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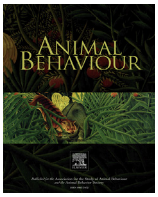

Does increasing habitat complexity favour particular personality types of juvenile Atlantic salmon, *Salmo salar*?

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The costs and benefits of a particular behavioural trait, such as boldness or aggression, may vary depending on the physical environment. We tested whether the common practice of adding physical structure (i.e. boulders) to streams to increase salmonid density has behavioural consequences, as open habitats are predicted to favour individuals that are more bold and aggressive. Wild young-of-the-year Atlantic salmon were captured from habitats of varying physical complexity and placed into semi-natural stream enclosures for 11 days while their behaviour was observed and tested in both open and structurally complex environments. We found evidence for personality, or consistent individual behavioural differences across contexts, for avoidance and site attachment, with repeatabilities of 0.287 and 0.206, respectively, but not for activity or frequency of aggression. Fish were significantly more active and aggressive in the open habitats, and more site-attached in the complex habitats. Active and aggressive fish also grew more in the wild, while site-attached fish grew less in the wild, but more in the enclosures. However, contrary to our expectation, the complexity of the original habitat was not a significant predictor of personality. Our results suggest stream restorations involving increasing habitat complexity will alter the behaviour of young-of-the-year Atlantic salmon, but will not favour any particular personality types.

Complex habitats differ from open habitats by providing physical structure that can be used as refuge from the physical environment, competitors and predators (Höjesjö, Johnsson, & Bohlin, 2004; Millidine, Armstrong, & Metcalfe, 2006), thus altering the costs and benefits of different behaviour patterns. Aggressive behaviour (Adams, 2001; Grant, 1993) is less effective in complex habitats where physical structure reduces visual contact between competitors and decreases the success of resource defence and monopolization (Basquill & Grant, 1998; Eason & Stamps, 1992). Consequently, overall levels of aggression tend to be lower in structured habitats (Höjesjö et al., 2004) in a variety of territorial species such as birds (Burger, 1974), lizards (Eason & Stamps, 1992) and fish (Danley, 2011; Imre, Grant, & Keeley, 2002). Similarly, in open habitats, bold behaviour is often rewarded through preferential access to food (Ward, Thomas, Hart, & Krause, 2004) or mating opportunities (Myhre, Forsgren, & Amundsen, 2013), but may also increase encounter rate with predators (Grabowski, 2004; Wong, 2013). Physical structure may also obstruct movement or increase activity costs (Brownsmith, 1977; Schooley, Sharpe, & Van Horne, 1996); accordingly, fish (Enefalk & Bergman, 2016; Radabaugh, Bauer, & Brown, 2010), primates (Jaman & Huffman, 2008) and ants (Crist & Wiens, 1994) show higher activity levels in open relative to complex habitats (but see Cenni, Parisi, & Gherardi, 2010). Variation in habitat complexity may also help maintain behavioural diversity within a population, by inducing spatial variation in selection pressures that facilitate the coexistence of different behavioural strategies (Brockmark, Neregård, Bohlin, Björnsson, & Johnsson, 2007; Höjesjö et al., 2004).

Although certain behaviours may be more effective in a particular habitat, behaviour is not infinitely plastic and can be limited by physiological, cognitive or sensory constraints (e.g. Hazlett, 1995; Johnson & Sih, 2007). Indeed, individuals often behave consistently over time or across different contexts, exhibiting personality (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). Although widespread, personality reflects a limit to plasticity, or behavioural adaptability to the environment, and may constrain optimal behaviour in certain situations (Conrad, Weinersmith, Brodin, Saltz, & Sih, 2011). Plasticity can also be its own quantifiable personality trait that varies among individuals, reflecting a trade-off between

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adaptability and consistency (e.g. Briffa, Rundle, & Fryer, 2008). Differences in personality may also correspond to differences in life history strategy (Réale, Martin, Coltman, Poissant, & Festa-Bianchet, 2009); accordingly, faster growth and higher fecundities are found in more aggressive, bold and active individuals across a broad range of taxa (Biro & Stamps, 2008). Differences in personality may also result in differences in habitat choice, whereby individuals with different personality traits are 'sorted' into different habitats (e.g. Duckworth, 2006; Hensley, Cook, Lang, Petelle, & Blumstein, 2012).

Salmonids are an excellent model system for investigating how habitat complexity may affect personality. Juvenile salmonids have personalities when observed in the laboratory (Adriaenssens & Johnsson, 2011; Höjesjö et al., 2004), and their territorial behaviour is affected by habitat structure. Physical structure is thought to increase the costs of territory defence (Eason & Stamps, 1992), causing the rate of aggression to decrease (Höjesjö et al., 2004) and territory size to shrink (Venter, Grant, Noel, & Kim, 2008), so that complex habitats can support higher densities (Dolinsek, Grant, & Biron, 2007a; Kalleberg, 1958). In addition, many salmonid populations that have been negatively affected by human activities are the focus of current substantive conservation efforts (Parrish, Behnke, Gephard, McCormick, & Reeves, 1998). Salmonid restoration projects often focus on adding physical structure to the stream environment (Nislow, Folt, & Parrish, 1999), including boulders, weirs and large woody debris to create a more heterogeneous physical environment (Whiteway, Biron, Zimmermann, Venter, & Grant, 2010). The costs of these restoration projects range from a few thousand to a few hundred thousand dollars per project, with the majority of restorations resulting in short-term increases in salmonid abundance (Whiteway et al., 2010). However, the effect of stream restoration projects on the behaviour of the target fish has not been widely assessed (but see Enefalk & Bergman, 2016). This study will be the first, to our knowledge, to determine whether increasing habitat complexity favours particular behavioural phenotypes in the population.

