ARTICLE

Social cues may advertise habitat quality to refuge-seeking conspecifics

C.K. Elvidge, E.L.L. Cooke, R.A. Cunjak, and S.J. Cooke

Abstract: Individuals travelling through landscapes may use the presence of conspecifics to evaluate habitat quality. Juvenile Atlantic salmon (*Salmo salar* L., 1758) are usually territorial and exhibit some degree of density-dependent regulation in wild populations. They are also vulnerable to heat stress and may need to locate a thermal refuge to offset metabolic costs above certain temperature thresholds. During July 2010, a heat wave resulted in water temperatures in the Miramichi River system exceeding 30 °C. During this period, salmon parr were observed aggregating in cold-water refugia at densities several orders of magnitude greater than usual. We tested whether groups of wild-caught salmon parr held at high densities (160 parr/m²) would have an attractant effect on free-swimming parr at three sites differing in temperature between 16.5 and 24 °C. Although neither temperature nor site influenced the number of parr that we observed, there were significantly more parr in close proximity (<1 m) to the artificial aggregations than to the controls. These results suggest that social cues from high-density aggregations of conspecifics during extreme temperature events may advertise the location of thermal refugia to others. Understanding how heat-stressed salmon locate refugia may prove valuable to ongoing conservation efforts given the likelihood of increasingly frequent and extreme high-temperature events.

Key words: aggregations, *Salmo salar*, Atlantic salmon, parr, heat stress, information use, territoriality, thermal refuge/refugia.

Résumé : Les individus qui se déplacent dans les paysages peuvent se servir de la présence de congénères pour évaluer la qualité de l'habitat. Les saumons atlantiques (*Salmo salar*, L. 1758), juvéniles sont habituellement territoriaux et font preuve d'un certain degré de régulation dépendant de la densité au sein de populations sauvages. Ils sont également vulnérables au stress thermique et, au-delà de certains seuils de température, peuvent devoir trouver un refuge thermique pour compenser les coûts métaboliques. Durant le mois de juillet 2010, une vague de chaleur a produit des températures de l'eau supérieures à 30 °C dans le réseau du fleuve Miramichi. Durant cette période, le regroupement de tacons de saumon a été observé dans des refuges d'eau froide à des densités de plusieurs ordres de grandeur supérieures à leurs densités habituelles. Nous avons vérifié si des groupes de tacons de saumon capturés à l'état sauvage maintenus à haute densité (160 tacons/m²) exercent un effet d'attraction sur des tacons nageant dans trois endroits de différentes températures allant de 16,5 à 24 °C. Si ni la température ni l'emplacement n'influençait le nombre de tacons observés, il y avait un nombre significativement plus grand de tacons tout près (<1 m) des regroupements artificiels que de témoins. Ces résultats portent à croire que des signaux sociaux provenant de regroupements de congénères de forte densité durant des épisodes de température extrême pourraient communiquer l'emplacement de refuges thermiques à d'autres individus. La compréhension de la manière dont les saumons en situation de stress thermique situent des refuges peut s'avérer utile pour les efforts de conservation en cours, étant donné la probabilité d'épisodes de haute température de plus en plus fréquents et extrêmes. [Traduit par la Rédaction]

Mots-clés : regroupement, *Salmo salar*, saumon atlantique, tacon, stress thermique, utilisation de l'information, territorialité, refuge thermique.

Introduction

To individuals moving through landscapes (Schmidt et al. 2010), the presence of conspecifics (Pizzatto et al. 2016) may be a reliable indicator of physical habitat quality (Muller et al. 1997), forage availability, and low levels of predation risk (Nocera et al. 2009). Fish possess sophisticated chemosensory capabilities, and a wide range of fish taxa have demonstrated the ability to discriminate between the odours of conspecifics of different social status (Todd et al. 1967) and physiological condition (Giaguinto and Hoffmann 2012), from different populations (Brown et al. 2009) and life-history stages (Harvey and Brown 2004; Parkos and Wahl 2010), and to determine the recent diets of predators from their metabolites (reviewed in Ferrari et al. 2010; Scherer and Smee 2016). In the context of habitat selection (Reed et al. 1993; Campomizzi et al. 2008), larval stages of some coral reef (Sweatman 1988; Igulu et al. 2011) and flatfishes (Ryer et al. 2007) appear to use the presence of conspecific adults to evaluate the quality of areas to settle in, although other species may avoid conspecifics (Roux et al. 2015). Larval fish can also use social and chemical cues indicating the presence of predators to avoid settling in risky areas (Manassa and McCormick 2013). In migratory fishes like the salmonids, chemical cues from conspecifics have long been believed to contribute to homing behaviours within stream systems during spawning runs (Nordeng 1977).

