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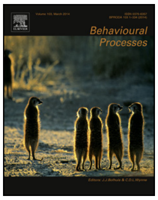

Behavioural responses of Pacific salmon to chemical disturbance cues during the spawning migration

Nolan N. Bett[a,*], Scott G. Hinch[a], Sang-Seon Yun[b,1]

[a] Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, BC V6T 1Z4, Canada
[b] Faculty of Land and Food Systems, University of British Columbia, Vancouver, BC V6T 1Z4, Canada

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ABSTRACT

Many fish that are exposed to a threat release disturbance cues, which are chemicals that alert conspecifics to the presence of the threat. The release of disturbance cues has been well demonstrated in various species of laboratory-reared fish. Migratory fish species often exhibit increased cortisol levels and are exposed to numerous stressors during their migrations, which could trigger the release of disturbance cues. We tested the responses of wild migrating sockeye salmon (*Oncorhynchus nerka*) and pink salmon (*O. gorbuscha*) to the odours of disturbed and undisturbed conspecifics to determine whether these fish release disturbance cues following exposure to a simulated stressor. Furthermore, we tested the responses of sockeye salmon to water-borne cortisol, following evidence from past studies that this chemical is excreted through the gills of stressed fish, and speculation that endogenous correlates of stress might function as disturbance cues. We found that sockeye salmon avoid the odour of disturbed conspecifics, whereas pink salmon do not. Avoidance occurred in both female and male sockeye salmon, and was associated with an increase in plasma cortisol levels in females, but not in males. We also found no behavioural response to water-borne cortisol, which suggests this chemical does not act as an exogenous disturbance cue in sockeye salmon. Avoidance of disturbed conspecifics could limit exposure to risks during the sockeye salmon spawning migration, but could also delay the rate of migration and thereby accrue reproductive costs.

1. Introduction

In the aquatic environment, many animals use chemical cues as indicators of danger (Liley, 1982; Smith, 1992). One category of these chemical cues is “disturbance cues”, which are released when danger is detected but no physical damage is incurred (Wisenden, 2000; Ferrari et al., 2010), as opposed to the more commonly studied “damage-released cues” (Mathis et al., 1995; Wisenden, 2000; Brown, 2003) that are released following injuries. Disturbance cues appear to function as an early warning, eliciting behavioural and physiological responses in conspecifics (Wisenden, 2015), including avoidance (Jordão and Volpato, 2000), increased vigilance (Wisenden and Barbour, 2005), decreased foraging (Giaquinto and Hoffmann, 2012), and increased plasma cortisol levels (Barcellos et al., 2011, 2014). They can also act as a primer for anti-predator behaviours in response to subsequent cues (Ferrari et al., 2008; Vavrek et al., 2008). These cues have been documented in various fish species, including Nile tilapia and jundiá (*Oreochromis niloticus* and *Rhamdia quelen*, respectively; Barcellos et al., 2011), zebrafish (*Danio rerio*; Barcellos et al., 2014), salmonids (Salmonidae; e.g. Ferrari et al., 2008) and pacus (*Piaractus mesopotamicus*; Jordão and Volpato, 2000).

Damage-released chemical cues have been well demonstrated in Pacific salmon and trout (*Oncorhynchus* spp.; e.g. Brown and Smith, 1997; Berejikian et al., 1999; Scholz et al., 2000; Mirza and Chivers, 2003; Scott et al., 2003; Tierney et al., 2006; McIntyre et al., 2012), as have disturbance cues (Toa et al., 2004; Ferrari et al., 2008; Vavrek et al., 2008; Brown et al., 2012). These studies, however, were conducted on juvenile salmonids reared in a hatchery or laboratory. To our knowledge, none have tested wild adult salmon during their spawning migration, despite the abundance of threats or stressors that migrating adult salmonids face. Stressors include predation risk, migration barriers (e.g. dams, rapids), and capture-and-release from commercial, recreational or subsistence fisheries. Avoidance of disturbance cues could limit exposure to such stressors, increasing migratory – and therefore spawning – success.

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* Corresponding author.
E-mail address: nolanbett@gmail.com (N.N. Bett).
[1] Present address: Fisheries Program, The Confederated Tribes of the Umatilla Indian Reservation, Walla Walla, WA, 99362, USA.

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In addition to an absence of information on wild adult salmonids, the chemical identities of disturbance cues remain largely unknown (Wisenden, 2015). There is evidence that they may be metabolites (Lebedeva et al., 1993) and that they may in part comprise ammonia (Kiesecker et al., 1999; but also see Vavrek et al., 2008) or urea (Brown et al., 2012). Plasma cortisol levels increase in response to danger, such as following a simulated stressor (e.g. chasing fish with a net or similar apparatus to simulate predation risk; Toa et al., 2004; Ellis et al., 2007; Barcellos et al., 2011; Donaldson et al., 2014), and excess cortisol is released into the water through the gills (Ruane and Komen, 2003; Ellis et al., 2004, 2007; Wong et al., 2008; Zuberi et al., 2011). Fish demonstrate behavioural differences after exposure to corticosteroids (Stacey, 2015), and it is possible that cortisol or other endogenous correlates of stress may not only influence the release of disturbance cues, but could also act as cues themselves (Wisenden, 2015).

