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# Salmon egg subsidies and interference competition among stream fishes

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**Abstract** Resource availability may modulate interference interactions among competitors. For example, competition among stream fishes for drifting eggs from salmon (*Oncorhynchus* spp.) spawning events may be influenced by the availability of this energy-rich food source. This study used camera-based techniques to evaluate the effect of varied prey availability (i.e., pink salmon (*O. gorbuscha*) eggs) on rates of interference competition within natural stream fish communities at 10 sites. Aggressive interactions were quantified across different levels of egg additions, ranging from 6 to 3575 *O. gorbuscha* eggs, at 10 sites on the Keogh River, British Columbia, Canada. There were fewer aggressive interactions among salmonids (*O. kisutch*, *O. mykiss*, and *O. clarkii clarkii*) when there were more available eggs. Aggressive interaction rates were species-dependent; for example, the number of aggressive acts relative to null expectations based on abundances were highest in juvenile coho (*O. kisutch)* towards conspecifics. For some interactions, size of fish appeared to be a key factor as well. Thus, higher densities of spawning salmon in streams may provide sufficient prey resources in the form of eggs to temporarily decrease interference competition among stream fishes.

**Keywords** Aggression · Fish community · Resource superabundance · Competitive interactions · *Oncorhynchus sp*

## Introduction

Competition for resources can create strong density dependence in stream salmonids (Grant and Kramer 1990) and ultimately set the carrying capacity of their populations (Ayllón et al. 2012). Heightened competition can increase the rates of mortality, decrease growth rates, and displace salmonids from their territories (Imre et al. 2004; Young 2004). For example, intraspecific competition expressed as territoriality amongst stream salmonids has been used to predict the abundance and composition of a multicohort brown trout *Salmo trutta* (Linnaeus, 1758) population (Ayllón et al. 2012). However, the rate of competitive interactions among stream fishes may be modulated by changing food availability as proposed by three competing hypotheses. i) Higher food availability could increase occurrences of interference competition because the costs of competition are outweighed by higher benefits (Keenleyside and Yamamoto 1962). Interference competition is defined as aggressive behaviours of an individual that restrict another's resource use (Birch 1957). ii) If fish establish territories based on food availability, manipulating food

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C. J. Bailey and L. C. Andersson contributed equally to this work.

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abundance may not alter rates of aggression among stream salmonids (Newman 1956; Imre et al. 2004). iii) Higher food availability could decrease interference and exploitative competition as fish become satiated, as observed by Slaney and Northcote (1974), Moutou et al. (1998) and Noble et al. (2007) in highly controlled studies (i.e., artificial stream channels). Thus, even though there can be strong inter-specific competition in stream fish communities (e.g., Glova 1986), the impact of changing resource availability on competitive interactions among species remains relatively unclear.

Pacific salmon *Oncorhynchus* spp. eggs can be a key prey resource for stream fishes in coastal streams connected to the North Pacific. A variety of species consume large quantities of eggs, including juvenile anadromous salmonids *Oncorhynchus* spp., resident char *Salvelinus* spp. and trout, and sculpins *Cottus* spp. (e.g., Denton et al. 2009; Quinn et al. 2012; Swain et al. 2014). These nutrient- and energy-rich egg subsidies can have profound effects on individual growth (Denton et al. 2009; Ruff et al. 2011; Bailey et al. 2018) and even can shift migration timing in these species (Bailey et al. 2018). Salmon eggs generally enter the stream drift during salmon spawning when eggs are incompletely buried or when nest digging overlaps other buried nests, releasing large quantities of eggs (Essington et al. 2000; Moore et al. 2008). Thus, annual variation in salmon spawner abundance can drive large variation in the availability of eggs (Moore et al. 2008). Although the importance of salmon eggs as a prey resource to stream fishes is widely appreciated, it is unknown if variation in salmon egg prevalence may influence interference competition, especially in natural stream fish communities with multiple species of egg predators.

This study examined how abundance of a key prey resource alters interference competition within stream fish communities. Specifically, we focused on the availability of salmon eggs. The study used experimental additions of salmon eggs and underwater video analysis to address how salmon egg availability affected rates of aggressive interactions within stream fish communities, and how the rates and directionality of aggression differed among and within species. We expected to observe differences between salmonids and sculpins because salmonids are drift-feeding predators (Kawai et al. 2014), whereas sculpins are cryptobenthic ambush predators (Baltz et al. 1982). Drift-feeders will likely compete amongst themselves, while cryptobenthic fishes are more likely to hide and less likely to interact with the drift-feeders. Our predictions were that i) the frequency of aggression among stream fishes would decrease when the environment was saturated with salmon eggs, and ii) most aggressive interactions would occur among salmonids, with few interactions exchanged between salmonids and sculpins (*Cottus* spp.).

