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Research Article

Nonconsumptive Effects of Predation and Impaired Chemosensory Risk Assessment on an Aquatic Prey Species

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Weak levels of acidity impair chemosensory risk assessment by aquatic species which may result in increased predator mortalities in the absence of compensatory avoidance mechanisms. Using replicate populations of wild juvenile Atlantic salmon (*Salmo salar*) in neutral and acidic streams, we conducted a series of observational studies and experiments to identify differences in behaviours that may compensate for the loss of chemosensory information on predation risk. Comparing the behavioural strategies of fish between neutral and acidic streams may elucidate the influence of environmental degradation on nonconsumptive effects (NCEs) of predation. Salmon in acidic streams are more active during the day than their counterparts in neutral streams, and are more likely to avoid occupying territories offering fewer physical refugia from predators. Captive cross-population transplant experiments indicate that at equal densities, salmon in acidic streams do not demonstrate relative decreases in growth rate as a result of their different behavioural strategies. Instead, altering diel activity patterns to maximize visual information use and occupying relatively safer territories appear sufficient to offset increased predation risk in acidic streams. Additional strategies such as elevated foraging rates during active periods or adopting riskier foraging tactics are necessary to account for the observed similarities in growth rates.

1. Introduction

Predation has long been recognized as an important and dramatic factor influencing population demographics, local persistence, distributions, and behaviours of prey species. Recently, many studies have begun differentiating between the lethal (after [1]) and nonlethal [2, 3] effects of predation risk on prey. These different processes have been referred to by several related terms, including direct versus indirect [4, 5], consumptive versus nonconsumptive [6, 7], and density- versus trait-mediated [8–10] effects. Nonconsumptive effects (NCEs) resulting from the perceived threat of predation have also been referred to with hyperbolisms including "the ecology of fear" [11] and "predator intimidation" [12, 13].

The strength of NCEs experienced by affected prey is influenced by multiple complementary predator cues from different sensory modalities [14, 15] and information on the specific types and levels of risk conveyed by any cues received [16]. For example, ambush strategists appear to exert greater NCEs on their prey than actively foraging predators [17], with the increased temporal variability in risk associated with the sit-and-wait approach likely driving the differences in prey response [18]. Environmental conditions, including the absence of visual cues at night [19] and physical barriers to transmission due to topographical variability [20–23], may alter both consumptive and nonconsumptive effects when they interfere with the transmission or detection of information on predation risk [24].

In both freshwater and marine systems, weak levels of acidity (pH < 6.6) deprive fishes of an important source of information on risk by rendering damage released chemical alarm cues nonfunctional [25, 26]. Consequently, water-bodies can be divided into functional categories of acidic or neutral around a boundary of pH 6.6 based on the different behavioural patterns demonstrated by resident fish. Acid-impacted juvenile Atlantic salmon (*Salmo salar*) have demonstrated both increased predator mortality in acidic streams relative to neutral ones when they were physically

constrained in a tethering experiment [27] and responses of greater strength to remaining visual threat cues [15] when they are free-swimming. However, visual cues are often unavailable and may be unreliable in aquatic habitats, so additional compensatory mechanisms are necessary to explain the persistence of prey populations in acidic streams given their apparent greater vulnerability to predation. Acidified aquatic habitats therefore present opportunities for studying how environmental degradation influences the strength of NCEs in natural settings.

Despite being nonlethal, the NCEs of predation may contribute indirectly to prey mortality via interactions between induced stress responses and other factors [28]. In elk (*Cervus elaphus*), for example, stress hormone levels have been positively associated with the perceived level of risk of predation by wolves (*Canis lupus*) [29], and these elevated stress levels have in turn been linked to decreases in female fertility and calf recruitment [30]. In fishes, similar reproductive effects as well as decreased growth rates in adults and juveniles have been demonstrated under elevated predation regimes [3, 31]. Persistent and heritable life history alterations, including the production of significantly larger eggs during reproduction following exposure to predators as juveniles [32, 33], indicate that some NCEs may be at least equally important to the evolutionary ecology of prey species as direct consumptive effects.