C.K. Elvidge, E.L.L. Cooke,* and S.J. Cooke. Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, ON K1S 5B6, Canada.
R.A. Cunjak. Canadian Rivers Institute and Department of Biology, University of New Brunswick, P.O. Box 4400, Fredericton, NB E3B 5A3, Canada.
Corresponding author: Chris K. Elvidge (email: chris.k.elvidge@gmail.com).
*Present address: Department of Ocean Sciences, Memorial University, St. John's, NL A1C 5S7, Canada.

Fig. 1. High-density aggregation of Atlantic salmon (*Salmo salar*) parr (1+ and 2+ age classes) in a cold-water refuge in the Little Southwest Miramichi River, New Brunswick, Canada, during a high water temperature event (>30 °C) in July 2010. Photo, which appears in colour on the Web, is by R.A. Cunjak.

The upper thermal tolerance limits of juvenile Atlantic salmon (*Salmo salar* L., 1758) are among the highest reported in the salmonids (Elliott 1991), with wild salmon fry (0+ age class) demonstrating increasing activity levels proportional to temperature up to 28 °C (Breau et al. 2011). The activity levels and oxygen consumption of salmon parr (1+ and 2+ age classes), however, plateau at 24 °C concurrent with elevated blood and muscle lactate levels indicative of metabolic dysfunction. Above this temperature threshold, salmon parr abandon their normal territorial feeding behaviours (Keenleyside and Yamamoto 1962; Bilhete and Grant 2016) and form high-density aggregations in cold-water refugia (Fig. 1; Breau et al. 2011). This ontogenetic reduction in thermal tolerance likely reflects the greater metabolic requirements associated with increasing body size (Schmidt-Nielsen 1984), as Atlantic salmon are generally considered to be the most temperature sensitive of the salmonids as spawning adults (Jonsson and Jonsson 2009). The combination of high-temperature sensitivity and long-standing conservation concerns for populations of Atlantic salmon (Parrish et al. 1998) make them an ideal and important sentinel species for quantifying the effects of climate change and habitat alteration on stream-dwelling fishes.

During an extreme high-temperature event in the mainstem Little Southwest Miramichi River, New Brunswick, Canada, in July 2010, water temperatures rose as high as 30.66 °C, a record in over 20 years of local monitoring (R.A. Cunjak and E. Corey, unpublished data). During this event, Atlantic salmon parr were observed aggregating in cold-water thermal refugia at densities over 100 parr/m² (Fig. 1), two orders of magnitude higher than the ~1 parr/m² typically observed at cooler temperatures (Keeley and Grant 1995). Thermal refugia likely play vital roles in the persistence of juvenile salmon populations during high-temperature events (Dugdale et al. 2013) because their presence enables escape from physiological impairment due to heat stress (Breau et al. 2011; Dugdale et al. 2016). Heat-stressed juvenile salmon may use chemosensory cues (odours) from conspecifics to locate these thermal refugia. Here, we describe an experiment examining the effect of artificial aggregations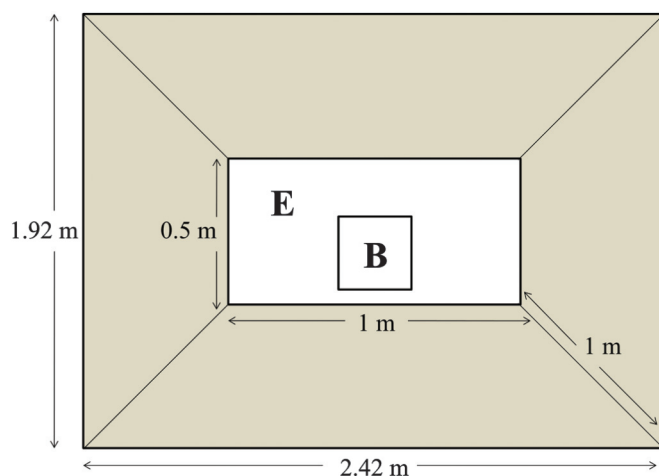 of salmon parr on ambient densities of free-swimming conspecifics under fully natural conditions. We predict that the presence of artificial aggregations of conspecifics will advertise the location of desirable habitat to free-swimming salmon parr via chemical cues and may serve as a trigger for the formation of aggregations independent of thermal gradients.

