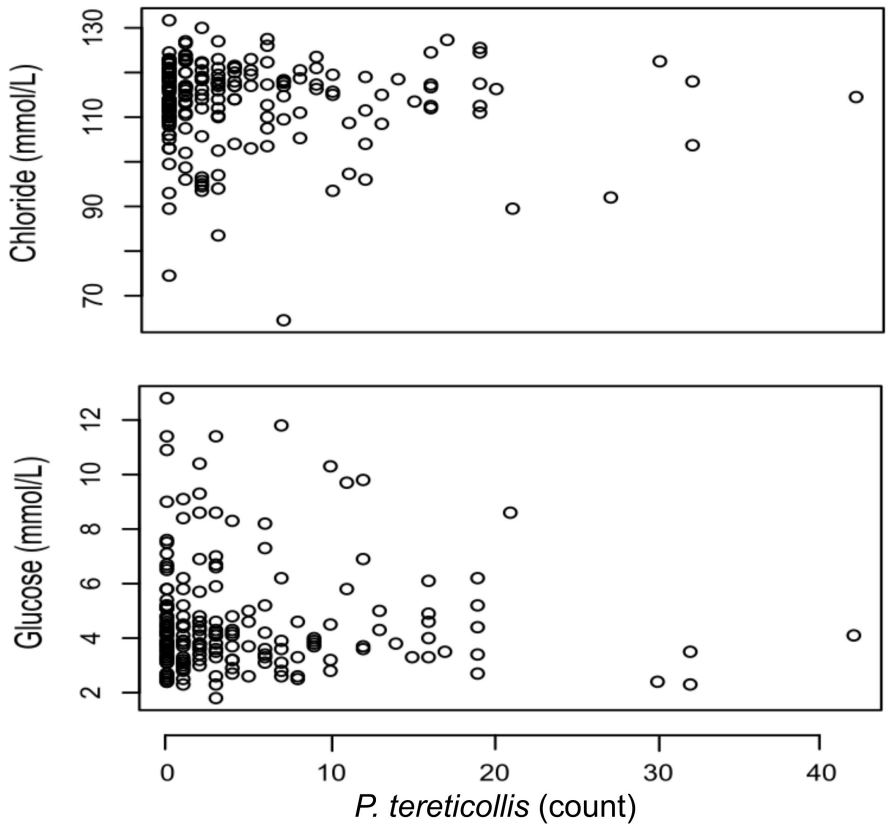

FIGURE 4 | Plasma chloride concentration (mmo/l) and blood glucose concentration (mmol/l) vs. *P. tereticollis* count for all smolts used in the experiment (n = 198).

TABLE 4 | Parameter estimates from the linear model where chloride was the response variable.

	Value	Std. Error	*t*-value	*p*-value
(Intercept)	116.899	6.076	19.241	<0.001
P. tereticollis	−0.060	0.053	−1.123	0.263
Treatment Group: 24SW	13.363	1.384	9.655	<0.001
Treatment Group: 72SW	14.998	1.389	10.796	<0.001
Fulton's K	−13.864	6.704	−2.068	0.040
Tank 2	−0.238	1.038	−0.229	0.819
Tank 3	−0.195	1.054	−0.185	0.854
Tank 4	−0.218	1.055	−0.207	0.836
Sex: Male	−0.198	0.773	−0.256	0.798
Operator: B	−0.354	0.730	−0.485	0.628

Intercept corresponds to females in treatment group 24FW in Tank 1 sampled by Operator A.

TABLE 5 | Parameter estimates from the linear model where glucose was the response variable.

	Value	Std. Error	*t*-value	*p*-value
(Intercept)	10.152	1.131	8.978	<0.001
P. tereticollis	0.013	0.009	1.422	0.157
Treatment Group: 24SW	−2.686	0.313	−8.575	<0.001
Treatment Group: 72SW	−3.481	0.316	−11.028	<0.001
Fulton's K	−3.743	1.224	−3.059	0.003
Tank 2	−0.193	0.183	−1.052	0.294
Tank 3	−0.134	0.186	−0.718	0.474
Tank 4	−0.167	0.193	−0.865	0.388
Sex: Male	−0.199	0.138	−1.439	0.152
Operator: B	−0.196	0.130	−1.509	0.133

Intercept corresponds to females in treatment group 24FW in Tank 1 sampled by Operator A.