Nonconsumptive effects may extend beyond physiological and reproductive consequences for prey species. Frequently observed NCEs include alterations in spatial distributions [3, 34], foraging patch preferences, and activity levels [35] that may collectively serve to reduce vulnerability to predation. Under some circumstances, however, prey may be able to at least partially compensate for lost foraging opportunities due to increased competition or changes in antipredator time budgets [7] by increasing the frequencies of risky behaviours. For example, green sea turtles (*Chelonia mydas*) of relatively poor body condition forage more frequently in the water column when tiger sharks (*Galeocerdo cuvier*) are present than conspecifics of higher condition [13].

Here, we describe a series of experiments designed to address whether juvenile Atlantic salmon in neutral and acidic nursery streams differ in their (1) preferences for more or less risky microhabitats, (2) diel activity patterning to reflect the absence of chemical information in acidic streams and the availability of visual cues only during light hours, and/or (3) growth patterns resulting from tradeoffs between antipredator behaviours and other compensatory fitness-related activities such as foraging.

2. Methods

2.1. Study Sites. All experiments were conducted during the summer months (July and August) from 2008 to 2011 in three neutral (pH ≥ 6.6) and two weakly acidic (pH < 6.6; after [15]) Atlantic salmon nursery streams in the Northwest Miramichi River system, NB, Canada (Table 1). These streams have served as the setting for several earlier studies on the chemically-mediated antipredator behaviours of juvenile salmon that reliably demonstrate differences attributable to the loss of alarm cue function [15, 25, 27]. The salmon used were exclusively young-of-year (0^+), hereafter referred to as "fry."

Table 1: GPS coordinates of study sites in five Atlantic salmon (*Salmo salar*) nursery streams in Northumberland County, NB, Canada.

Stream	Class[1]	Location	
Catamaran Brook	Neutral	46°52.747′ N	66°06.235′ W
Otter Brook	Neutral	46°52.749′ N	66°02.214′ W
Lower Devil's Brook	Neutral	46°52.377′ N	66°13.545′ W
Upper Devil's Brook	Acidic	46°52.386′ N	66°13.610′ W
Correy Creek	Acidic	46°52.424′ N	66°13.603′ W

[1]Neutral: pH ≥ 6.6; acidic: pH < 6.6.

2.2. Experiment 1: Microhabitat Selection. Individual free-swimming salmon fry were located by a snorkelling observer and monitored for ≥ 3 min in order to identify their central foraging station [36]. The occupied sites of twenty individual salmon in each of four streams (neutral: Catamaran Brook and Lower Devil's Brook; acidic: Upper Devil's Brook and Correy Creek; $n = 40$ sites in each stream class), as well as unoccupied nearby control sites ~1 m directly upstream, were marked with flagged rocks and compared to quantify differences in microhabitat preferences between stream classes. Habitat measurements consisted of pH, temperature (°C), channel width (m), distance from nearest riverbank (m), shore index (distance from bank/channel width), depth (m), flow rate ($m\,s^{-1}$) at 50% depth, substrate complexity (described in [15, 37]), canopy cover (proportion of the sky directly overhead covered with tree canopy or other vegetation, after [25]), and substrate composition (per cent of area within a 0.5 m radius covered with substrate < 1 cm, 1 cm ≤ x < 5 cm, 5 cm ≤ x < 15 cm, and ≥15 cm) based on the grain size classes delineated by the Wolman [38] Pebble Count. Physical measures were combined into a multivariate response and analyzed with two-way MANOVA against stream class (neutral or acidic) and fry preference (occupied or unoccupied).

2.3. Experiment 2: Diel Activity Patterning. A series of snorkelling surveys ($n = 3$ for each time/stream combination) were conducted at 3-week intervals during 2008 at midday (10:00–14:00) and midnight (22:00–02:00, using an underwater flashlight) in two 30 m reaches in each of four streams (neutral: Catamaran Brook and Otter Brook; acidic: Upper Devil's Brook and Correy Creek). Haphazard transect lines were followed in zig-zag patterns from bank to bank and every salmon fry sighted during each survey were recorded. These counts were transformed into density estimates in areas defined by reach length and mean channel width based on $n = 3$ measurements taken perpendicular to the stream axis. Due to the low overall numbers of active, nonsheltering fish throughout the study streams during this particular sampling period, density estimates were square-root transformed to reduce the magnitude of positive skew and then examined in

a one-way ANOVAs against diel period in each stream class (neutral or acidic). Direct comparisons of abundance/density estimates between streams and stream classes were avoided in order to focus on diel patterning within classes and limit potential confounds arising from different absolute abundance or densities between populations.