Materials and methods

Three sites were selected based on their typical differences in water temperature: (1) the mouth of Catamaran Brook is a known cool-water refuge and the site of the high-density aggregations observed during a heat wave in July 2010 (Fig. 1); (2) a "control" site in Little Southwest ~100 m downstream of Catamaran Brook demonstrates an intermediate temperature; and (3) a shallow reach in Little Southwest ~25 m upstream of its confluence with Otter Brook (~6 km downstream of Catamaran Brook) that is consistently warmer than the control site in Little Southwest. Two enclosures (1 m wide × 0.5 m long, relative to the stream axes) consisting of rigid plastic mesh (0.8 cm mesh size) held in place via aluminum conduit poles (1.25 m long) driven into the substrate were placed in parallel separated by 2–3.5 m at each site to serve as paired control (no parr) and aggregation (captive parr) sites. Aggregation and control treatments alternated daily between the paired enclosures during August 2015. All sites were selected based on qualitative assessments of their physical similarities (depth, flow, substrate complexity).

Salmon parr (age 1+ and 2+, $n = 240$, standard length (L_s) = 63–125 mm, mean (±SD) L_s = 92.3 ± 13.3 mm) were collected from the Little Southwest Miramichi River within 300 m of the mouth of Catamaran Brook using a backpack electrofisher (Smith-Root, Inc., Model 12B) with permission from Fisheries and Oceans Canada (permit No. SG-RHQ-15-060A). All work complied with the regulations of the Canadian Council on Animal Care (University of New Brunswick Animal Care protocol No. 15018). Groups of 10 parr were placed into wire-mesh boxes (25 cm long × 25 cm wide × 25 cm high, mesh size = 1 cm) at densities of 160 parr/m² and each box was placed into one of the paired enclosures at each site

Fig. 2. Schematic diagram of the experimental apparatus showing the wire-mesh holding box (B) placed inside the black plastic enclosures (E) and the surrounding area (shaded) snorkeled to estimate ambient parr density. Artificial aggregation treatments consisted of 10 Atlantic salmon (*Salmo salar*) parr in the mesh holding boxes, and control treatments were physically identical but did not have parr in the holding boxes. Figure appears in colour on the Web.
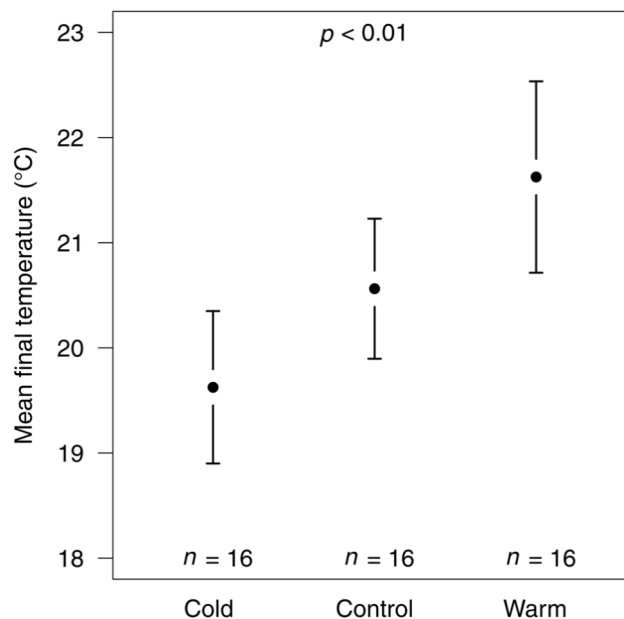

(Fig. 2). The boxes were completely submerged, as depth within the enclosures ranged from 35 to 55 cm. Prior to placement of the experimental parr, visual snorkeling surveys were conducted in the area directly surrounding the enclosures between the hours of 1100 and 1400. Subsequent snorkeling surveys were conducted after the boxes containing parr had been in place for 2–5 h between the hours of 1400 and 1900, after which the captive parr were removed and released back at their approximate site of capture. Temperature was recorded with an alcohol thermometer during each survey period. One trial block (paired control and aggregation treatments) was conducted at each site daily for eight consecutive days (*n* = 8 replicates/site).