parasites, which our DNA barcoding indicated to be *P. tereticollis*, consistently survived the first 72 h that smolts spent in salt water. However, although salinity in the saltwater tanks (∼26 PPT) was representative of local coastal waters, it was lower than in the open ocean habitat of the North Atlantic (∼35 PPT). This lower salinity may have made the environment in the saltwater tanks more tolerable for these acanthocephalan parasites than open ocean environments but was representative of local conditions experienced by these smolts in the wild in their first few days in coastal waters. However, given that the PTL1 strain of *P. tereticollis* (the only strain recorded in Ireland thus far) is believed to have co-evolved with salinity tolerant hosts (O'Mahony et al., 2004; Perrot-Minnot et al., 2018; Andreou et al., 2020), it is also possible that these acanthocephalans can survive for prolonged periods while their hosts are in open ocean environments.

The apparently widespread distribution of *P. tereticollis* (formerly called *P. laevis*) in Ireland (Hine and Kennedy, 1974; Munro et al., 1990; Molloy et al., 1993; Byrne et al., 2003), combined with the preferential use of salmonid definitive hosts by the PTL1 strain in Ireland (Pippy, 1969; Perrot-Minnot et al., 2018; Andreou et al., 2020; Tierney et al., 2020), implies that anadromous Irish salmonids often enter the marine environment while infected with these acanthocephalan parasites. Indeed, we found that infection prevalence amongst salmon smolts that were captured at the tidal limit of the Burrishoole catchment during the 2016, 2017, and 2018 smolt runs exceeded 65% in all years, with mean infection intensities of 9.2, 7.3, and 6.9, respectively. These infection rates are in line with those reported from other Irish catchments where *S. salar* and *P. laevis s.l.* coexist (Pippy, 1969), and previous studies have also found strong overdispersion in *P. laevis s.l.* abundance amongst host fish (Kennedy, 1974, 1996; Brown, 1989). Some authors have suggested that post-cyclic transmission (i.e., transmission occurring when a definitive host eats another definitive host) causes such acanthocephalan overdispersion patterns in definitive host species (Lassiere and Crompton, 1988; Valtonen and Crompton, 1990; Kennedy, 1999). However, the small body size and therefore presumably pre-piscivorous diet of the sampled smolts (no fish parts were observed in the stomach contents of the 175 smolts dissected at time of capture in 2016 and 2017) makes post-cyclic transmission from other host fish unlikely in this case. Given the extensive habitat heterogeneity within the Burrishoole catchment (ranging from fast-flowing streams to deep lakes) (Whelan et al., 1998), it is perhaps more likely that differing feeding behavior in areas with differing densities of the intermediate host *Gammarus duebeni* resulted in contrasting infection opportunities amongst these smolts.

Infection intensity amongst infected smolts was not associated with significant variation in any measure of smolt size (fork length, weight or Fulton's K). Infected males sampled in 2016 contained significantly more parasites per individual than infected females from the same year (12.8 vs. 4.9) although no sex bias in infection intensity was evident in 2017 or 2018. While no significant associations were found between infection prevalence and absolute measures of smolt size (i.e., fork length and weight), infected smolts were actually in better condition (at least as expressed by Fulton's K) than uninfected smolts. At first glance this is surprising, given that smolt condition might be expected to be negatively impacted by parasitic infection. However, salmon are known to undergo a rapid increase in length during smoltification that is not matched by an equivalent increase in weight, leading to a reduction in condition factor (Wedemeyer et al., 1980). Thus, if infection by *P. tereticollis* caused a reduction in growth (i.e., length gain) during the parr-smolt transformation period, it could account for the comparatively high condition factor observed amongst infected individuals relative to uninfected individuals. Alternatively, though, this finding could simply reflect the fact that pre-smolts that feed more actively in the weeks or months preceding their marine migration may attain increased condition relative to less active feeders but also have higher chances of consuming intermediate hosts (i.e., *G. duebeni*) infected with *P. tereticollis*, given that new infections of salmonids in Irish waters tend to peak in spring (Fitzgerald and Mulcahy, 1983; Molloy et al., 1995). Such seasonal patterns of parasite infections in salmonids are often associated with temporal changes in diet (Prati and Henriksen, 2020). Previous research has shown that many species of acanthocephalan parasites cause substantial damage to their hosts' intestines (Kim et al., 2011), reducing growth rates when infection intensities are high and leading to mortality in extreme cases (Latham and Poulin, 2002; Mayer et al., 2003). However, if many of the *P. tereticollis* found in the sampled smolts were relatively recent infections, there may have been insufficient time for their presence to cause a discernible effect on growth. As marine survival can be strongly associated with smolt size (Jonsson et al., 2017; Gregory et al., 2018), any parasite-induced impact on growth or condition factor is likely to have fitness consequences.