2.4. Experiment 3: Captive Growth Trials. Wild salmon fry were captured individually via dipnet from neutral Catamaran Brook, weighed (W), measured (standard length in mm, L_S), and placed into one of two mesh enclosures in either Catamaran Brook or the weakly acidic Correy Creek. The enclosures consisted of nylon nets (6 m length × 1 m width × 0.75 m height, mesh size 3 mm) supported by aluminium conduit poles driven into the substrate and anchored to nearby trees with nylon rope. River gravel was shovelled in to a depth of ~3 cm and several large rocks (>15 cm diameter) were added to mimic natural substrate offering refuge from both predators and high water flows. These enclosures effectively retained captive fish and delivered natural drift forage while excluding aquatic, aerial, and terrestrial predators and have previously been used in field studies of juvenile Atlantic salmon behaviour [39]. Fish were transported between sites using 200l aluminium tanks on loan from the Miramichi Salmon Association, Southesk, NB. Six salmon were placed into each enclosure at a density of $1\,m^{-2}$ for seven days, during which each enclosure was exposed to daily (11:00 or 14:00) 100 mL injections of either damage-released chemical cues (described in [15]) or stream water as a control to simulate high and low risk conditions. Fish were removed 24 hours after the last injection, reweighed and measured, and released at their approximate site of capture in Catamaran Brook. Five replicate trials were conducted in each stream, involving a total of 120 fish ($n = 6$ for each stream × treatment combination and $n = 30$ fish per treatment per stream). Specific growth rates ($\ln(W_2/W_1) \div$ time), mean changes in body size (L_S), and Fulton's condition index ($K = 100(WL_S^{-3})$) were examined against stream class (neutral versus acidic) and treatment (high versus low risk) in two-way ANOVAs. All statistical analyses and figures were generated using R version 3.1.1 [40].

3. Results

3.1. Experiment 1: Microhabitat Selection. Territories occupied by wild Atlantic salmon fry demonstrated several statistically significant differences in physical measures compared to unoccupied control sites within each stream class (Figure 1). Fish under acidic conditions occupied sites that had slower rates of flow relative to control sites ($F_{1,78} = 6.442$, $P = 0.013$, Figure 1(a)). While lower flow rates may result in greater temporal persistence of chemical cues within a given area, the loss of function of chemical alarm cues due to acidification is unlikely to play a role in driving the establishment of this apparent preference. Lower rates of flow may also result in longer residence times within an area for drift-borne forage material, as well as more abundant benthic fauna, potentially resulting in greater forage abundance facilitating more risk-averse foraging strategies relative to high flow conditions. Conversely, high flow sites may deliver drift forage opportunities at a greater rate than low flow sites while also reducing the temporal persistence of chemical cues.

Salmon under neutral conditions demonstrated significant preferences for sites with greater proportions of smaller substrate particles (substrate grain size: diameter < 1 cm: $F_{1,78} = 5.849$, $P = 0.0179$, Figure 1(c); 1 cm ≤ x < 5 cm: $F_{1,78} = 2.899$, $P = 0.093$) and for sites with lower proportions of the largest substrate grain size (diameter > 15 cm: $F_{1,78} = 9.175$, $P = 0.0033$, Figure 1(d)). Salmon in acidic streams, by contrast, demonstrated nonsignificant trends towards occupying sites with lower proportions of the smaller substrate grain size classes (Figure 1). Larger-grained substrate particles, while potentially reducing line-of-sight distances, may also provide a greater abundance of physical refugia and decreased rate of flow due to turbulence. The latter potential consequence of larger grain size is demonstrated by the observation that fish under acidic conditions occupied sites characterized by slower flow rates relative to unoccupied sites (Figure 1(a)).

Fish in the neutral streams preferred habitats with greater substrate complexity ($F_{1,78} = 8.844$, $P = 0.0039$) independent of substrate grain size. There was no demonstrated difference in preference for channel position (distance from nearest bank · channel width^{-1}) within either stream class, although a general preference for near-shore habitats appears to generate lower values for channel position within the wider neutral streams. Occupying locations closer to a shore may potentially limit the angle of attack available to foraging predatory fishes but may also increase vulnerability to attack from terrestrial predators.