Temperatures recorded during the final density surveys were compared between sites in a one-way ANOVA. The effect of the artificial aggregations on final ambient parr densities was examined as a generalized linear mixed model (Pinheiro et al. 2011) using maximum likelihood with treatment (aggregation or control) as a fixed effect, initial parr density and final temperature as linear covariates, and site as a repeated measure. The most parsimonious model was selected via stepwise Akaike's information criterion (AIC) comparisons (Venables and Ripley 2002). Pairwise differences in final densities between treatments (density near the artificial aggregations minus density at the control sites) were tested for relative increases with a one-tailed Welch's *t* test. All analyses were conducted using R version 3.2.1 (R Core Team 2015).

Results

Temperatures at the sites ranged from 16.5 to 24 °C and generally increased between snorkeling surveys, i.e., from morning to afternoon. We observed significant differences in mean final temperature between the three sites consistent with their selection criteria as relatively cool, intermediate, and warm ($F_{[2,45]}$ = 7.59, p = 0.0014; Fig. 3). However, site did not have a significant effect on the final parr densities as a repeated measure (p > 0.05) and this error term actually increased the AIC value of the basic ANCOVA (ΔAIC = +2.0). In addition, variance components analysis (Paradis et al. 2004) revealed that site as a repeated measure explained less than 0.1% of the variance in final parr densities so the nested factor (site) was excluded from further analyses. Based on the

Fig. 3. Mean (±95% CI) temperature during final Atlantic salmon (*Salmo salar*) parr density surveys at each site. The *p* value is from one-way ANOVA; sample sizes reflect paired temperature measurements at control and aggregation enclosures at each site.
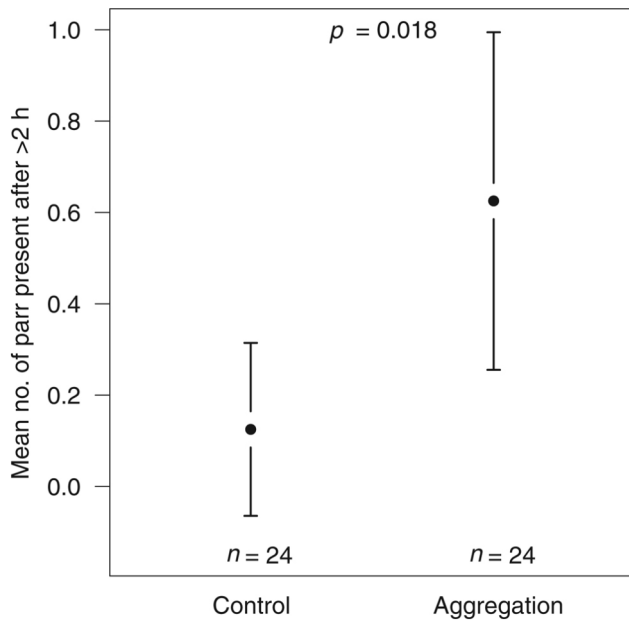

results of the remaining one-way ANCOVA, final parr densities were significantly higher around the artificial aggregations than around the paired control sites ($F_{[1,44]}$ = 6.012, p = 0.018; Fig. 4). These final densities were independent of both initial (pretreatment) parr densities and final temperatures (both p > 0.4). Final density differences (postsurvey counts minus presurvey counts) for each paired replicate (artificial aggregation vs. control) were significantly greater than zero ($t_{[23]}$ = 2.3, n = 1, p = 0.031), demonstrating that the artificial aggregations served as an attractant to free-swimming parr and elicited greater ambient densities than the control sites.

Discussion

Although the aggregations of Atlantic salmon parr that have been observed under natural conditions occurred during high-temperature events (>24 °C; Breau et al. 2011; Dugdale et al. 2016), our findings suggest that the formation of aggregations may also be influenced by social, chemical cues advertising the presence of nonterritorial conspecifics to other salmon. In functional components, we propose that (*i*) elevated temperatures result in physiological stress that triggers the abandonment of territories and search for a thermal refuge, and (*ii*) refuge-seeking fish locate thermal refuges by some combination of thermal and chemical cues with the relative importance of each factor determined by its quality and reliability (Doligez et al. 2003). Heat-stressed salmon parr may inadvertently advertise their condition (Nocera et al. 2006), and refuge-seeking fish may avoid these stress cues in favour of the cues of unstressed conspecifics as a mechanism for locating colder waters. Social, chemical cues would therefore provide a positive feedback mechanism that advertises and attracts individual salmon to aggregations, where their own cues may reinforce the strength of the chemical signal conveyed to refuge-seeking receivers (Fletcher 2006). This mechanism applies generally to the cognitive process underlying settling in motile fishes, as newly entered habitat containing conspecifics may be more attractive than habitat of equal quality but lacking resident conspecifics (Igulu et al. 2011, but see Roux et al. 2015).