## Materials and methods

### Site description

Experimental pink salmon *Oncorhynchus gorbuscha* (Walbaum 1792) egg addition and underwater filming took place in the Keogh River (50° 40′ 43.56” N, 127° 20′ 55.23” W), Vancouver Island, British Columbia, Canada. The Keogh River is small (31.2 km long, 130 km$^2$ watershed area; Smith and Slaney 1980), nutrient-poor (Johnston et al. 1990), and has been studied extensively since 1972, including projects such as long-term salmonid enumeration and migration monitoring (e.g., Ward and Wightman 1989; Smith and Ward 2000; McCubbing 2002; Bailey et al. 2018). Potential stream-fish egg predators in the Keogh River include juvenile steelhead trout *Oncorhynchus mykiss* (Walbaum, 1792), cutthroat trout *Oncorhynchus clarkii clarkii* (Richardson, 1836), Dolly Varden char *Salvelinus malma* (Walbaum, 1792), and sculpin *Cottus* spp. [*C. asper* (Richardson, 1836) and *C. aleuticus* (Gilbert, 1896)]. Readers can refer to the supplementary material for details on the diets of these species as described in previous literature (online resource 1). Over the last four decades, estimated pink salmon spawning abundance in the Keogh River has ranged from less than 1000 to greater than 100,000 fish (Bailey et al. 2018), providing a variable but potentially important food source for this stream fish community. Pink salmon from the Keogh River typically school off of the mouth of the river from August to early September before entering the river to spawn from late September through October (McCubbing et al. 1999). All experimentation was completed before pink salmon began to migrate above the tidally-influenced portion of the river.

### Field experiment

Eggs were harvested from adult female pink salmon captured in the Keogh River estuary, water hardened, and separated from their skeins into single eggs. Eggs were counted by hand into six different treatment quantities along a logarithmic scale: 6, 26, 72, 303, 865, and 3575. Egg treatments spanned logarithmic increments for two reasons: 1) to ensure that habitats became saturated with eggs at the highest treatment, and 2) drifting egg densities increase exponentially as a function of salmon spawner abundance due to increasing nest overlap (Moore et al. 2008).

Site selection and delineation was designed to represent the diversity of habitats and natural fish communities that occur in the Keogh River. Sites were selected on a stratified random basis of macrohabitat types (pool, riffle or glide), and were spaced a minimum of 20 m apart. At each river access point, a macrohabitat type was drawn at random and then located by wading upstream until an instance of that macrohabitat was encountered (as characterized by Bain and Stevenson 1999; Fausti et al. 2004). Each site was 5 m long, defined by a minnow seine net (1/4″ mesh) across the river at the downstream end, and a piece of rebar installed upright in the river substrate at the upstream end in the thalweg (Fig. 1). A spawning cue in the form of a sealed bag punched with small holes and filled with water that eggs had soaked in for >24 h was weighted and placed against the upstream surface of the rebar. The purpose of the cue was to simulate the scents released by spawning pink salmon, signalling stream fish that eggs may enter the stream drift and become available for consumption. The minnow seine was placed at the downstream end of a site to prevent other fishes further downstream from following the spawning cue to its origin and artificially increasing stream fish abundance at a site. This was done to conserve natural variation in stream fish community composition and abundance among sites. The upstream limits of sites were not closed off by nets to minimize disturbance to the sites. Furthermore, the spawning cue would only move downstream in the direction of flow, thus upstream fish would not be attracted by the cue.

A GoPro (Silver hero4) video camera was attached to the rebar approximately 1/3 of the depth of the river below the surface at a downwards angle of approximately 15° below level. Although Ebner et al. (2009) suggest setting cameras horizontally, we angled our camera down slightly to compromise between being able to view fish behind cobble and gravel and view interactions near the stream surface. Fifteen minutes after a spawning cue was added to a site, a re-sealable bag containing one of the six egg-treatment levels was submerged, opened, and everted just above the river bottom immediately downstream of the rebar. Video was recorded at 59.94 frames s$^{-1}$ for 30 min per site at 13 sites, and recording began just before the spawning cue was added.