3.2. Experiment 2: Diel Activity Patterning. Overall, juvenile salmon demonstrated trends towards greater median abundances at midday relative to midnight in the acidic study streams (Figure 2). In order to prevent overrepresentation of estimates of salmon fry abundance from the neutral streams in which they were more abundant during the study period, the analyses were repeated on a subset of the data consisting of one stream of each class in which salmon were most commonly recorded (Catamaran Brook and Upper Devil's Brook). In this subset of the data, juvenile salmon were significantly more abundant during the day than at night in the acidic Upper Devil's Brook ($F_{1,10} = 5.993$, $P = 0.0034$; Figure 2(b)). While this is consistent with other studies that found fry to be more active during the day [41], the observed difference between stream classes suggests that this patterning is mediated by environmental degradation and the availability of chemical information.

3.3. Experiment 3: Captive Growth Trials. Mean physical measurements recorded within the captive growth enclosures during each replicate did not differ between streams (Table 2). Captive salmon exposed to both the high risk (AC) and control (SW) treatments in neutral Catamaran Brook and acidic Correy Creek demonstrated positive specific growth rates in both weight (Figure 3(a)) and length (Figure 3(b)) over the course of the experiment. While the growth rates of subjects exposed to the different risk treatments did not differ within streams, salmon exposed to both treatments