Above a physiological temperature threshold of 24 °C, Atlantic salmon parr abandon their territorial feeding behaviours and

Fig. 4. Mean (±95% CI) number of Atlantic salmon (*Salmo salar*) parr present outside of the experimental enclosures 2–5 h after starting a trial on consecutive days. The *p* value is from one-way ANOVA; sample sizes reflect eight daily snorkeling observations at the three sites.

cease aggressive intraspecific interactions as they aggregate at high densities in cold-water refugia (Breau et al. 2011; Dugdale et al. 2016). Territorial behaviour in salmonids is expressed with some degree of plasticity, because factors including artificially manipulated population densities and social status (Wood et al. 2012; Lindeman et al. 2015; Dugdale et al. 2016), food abundance (Keeley and Grant 1995; Imre et al. 2004), and habitat complexity (Dolinsek et al. 2007; Bilhete and Grant 2016) all influence the size of territories defended by individuals. Interestingly, yellow bullhead (*Ameiurus natalis* (Lesueur, 1819)) were found to switch behavioural strategies when they were exposed to odours from solitary (aggressive) or gregarious (peaceful) to reflect the strategy of the odour donors (suggested to be in response to a putative "love-in" pheromone released by the gregarious donors: Todd et al. 1967). Similar chemical triggers may contribute to the abandonment of territoriality and enable the formation of aggregations in heat-stressed salmon parr.

The attraction effect of aggregated salmon parr that we describe above suggests several questions for future research, particularly whether (*i*) the relative attractiveness of parr aggregations changes around the heat-stress threshold of 24 °C and (*ii*) chemical cues from heat-stressed or unstressed parr have different effects on the formation of aggregations independent of ambient temperature. These questions are especially relevant given the global trend towards warmer surface waters (Morgan et al. 2001) that will result in more frequent and more extreme high-temperature events and may detrimentally affect the abundance and persistence of cold-water refuges (Kurylyk et al. 2015) throughout the southern limits of salmon distribution in Atlantic Canada (Daigle et al. 2015).

Acknowledgements

References

Bilhete, C., and Grant, J.W.A. 2016. Short-term costs and benefits of habitat complexity for a territorial fish. Ethology, **122**(2): 151–157. doi:10.1111/eth.12456.

Breau, C., Cunjak, R.A., and Peake, S.J. 2011. Behaviour during elevated water temperatures: can physiology explain movement of juvenile Atlantic salmon to cool water? J. Anim. Ecol. **80**(4): 844–853. doi:10.1111/j.1365-2656.2011.01828.x. PMID:21401593.

Brown, G.E., Macnaughton, C.J., Elvidge, C.K., Ramnarine, I., and Godin, J.-G.J. 2009. Provenance and threat-sensitive predator avoidance patterns in wild-caught Trinidadian guppies. Behav. Ecol. Sociobiol. **63**(5): 699–706. doi:10.1007/s00265-008-0703-4.

Campomizzi, A.J., Butcher, J.A., Farrell, S.L., Snelgrove, A.G., Collier, B.A., Gutzwiller, K.J., Morrison, M.L., and Wilkins, R.N. 2008. Conspecific attraction is a missing component in wildlife habitat modeling. J. Wildl. Manage. **72**(1): 331–336. doi:10.2193/2007-204.

Daigle, A., Jeong, D.I., and Lapointe, M.F. 2015. Climate change and resilience of tributary thermal refugia for salmonids in eastern Canadian rivers. Hydrol. Sci. J. **60**(6): 1044–1063. doi:10.1080/02626667.2014.898121.

Doligez, B., Cadet, C., Danchin, E., and Boulinier, T. 2003. When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. Anim. Behav. **66**(5): 973–988. doi:10.1006/anbe.2002.2270.

Dolinsek, I.J., Grant, J.W.A., and Biron, P.M. 2007. The effect of habitat heterogeneity on the population density of juvenile Atlantic salmon *Salmo salar* L. J. Fish Biol. **70**(1): 206–214. doi:10.1111/j.1095-8649.2006.01296.x.