Within the *Oncorhynchus* genus, species appear to differ in their sensitivity to olfactory cues. For example, sockeye salmon (*O. nerka*) have very high natal site fidelity (Keefer and Caudill, 2014), whereas the closely related pink salmon (*O. gorbuscha*), whose distribution overlaps with sockeye salmon, stray more frequently to non-natal areas. One explanation for this difference may be that pink salmon spend considerably less time imprinting on freshwater cues prior to smolting and migrating to the ocean compared to sockeye salmon, although there is some evidence that sockeye salmon may possess greater olfactory sensitivity. Yamamoto et al. (2008) tested the responses of both species to mixtures of amino acids, believed to be a major component of the olfactory cues that signify natal water (Ueda, 2011). The authors exposed the fish to amino acid mixtures that mimicked the profile of their natal water, and found a much stronger attraction response in sockeye salmon relative to pink salmon. A stronger olfactory sensitivity to migratory cues could be associated with a stronger sensitivity to other chemicals such as disturbance cues, though this has not been investigated (reviewed by Bett and Hinch, 2016).

In this study we examined whether wild adult sockeye and pink salmon exhibit avoidance responses to the odours of disturbed conspecifics. We subjected salmon to a disturbance consisting of a handling event, and then measured the effect of their odours on the behaviour of conspecifics. We predicted that sockeye and pink salmon would avoid the odour of disturbed conspecifics. Additionally, we tested the response of sockeye salmon to waterborne cortisol to determine whether this chemical, which could be excreted through the gills of disturbed salmon, might act as a disturbance cue.

2. Methods

2.1. Study location and animals

The experiments took place on August 18–23 and September 17–23 of 2013, and August 16–25 and October 7–9 of 2014. They were conducted on the north bank of the Seton River, a tributary of the Fraser River, in the interior of southwestern British Columbia, Canada. Sockeye salmon in this river system spawn in Portage Creek and Gates Creek, located 25 km and 55 km upstream from the capture site, respectively. Pink salmon spawn throughout the watershed, including the area surrounding the capture location. Both species must migrate approximately 300 km up the Fraser River from the ocean to reach the Seton River (the study site has been further described by Roscoe et al. (2011) and Burnett et al. (2014)). We captured all sockeye and pink salmon by dipnet from the top pool of the Seton Dam fishway, located on the Seton River 5 km from the Seton-Fraser confluence. Captures all took place during the peak of the respective populations' runs. Our experimental set-up was located approximately 100 m from the capture location.

2.2. Experimental set-up

We used submersible pumps to move water from the Seton River into two 11,365 L polyethylene head tanks (Premier Plastics Inc., Delta, BC), from which the water was gravity fed through 2" diameter water suction hoses (Greenline, Delta, BC) to two 1136 L polyethylene source tanks (Premier Plastics Inc.). Water was gravity fed from each source tank through 4" diameter water suction hoses into a Y-maze (Fig. 1). We used a Y-maze constructed from plywood and wood supports, and sealed the interior with fiberglass and a fish-safe gelcoat (Rebel Fiberglass, Kamloops, BC). The Y-maze was rectangular in shape, 4.88 m long × 1.22 m wide × 1.22 m high. A 2.44-m-long divider, made from fiberglassed plywood, divided the upstream end into two equally sized halves (or two "arms"). We conducted a dye test to ensure no mixing occurred between the two arms. Water exited the Y-maze through a standpipe, and the water depth was 17 cm. We used valves to maintain the amount of water entering each arm at 40 L min^{-1}. We also used plywood to cover the top of the Y-maze. We monitored behaviour through a video system, using an infrared camera (securitycamera2000.com, Hong Kong) connected to a monitor.

2.3. Experimental protocol

We conducted the experiments during daylight hours (0700–1700). At the beginning of each day, we captured 8–12 sockeye or pink salmon and immediately transferred them to an aerated 1000 L transport tank, which we then drove to the experimental set-up. We held the salmon in individual isolation chambers, constructed from PVC pipe (75 cm length × 15.3 cm diameter) with mesh ends, which we placed inside a 10,000 L holding tank receiving a continuous flow of water from Seton River. We transferred the salmon individually from the holding tank to the Y-maze, located directly adjacent, until each fish had been tested. The isolation chambers allowed us to remove individual fish from the holding tank without disturbing the others. Concurrently, we captured an additional 3 salmon from the same capture location at the beginning of each day, and we transferred them to one of the two source tanks. The "source fish" remained in the source tank for the duration of the day and provided an odour to one arm of the Y-maze. Each batch of source fish contained at least one member of each sex (i.e. two males and one female, or two females and one male). In the sockeye salmon experiment, the source fish were divided into two treatment groups: "disturbed" and "control". The disturbed source fish underwent the following handling procedure: first, air exposure for approximately 15 s during the transfer from the fishway to the transport tank using a dipnet, followed by 0.5-1.5 h in the aerated transport tank, then another 15 s of air exposure during transfer from the transport tank to the source tank. They remained in the source tank for up to 8 h. Physiological stress responses to handling events last up to 24 h in Pacific salmon (Donaldson et al., 2014), and this, in addition to confinement stress, ensured the source fish remained in a disturbed state for the duration of the tests. Manipulating wild fish is inherently stressful for them, so it was not possible to capture, transport, and confine source fish in the control group in a truly undisturbed state. Roscoe et al. (2011), for example, found an increase in plasma glucose, a commonly used indicator of stress in salmonids (Barton, 2002), in Gates Creek sockeye salmon following 5 h of confinement in net pens in the Seton River. Instead, we sacrificed the control fish immediately upon capture (<10 s) by cerebral percussion, before a physiological stress response could