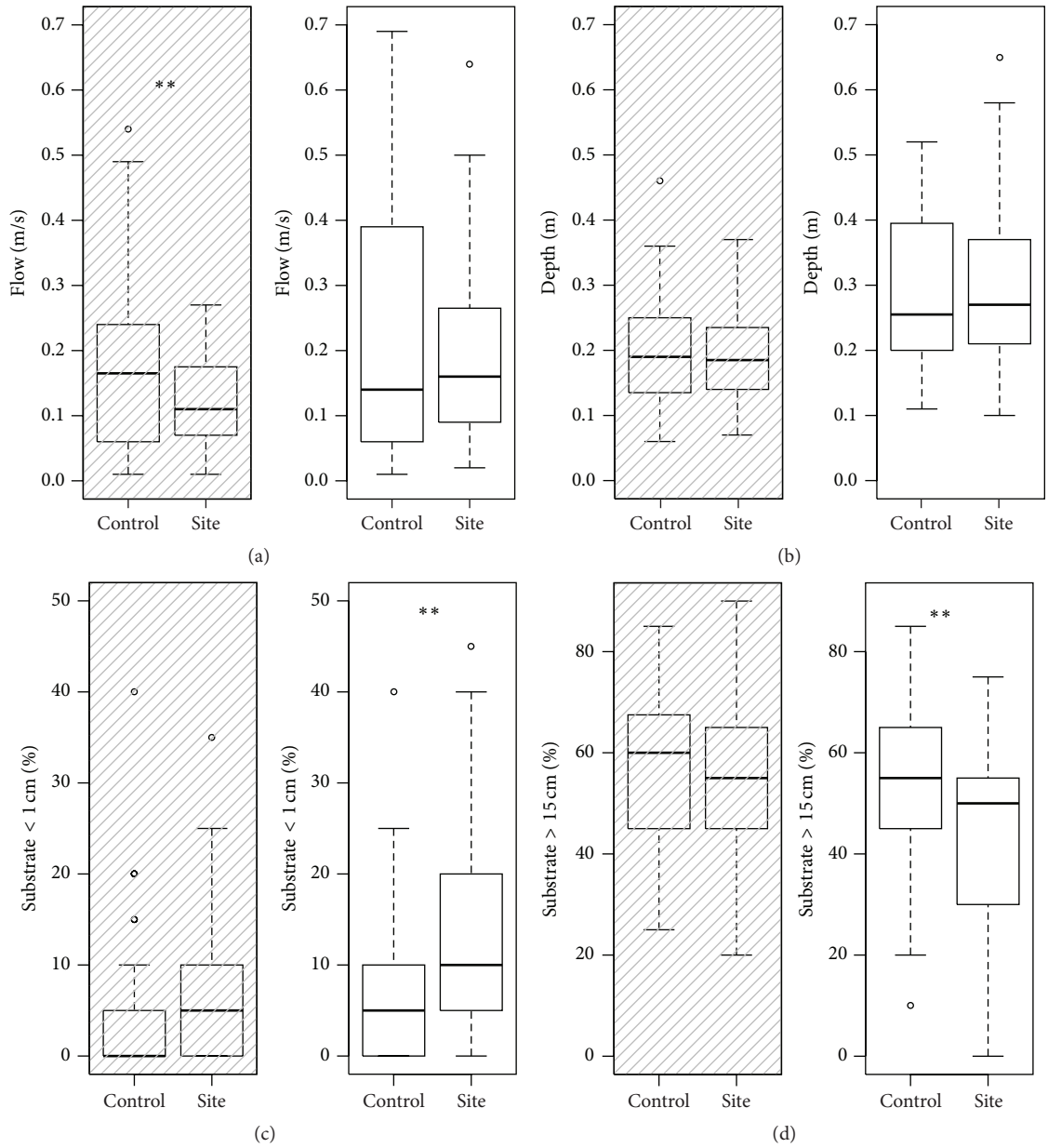

Figure 1: Boxplots showing the median, first and third quartiles, and 95% CI of different physical habitat measurements within a 1 m radius of occupied central place foraging sites (Site) of Atlantic salmon (*Salmo salar*) fry compared to unoccupied control sites (Control) 2 m directly upstream in two neutral (open plots) and two acidic (shaded plots) streams. (a) Depth (m); (b) flow rate (m s^{-1}); (c) percent substrate particles < 1 cm diameter; (d) percent substrate particles > 15 cm diameter ($n = 40$ per box). Asterisks denote significant differences from zero in one-sample t-tests ($^{**}P < 0.01$).

Table 2: Mean (±SD) values of physical characteristics captive 0^+ Atlantic salmon (*Salmo salar*) were exposed to inside mesh enclosures during a cross-population transplant experiment[1].

Stream	Class	Treatment	Temperature (°C)	Depth (m)	Flow rate (m s^{-1})
Catamaran Brook	Neutral	AC	18.74 ± 1.64	0.216 ± 0.07	0.0812 ± 0.03
		SW	18.74 ± 1.64	0.203 ± 0.06	0.0631 ± 0.02
Correy Creek	Acidic	AC	18.19 ± 1.54	0.227 ± 0.05	0.0827 ± 0.04
		SW	18.19 ± 1.54	0.224 ± 0.05	0.0825 ± 0.04

[1] $n = 5$ replicates per stream × treatment combination. AC = alarm cue (high risk), SW = stream water (control).