Dugdale, S.J., Bergeron, N.E., and St-Hilaire, A. 2013. Temporal variability of thermal refuges and water temperature patterns in an Atlantic salmon river. Remote Sens. Environ. **136**: 358–373. doi:10.1016/j.rse.2013.05.018.

Dugdale, S.J., Franssen, J., Corey, E., Bergeron, N.E., Lapointe, M., and Cunjak, R.A. 2016. Main stem movement of Atlantic salmon parr in response to high river temperature. Ecol. Freshw. Fish, **25**(3): 429–445. doi:10.1111/eff.12224.

Elliott, J.M. 1991. Tolerance and resistance to thermal stress in juvenile Atlantic salmon, *Salmo salar*. Freshw. Biol. **25**(1): 61–70. doi:10.1111/j.1365-2427.1991.tb00473.x.

Ferrari, M.C.O., Wisenden, B.D., and Chivers, D.P. 2010. Chemical ecology of predator–prey interactions in aquatic ecosystems: a review and prospectus. Can. J. Zool. **88**(7): 698–724. doi:10.1139/Z10-029.

Fletcher, R.J., Jr. 2006. Emergent properties of conspecific attraction in fragmented landscapes. Am. Nat. **168**(2): 207–219. doi:10.1086/505764. PMID:16874630.

Giaguinto, P.C., and Hoffmann, A. 2012. The scent of stress: Pintado catfish differentially respond to chemical cues from stressed conspecifics. Behaviour, **149**(9): 941–951. doi:10.1163/1568539X-00003022.

Harvey, M.C., and Brown, G.E. 2004. Dine or dash?: Ontogenetic shift in the response of yellow perch to conspecific alarm cues. Environ. Biol. Fishes, **70**(4): 345–352. doi:10.1023/B:EBFI.0000035432.12313.87.

Igulu, M.M., Nagelkerken, I., Fraaije, R., van Hintum, R., Ligtenberg, H., and Mgaya, Y.D. 2011. The potential role of visual cues for microhabitat selection during the early life phase of a coral reef fish (*Lutjanus fulviflamma*). J. Exp. Mar. Biol. Ecol. **401**(1–2): 118–125. doi:10.1016/j.jembe.2011.01.022.

Imre, I., Grant, J.W.A., and Keeley, E.R. 2004. The effect of food abundance on territory size and population density of juvenile steelhead trout (*Oncorhynchus mykiss*). Oecologia, **138**(3): 371–378. doi:10.1007/s00442-003-1432-z. PMID:14669003.

Jonsson, B., and Jonsson, N. 2009. A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. J. Fish Biol. **75**(10): 2381–2447. doi:10.1111/j.1095-8649.2009.02380.x. PMID:20738500.

Keeley, E.R., and Grant, J.W.A. 1995. Allometric and environmental correlates of territory size in juvenile Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **52**(1): 186–196. doi:10.1139/f95-019.

Keenleyside, M.H.A., and Yamamoto, F.T. 1962. Territorial behaviour of juvenile Atlantic salmon (*Salmo salar* L.). Behaviour, **19**(1): 139–168. doi:10.1163/156853961X00231.

Kurylyk, B.L., MacQuarrie, K.T.B., Linnansaari, T., Cunjak, R.A., and Curry, R.A. 2015. Preserving, augmenting, and creating cold-water refugia in rivers: concepts derived from research on the Miramichi River, New Brunswick (Canada). Ecohydrology, **8**(6): 1095–1108. doi:10.1002/eco.1566.

Lindeman, A.A., Grant, J.W.A., and Desjardins, C.M. 2015. Density-dependent territory size and individual growth rate in juvenile Atlantic salmon (*Salmo salar*). Ecol. Freshw. Fish, **24**(1): 15–22. doi:10.1111/eff.12120.

Manassa, R.P., and McCormick, M.I. 2013. Social learning improves survivorship at a life-history transition. Oecologia, **171**(4): 845–852. doi:10.1007/s00442-012-2458-x. PMID:22976775.

Morgan, I.J., McDonald, D.G., and Wood, C.M. 2001. The cost of living for fresh-

water fish in a warmer, more polluted world. Global Change Biol. **7**(4): 345–355. doi:10.1046/j.1365-2486.2001.00424.x.

Muller, K.L., Stamps, J.A., Krishnan, V.V., and Willits, N.H. 1997. The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). Am. Nat. **150**(5): 650–661. doi:10.1086/286087. PMID:18811306.