We found that *P. tereticollis* deeply penetrated all layers of their host's intestinal wall with their praesoma (hooked proboscis), and in some cases even penetrated the peritoneum and adjacent muscle wall, passing completely out of the intestines in the process (**Figure 2A**), similar to previous reports (Dezfuli et al., 2002a). The anchoring method used by *P. laevis s.l.* has been shown to destroy intestinal mucosa (Wanstall et al., 1988), eliciting a localized inflammatory response (Wanstall et al., 1986; Dezfuli et al., 2008, 2011) and copious mucus secretion (Harris, 1972; Dezfuli et al., 2016). Although there is only limited evidence indicating that salmonids infected with *P. laevis s.l.* suffer reduced growth (Wanstall, 1984), it appears that these infections may cause modifications to the physiological functioning of their host's alimentary tract, potentially reducing control of transepithelial ion transport (Dezfuli et al., 2002a). Thus, we expected that negative impacts from *P. tereticollis* infection might only manifest when the host entered salt water, where effective osmoregulation requires efficient control of transepithelial ion transport by the intestine (Whittamore, 2012).

As anticipated (i.e., Bowers et al., 2000; Urke et al., 2014; Stewart et al., 2016), plasma chloride concentrations were significantly higher in smolts sampled after 24 and 72 h in salt water than in smolts sampled after 24 h in fresh water. However, *P. tereticollis* abundance was not associated with variation in chloride levels in any treatment group, indicating that any intestinal damage caused by *P. tereticollis* was insufficient to cause hyper or hypo-osmoregulatory failure. The range of plasma chloride concentrations in the freshwater and saltwater treatment groups were similar to those reported from other studies of Atlantic salmon in freshwater and saltwater environments (Oppedal et al., 1999; Wells et al., 2006; Kolarevic et al., 2014). However, no sampled smolts displayed highly elevated chloride levels in line with levels that have been recorded in salmon smolts infected with high numbers of salmon lice (*L. salmonis*), which would indicate compromised hypo-osmoregulatory function (Grimnes and Jakobsen, 1996; Wagner et al., 2003).

Hyperglycemia (elevated blood glucose) is a secondary stress response in fish that has been widely used as an indicator of parasite-induced stress in smolts (Wagner et al., 2003; Finstad et al., 2007; Long et al., 2019). No association between glucose and *P. tereticollis* count was detected in any of the treatment groups,

which would suggest that *P. tereticollis* infection intensities observed in this study were insufficient to cause a discernible stress response in smolts in hypo-osmotic environments or within 24- to 72-h of entry into hyper-osmotic environments. However, blood glucose is just one of many possible indicators of a complex, multi-dimensional stress response and thus it remains possible that other measures such as plasma cortisol could reveal parasite-induced effects on host stress levels that we were unable to detect.

Glucose levels were lowest in the group sampled after 72-h in salt water, which might relate to the longer period of fasting that this group experienced prior to sampling (72 h vs. 24 h in the other treatment groups). Plasma glucose is known to be affected by the feeding history and metabolic status of fish (Wells et al., 2006) and so it is possible that the comparatively low glucose levels found in the 72SW treatment group resulted from increased caloric deficit.