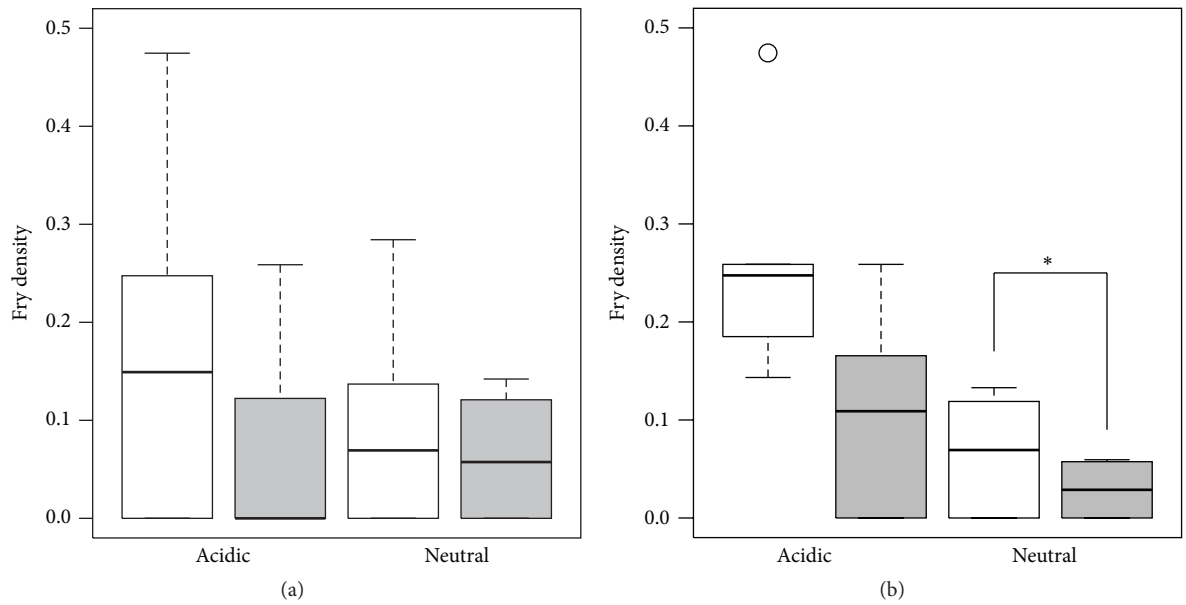

Figure 2: Boxplots showing the median, first and third quartiles, and 95% CI of square root-transformed density estimates (no. m^{-2}) of 0^+ Atlantic salmon (*Salmo salar*) fry observed via snorkelling at midday (open bars) and midnight (closed bars) in (a) two acidic and two neutral nursery streams and (b) Upper Devil's Brook (acidic) and Catamaran Brook (neutral). Asterisks denote significant differences between diel periods within stream classes from 1-way ANOVA ($^*P < 0.05$).

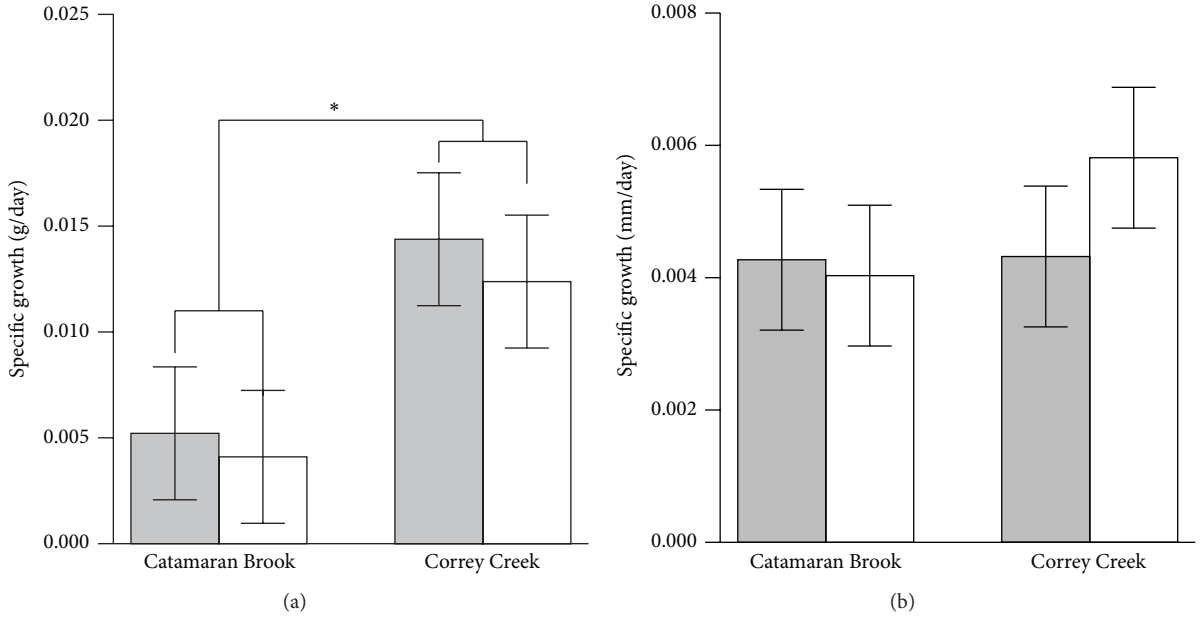

Figure 3: Mean (±SE) specific growth rates of wild-caught 0^+ Atlantic salmon (*Salmo salar*) fry from Catamaran Brook in their neutral natal stream or transplanted into acidic Correy Creek. Changes in (a) weight (g) and (b) standard length (mm) over 8 days with daily exposure to injections of damage-released chemical cues (shaded bars) or a stream water control (open bars; $n = 30$ measurements per bar). Asterisks denote significant differences between streams from 1-way ANOVA ($^*P < 0.05$).