Nocera, J.J., Forbes, G.J., and Giraldeau, L.-A. 2006. Inadvertent social information in breeding site selection of natal dispersing birds. Proc. R. Soc. B Biol. Sci. **273**(1584): 349–355. doi:10.1098/rspb.2005.3318.

Nocera, J.J., Forbes, G.J., and Giraldeau, L.-A. 2009. Aggregations from using inadvertent social information: a form of ideal habitat selection. Ecography, **32**(1): 143–152. doi:10.1111/j.1600-0587.2008.05614.x.

Nordeng, H. 1977. A pheromone hypothesis for homeward migration in anadromous salmonids. Oikos, **28**(2–3): 155–159. doi:10.2307/3543965.

Paradis, E., Claude, J., and Strimmer, K. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics, **20**(2): 289–290. doi:10.1093/bioinformatics/btg412. PMID:14734327.

Parkos, J.J., and Wahl, D.H. 2010. Influence of body size and prey type on the willingness of age-0 fish to forage under predation risk. Trans. Am. Fish. Soc. **139**(4): 969–975. doi:10.1577/T09-098.1.

Parrish, D.L., Behnke, R.J., Gephard, S.R., McCormick, S.D., and Reeves, G.H. 1998. Why aren't there more Atlantic salmon (*Salmo salar*)? Can. J. Fish. Aquat. Sci. **55**(S1): 281–287. doi:10.1139/d98-012.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and R Core Development Team. 2011. nlme: linear and nonlinear mixed effects models. R package version 3.1-101 [computer program]. Available from https://cran.r-project.org/web/packages/nlme/.

Pizzatto, L., Stockwell, M., Clulow, S., Clulow, J., and Mahony, M. 2016. Finding a place to live: conspecific attraction affects habitat selection in juvenile green and golden bell frogs. Acta Ethol. **19**(1): 1–8. doi:10.1007/s10211-015-0218-8.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.r-project.org.

Reed, J.M., and Dobson, A.P. 1993. Behavioural constraints and conservation biology: conspecific attraction and recruitment. Trends Ecol. Evol. **8**(7): 253–256. doi:10.1016/0169-5347(93)90201-Y. PMID:21236161.

Roux, N., Brooker, R.M., Lecellier, G., Berthe, C., Frédérich, B., Banaigs, B., and Lecchini, D. 2015. Chemical spying in coral reef fish larvae at recruitment. C.R. Biol. **338**(10): 701–707. doi:10.1016/j.crvi.2015.05.004. PMID:26318049.

Ryer, C.H., Stoner, A.W., Spencer, M.L., and Abookire, A.A. 2007. Presence of larger flatfish modifies habitat preference by age-0 northern rock sole *Lepidopsetta polyxystra*. Mar. Ecol. Prog. Ser. **342**: 227–238. doi:10.3354/meps342227.

Scherer, A.E., and Smee, D.L. 2016. A review of predator diet effects on prey defensive responses. Chemoecology, **26**(3): 83–100. doi:10.1007/s00049-016-0208-y.

Schmidt, K.A., Dall, S.R.X., and van Gils, J.A. 2010. The ecology of information: an overview on the ecological significance of making informed decisions. Oikos, **119**(2): 304–316. doi:10.1111/j.1600-0706.2009.17573.x.

Schmidt-Nielsen, K. 1984. Scaling: Why is animal size so important? Cambridge University Press, Cambridge.

Sweatman, H. 1988. Field evidence that settling coral reef fish larvae detect resident fishes using dissolved chemical cues. J. Exp. Mar. Biol. Ecol. **124**(3): 163–174. doi:10.1016/0022-0981(88)90170-0.

Todd, J.H., Atema, J., and Bardach, J.E. 1967. Chemical communication in social behavior of a fish, the yellow bullhead (*Ictalurus natalis*). Science, **158**(3801): 672–673. doi:10.1126/science.158.3801.672. PMID:6051493.

Venables, W.N., and Ripley, B.D. 2002. Modern applied statistics with S. 4th ed. Springer, New York.

Wood, J.L.A., Grant, J.W.A., and Belanger, M.H. 2012. Population density and territory size in juvenile rainbow trout, *Oncorhyncus mykiss*: implications for population regulation. Can. J. Fish. Aquat. Sci. **69**(6): 1121–1128. doi:10.1139/f2012-048.