The results of this study are based on the use of four replicate tanks for each treatment group. However, despite having 66 smolts in each treatment group (i.e., moderate to large sample sizes), only a small number of smolts had high infection intensities (**Figure 1**), and this may have reduced our ability to detect subtle parasite-induced changes in the blood parameters that we investigated. Also, all *P. tereticollis* found in each treatment group were alive and the vast majority were securely anchored to the intestinal wall by their praesomae, with no sign that others had recently detached (i.e., no vacant perforations in the intestinal wall). When *P. tereticollis* are anchored to the intestinal wall, their praesoma and inflated proboscis bulb appear to form an effective plug, preventing movement of liquid through the surrounding intestinal perforation. The *P. tereticollis* that parasitize juvenile salmon in the Burrishoole catchment are generally absent from adult salmon when they return to the river system for spawning (Deirdre Cotter, pers. obs.). Similarly, Pippy (1980) found no *P. laevis s.l.* in adult salmon caught off Greenland, concluding that the parasites could not endure the prolonged migration period of their host. Furthermore, Molloy et al. (1993) found that sea trout returning to the Burrishoole catchment had lower infection prevalence and intensity than were found in emigrating trout smolts, indicating that *P. tereticollis* are lost during the marine migration. Given that the lifespan of *P. laevis s.l.* in freshwater barbel (*Barbus barbus*) hosts has been estimated at between 6 and 8 months (Nachev and Sures, 2016), it is likely that *P. tereticollis* generally die before migrating salmon hosts return to fresh water. Presumably, after some period in the marine environment these acanthocephalans detach from their hosts' intestines, leaving intestinal perforations unplugged and thereby potentially facilitating ingress of salt water into the peritoneal cavity. However, as *P. tereticollis* in the sampled smolts remained alive and attached after 72 h in salt water we were unable to investigate this possible delayed pathology. As suggested by Pippy (1969), it would be useful for future studies to accurately establish the lifespan of *P. laevis s.l.* in Atlantic salmon at sea.

The shifts between freshwater and marine environments that define diadromous fishes are inherently stressful, demanding complex physiological responses from migrants that are simultaneously exposed to unfamiliar predators, parasites and pathogens. Mortality rates during this transitional period can be particularly high, and any pre-existing factor that increases stress or interferes with physiological processes such as osmoregulation may compromise long-term survival at sea (Finstad et al., 2012, 2007; Hostetter et al., 2012, 2011). While the contribution of non-lethal stressors to delayed marine mortality is often difficult to detect, particularly in cases where multiple stressors have a cumulative effect, their impacts are likely to play an important role in determining the performance of anadromous populations. We have shown that a high proportion of wild Atlantic salmon smolts entering the marine environment from the Burrishoole catchment in recent years are infected with *P. tereticollis* and, based on the literature, it appears likely that similar infection rates of smolts are common in Ireland but not elsewhere. However, we found no evidence to indicate that the infection intensities observed amongst the sampled smolts were associated with altered osmoregulatory performance or blood glucose levels in freshwater or saltwater environments. Despite this, it is possible that infection by *P. tereticollis* causes pathologies that we did not test for or that occur later in the marine environment as salinity increases or as the parasites detach from the intestine. Given the high prevalence of *P. tereticollis* infection amongst anadromous salmonid populations in Ireland, it would be valuable to investigate whether such delayed parasite-induced pathologies occur at sea. Such an investigation could be undertaken in a similar manner to the present study, but conducted over a longer time period at a higher salinity, potentially providing results with applied relevance in the context of fishery management and aquaculture (e.g., marine rearing of farmed Atlantic salmon).

In conclusion, our study adds to a growing body of work examining ecophysiological processes underpinning the performance of migratory fishes (McCormick et al., 1998, 2009; Hinch et al., 2005; Cooke et al., 2008, 2012; Groot, 2010; Björnsson et al., 2011; Eliason and Farrell, 2016) and draws particular attention to the potential role of parasites in determining osmoregulatory abilities. The physiological impacts of parasitism often depend on the extent and patterns of historical coevolution between hosts and their parasites (Prenter et al., 2004; Britton et al., 2011; but see Lymbery et al., 2014). Migratory species are particularly interesting in this context as they are exposed to native and non-native parasites in multiple geographic locations and habitat types. Consequently, infection or infestation may have delayed fitness consequences that occur in a different habitat to where the parasites are initially encountered. We therefore encourage further ecophysiological work on the impacts of parasites on the performance of migratory animals across variable and rapidly changing environments.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by Marine Institute Animal Welfare Committee (MI Establishment Authorisation No: AE19121) and the Health Professionals Regulatory Authority (HPRA Classification Request Number: 066).

AUTHOR CONTRIBUTIONS

RF, TR, and RP conceived and designed the experiment. RF, RP, and GR collected the data. ED conducted the genetic barcoding. RF and TR analyzed the data. RF wrote the first draft of the manuscript. All authors contributed to drafts of the manuscript and gave final approval for publication.

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