demonstrated significantly greater rates of weight increase in the acidic transplant stream, Correy Creek, than they did in their native Catamaran Brook ($F_{1,16} = 5.97$, $P = 0.0266$). Salmon exposed to three out of the four stream × treatment combinations actually demonstrated a decrease in Fulton's condition index (K), with the sole positive change occurring in the group transplanted into Correy Creek and exposed to chemical alarm cues (Table 3). This group of fish demonstrated rates of increase in weight similar to those fish transplanted into Correy Creek and exposed to the control (Figure 3(a)) but a smaller rate of mean increase in length (Figure 3(b)), leading to a positive change in the condition

Table 3: Mean values of fish size and Fulton's condition index (K) of 0^+ Atlantic salmon (*Salmo salar*) at the beginning and end of captive cross-population transplants[1]. Positive differences are indicated in bold font.

Stream	Cue	L_{S1}	L_{S2}	ΔL_S	W_1	W_2	ΔW	K_1	K_2	ΔK
Catamaran Brook	AC	44.27	45.47	**1.2**	1.20	1.24	**0.04**	1.38	1.31	−0.07
	SW	44.37	45.45	**1.08**	1.16	1.18	**0.02**	1.32	1.25	−0.07
Correy Creek	AC	44.00	45.23	**1.23**	1.15	1.25	**0.1**	1.34	1.35	**0.01**
	SW	44.07	45.68	**1.61**	1.17	1.26	**0.09**	1.36	1.33	−0.03

[1] L_S = standard length (mm); W = weight (g). Means are from 5 × 8 day replicates in each stream (n = 6 fish per replicate, n = 60 total).

index as K is inversely proportional to length. Overall, there was no significant difference in growth between streams or treatments.

4. Discussion

The three experiments presented above were intended to elucidate and quantify the NCEs of environmentally-mediated chemosensory impairment of acid-impacted and control populations of juvenile Atlantic salmon. The fact that salmon fry were present in these streams throughout the study period (2008–2011) and beyond indicates that acid-mediated sensory impairment does not result in absolute mortality of juveniles nor do adult spawners avoid weakly acidic nursery streams. Persistence in the study streams does not preclude the possibility of significant acid-mediated differences in interannual survival of juveniles or frequencies of return of spawning adults, although detecting any such differences was beyond the logistic parameters of these experiments. While we have attributed our findings to the acid-mediated loss of alarm cue function, we cannot entirely dismiss the possibility that other environmental factors may contribute to the observed behavioural patterns.

In terms of habitat selection (Experiment 1), juvenile salmon living under neutral conditions appear to occupy sites characterized by relatively small substrate grain size and greater flow rate. Both of these physical characteristics are associated with greater frequencies of drift forage arrival in less turbulent currents. They also demonstrated a preference for sites with greater substrate complexity, which may obstruct some portion of the field of view. This preference may reflect a behavioural tradeoff between heightened ambient risk level arising from decreased visual fields and increased drift foraging opportunities mediated by the availability of chemical risk cues. By contrast, juvenile salmon under acidic conditions appear to prefer sites with lower flow rates and substrate complexity. They also prefer larger substrate grain sizes, a combination that may minimize both exposure to visually foraging predators and the direct costs of predation associated with chemosensory impairment while also reducing drift foraging opportunities.

Selective habitat use in response to predation may result in the fragmentation of populations as prey avoid high risk areas [42]. This is of particular importance for stream-dwelling fishes as the dendritic nature of river systems constrains migratory fish to the channel network [43]. Avoidance of high risk connecting channels will therefore limit both the habitat availability and connectedness of subpopulations. Interestingly, a meta-analysis of altered habitat preferences in aquatic systems suggests that increased use of refuges increases the magnitudes of NCEs [44]. One possible explanation for this could be that refuging increases prey density, thereby increasing levels of resource competition, which itself has been demonstrated to increase the strength of NCEs [45, 46]. However, other studies suggest that increasing habitat complexity and reducing the visual field of salmon fry result in increased local densities [47, 48] due to reduced territorial behaviour [49, 50]. Recently, it was shown that smaller territory sizes do not result in differences in growth rate due to limited foraging opportunities in salmon fry [51, 52].