In this study, we explore the relationship between habitat complexity and behaviour in young-of-the-year (YOY) Atlantic salmon, *Salmo salar*. YOY salmon were captured from habitats with varying degrees of physical complexity and placed into seminatural stream enclosures, where their behaviour was observed and tested in both an open and complex habitat. We determined whether (1) personality exists in YOY Atlantic salmon, when measured in a seminatural setting, by quantifying four aspects of personality: neophobia, aggression, shyness/boldness and activity. Body size and growth during the trial were used as correlates of fitness. If habitat sorting by personality occurs, then we would expect to see personality types, evident through individual behavioural differences observed within the enclosures, to differ in the habitat complexity of the site of capture. Specifically, we tested the predictions that (2) fish captured from open habitats would be more aggressive, bold and active than those from complex habitats. Independent of habitat of capture, we also tested the predictions that (3) fish would have higher rates of aggression, boldness and activity in the open enclosure habitat than in the complex enclosure habitat. Finally, we tested the predictions that growth rate would be higher for fish that were (4) captured from open habitats and (5) were more aggressive, bold and active.

METHODS

Enclosures

The study was conducted in Catamaran Brook, a third-order tributary of the Little Southwest Miramichi River located in Northumberland County, New Brunswick (46°53′N, 66°06′W). This pristine habitat serves as a nursery stream for a naturally reproducing population of wild salmon (Dolinsek et al., 2007a). We used the lower 2 km of Catamaran Brook to capture fish for the experiment and to set up stream enclosures.

YOY salmon were captured with dip-nets while snorkelling in sites of varying habitat complexity. While we could not capture every fish that was encountered, our success rate was similar in both habitats. Hence, any bias in personality caused by our sampling method was likely similar in both habitats. All sites of capture were marked with a small numbered cobble, and fish were placed individually into covered plastic bins (35.6 × 20.3 × 11.7 cm) on the side of the stream. Water within the bins was refreshed at regular intervals to maintain a constant temperature. Our measure of habitat complexity at the site of capture was the mean visual distance measured in eight cardinal directions (N, NE, E, SE, S, SW, W, NW) to a maximum of 100 cm, with the upstream direction selected as North. Water depth was also measured at each of these locations.

All fish were weighed to the nearest 0.01 g, and fork length measured to the nearest 0.5 mm (mean ±SD: weight: 0.79 ± 0.42 g; length: 3.83 ± 0.59 cm). Fish were then tagged subcutaneously with elastomer in one of three colours (pink, orange, green) in one of three different body regions (upper-dorsal, mid-dorsal, caudal), such that each fish's tag was visible from above. Fish were given approximately 1 h to recover from tagging in the bins before being released into the enclosures.

A total of six enclosures (4 × 1 × 1 m) were used at a given time with six fish per enclosure, a population density typical in high-density regions in the stream (Imre, Grant, & Cunjak, 2005). Substrate for each enclosure consisted of gravel (<5 cm in diameter), small cobbles (5–7 cm in diameter) and boulders (~20 cm in diameter) obtained from the surrounding stream bed. Each enclosure was randomly chosen to initially have either an open or complex habitat. For both treatments (hereafter habitats), gravel and small cobbles were added to the bottom of the enclosures. Boulders were added at a density of 6 per m^2 to the complex habitats (Dolinsek et al., 2007a, b), for a total of 24 well-spaced boulders within each complex enclosure.

Groups of six fish were added to each enclosure. The original design was to capture fish from extreme habitats (i.e. open versus complex) and place three fish from each habitat into each enclosure. However, due to the low densities of YOY (K. D. W. Church, personal observation), we captured fish from a variety of habitats (see Results) and placed them into the enclosures in the approximate order of capture (see Results), to minimize the time fish spent in the covered bins. The six enclosures were used three times with different salmon, for a total of 18 replicates over the period of July to August 2015. The shallow depth (mean ±SD: 19.4 ± 8.4 cm, $N = 18$) in the enclosures allowed the fish to be clearly seen when viewed from above. Nylon cords were strung between the support posts at the corners of each enclosure to determine the x, y coordinates of all possible locations within the enclosure. Enclosures were open on top, leaving the fish exposed to some of their natural predators, including fishing spiders (*Dolomedes triton*) and kingfishers (*Megaceryle alcyon*), although aquatic predators, such as brook trout, *Salvelinus fontinalis*, were excluded. Personality tests were conducted daily on all visible fish, excluding acclimation periods and days with inclement weather.

Fish were given 48 h to acclimate to the enclosures before observations began. After all visible fish were observed (see below) on two separate occasions within the initial treatment, a period that ranged from 3 to 5 days depending on the weather and visibility, the habitats were switched. Large boulders were removed from the complex habitats and added to the open habitats, while the fish