In Experiment 2, salmon fry under acidic conditions demonstrated a trend towards greater levels of activity during the day than at night, while under neutral conditions they demonstrated no preference. In both stream classes, predatory book trout (*Salvelinus fontinalis*) were more active at night. These findings are mostly in agreement with other studies that demonstrated a preference for diurnal activity in salmon fry [41], with the caveat that this preference is more pronounced in acidified streams. Under acidic conditions, diurnal behavioural patterns may mitigate the importance of chemical cues to prey survival due to the increased availability of visual cues during active periods while reducing the likelihood of encountering nocturnal predators such as brook trout. Temporal avoidance of fish predators under neutral conditions, by contrast, may provide smaller survival benefits given the availability of chemical cues conveying information on risk levels under light-limited conditions. Similar diel activity patterning has been demonstrated in coral reef fishes reflecting the active foraging periods of predators [53].

In Experiment 3, there were no significant differences in growth rates between high and low risk treatments in the neutral and acidic streams. Given the shared provenance of the salmon fry and the greater rates of weight gain in the acidic stream, it appears that the acidic transplant stream may have actually provided a better set of conditions for growth in the predator-excluding mesocosms than the native stream. Unfortunately, including only one neutral stream population does not eliminate the possibility that the observed greater weight increase was the result of predator release and risk-prone foraging behaviour in the absence of chemical alarm cues. Increases in both body size (L_S) and weight indicate that weak acidification does not negatively affect growth either directly through physiological impairment or indirectly through shifts in forage abundance and/or composition within the enclosures. Conversely, the absence of differences between high and low risk treatments within the neutral

stream supports the notion that prey fish are able to adjust their antipredator strategies in order to maintain sufficient foraging activities at this density (i.e., 1 m^{-2}). In the context of the short-term behavioural responses to chemical alarm cues previously demonstrated by salmon fry [15], energetic costs incurred from immediate decreases in foraging following exposure to short-lived risky cues may be offset or replaced by increased rates of foraging following resumption of normal activities. This type of compensatory foraging pattern has recently been demonstrated in wild-caught Trinidadian guppies (*Poecilia reticulata*) [54] under natural settings and Hart's rivulus (*Anablepsoides hartii*; Elvidge and Brown, unpublished data) under laboratory conditions.

A recent meta-analysis of 453 peer-reviewed studies examining NCEs on prey species found that the majority (83%) involved aquatic systems under laboratory or mesocosm conditions and focused specifically on chemical information (73%) on risk level as the primary sensory modality [55]. These experiments therefore represent an important extension of this research area into natural settings. Environmental degradation in the form of freshwater acidification results in the loss of public chemical information on ambient risk levels. Compensatory mechanisms adopted by Atlantic salmon fry, including the changes in habitat preference, diel activity patterning, and foraging strategies demonstrated in the present study, are indicative of behavioural NCEs of perceived predation risk under natural settings. Our results suggest that these types of subtle differences are likely common between populations exposed to different predation regimes and environmental stressors.

5. Conclusion

Fishes living in weakly acidic water (pH < 6.6) are deprived of chemical information on ambient predation risk levels to interference with damage-released alarm cues. Previous work has shown that when acid-impacted juvenile Atlantic salmon are physically constrained from adopting compensatory behavioural mechanisms to offset this loss of information, they experience increased levels of predation risk. Our findings indicate that free-swimming wild salmon effectively compensate for chemosensory impairment by (1) occupying safer habitats that offer more abundant physical refugia from predators and (2) altering their diel activity patterns to maximize the availability of remaining (visual) information on risk by reducing their activity levels at night and increasing them during the day. Importantly, (3) these combined mechanisms appear sufficient to enable survival without reducing growth rates. These differences in behaviour represent NCEs of predation risk mediated by environmental degradation in Atlantic salmon habitats which may have important consequences on impacted salmon populations, particularly the possibility of increased competition within more desirable habitats in acidic streams.

Ethical Approval

The work reported herein was approved by Concordia University Animal Research Ethics Committee (protocol AREC-2010-BROW) and conducted with permission from Fisheries & Oceans Canada and the New Brunswick Ministry of Natural Resources.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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