Several environmental variables that may affect stream fish aggression in general or in the context of the experiment were measured: stream velocity, substrate size, and depth at the point of egg addition (Table 1). Increased stream velocity has been shown to reduce rates of aggressive interactions in Arctic charr *Salvelinus alpinus* (Linnaeus, 1758) by enforcing swimming to maintain position (Adams et al. 1995). Similarly, increased substrate size increases water turbulence which may reduce the ability of fish to make aggressions. For depth at the point of egg addition (hereon referred to as egg depth), greater depth may reduce competition for space near eggs and the scent cue. Stream velocity was measured using a meter stick and a float and recording the time the float needed to travel 1 m from the rebar to the

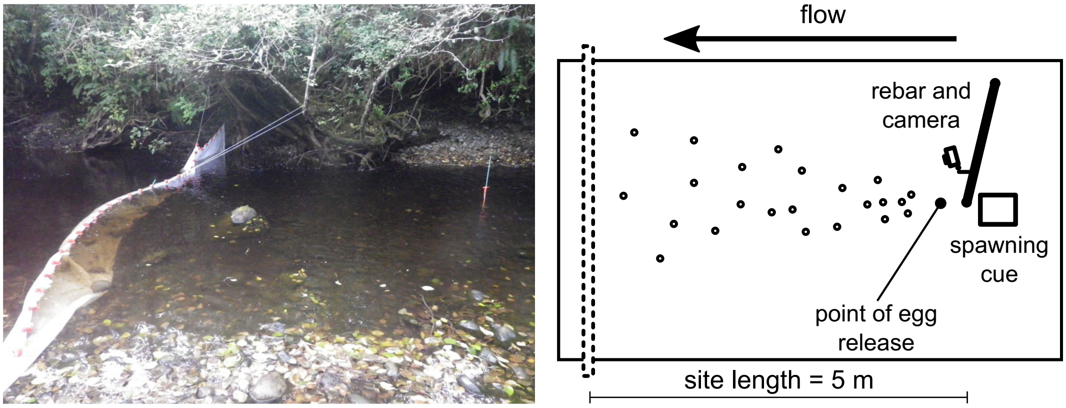

**Fig. 1** Photo and diagram of the layout of the field experiment

**Table 1** Summary of site environmental variables and treatments. Species and salmonid abundances are reported as the average of 5 frame counts

| Site | Mean velocity (m s$^{-1}$) | Mean substrate size (m) | Egg depth (m) | No. eggs | Average abundance | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | Salmonids frame$^{-1}$ (SD) | *Cottus* spp. frame$^{-1}$ (SD) | *O. kisutch* frame$^{-1}$ (SD) | *O. mykiss* frame$^{-1}$ (SD) | *O. clarkii clarkii* frame$^{-1}$ (SD) |
| 1 | 0.08 | 0.062 | 0.28 | 72 | 1.0 (1.2) | 0.4 (0.5) | 0.8 (0.8) | 0.2 (0.4) | 0 (0) |
| 2 | 0.27 | 0.072 | 0.43 | 6 | 0.8 (1.3) | 0.6 (0.5) | 0.4 (0.5) | 0.2 (0.4) | 0.2 (0.4) |
| 3 | 0.20 | 0.077 | 0.34 | 3575 | 4.4 (1.7) | 0 (0) | 0.6 (0.5) | 2.4 (1.1) | 1.4 (0.9) |
| 4 | 0.18 | 0.052 | 0.47 | 303 | 8.4 (0.9)) | 0 (0) | 7.8 (0.8) | 0.6 (0.5) | 0 (0) |
| 5 | 0.50 | 0.208 | 0.32 | 72 | 2.0 (1.4) | 0 (0) | 0.8 (1.3) | 1.0 (1.2) | 0.2 (0.4) |
| 6 | 0.75 | 0.130 | 0.26 | 3575 | 0.6 (0.5) | 0 (0) | 0 (0) | 0.6 (0.5) | 0 (0) |
| 7 | 0.30 | 0.062 | 0.21 | 72 | 16 (0.5) | 0 (0) | 0 (0) | 1.6 (0.5) | 0 (0) |
| 8 | 0.38 | 0.083 | 0.43 | 26 | 2.0 (0.7) | 0 (0) | 1.0 (0.7) | 1.0 (1.0) | 0 (0) |
| 9 | 0.27 | 0.081 | 0.27 | 865 | 0.2 (0.4) | 0 (0) | 0 (0) | 0.2 (0.4) | 0 (0) |
| 10 | 1.00 | 0.184 | 0.29 | 303 | 3.2 (0.4) | 0 (0) | 0.2 (0.4) | 3.0 (0.7) | 0 (0) |

end of the meter stick. Velocity measures were repeated three times and averaged. Stream depth was measured at the rebar, and again at five points across the stream level with the rebar and perpendicular to the direction of flow according to standard methods outlined by Bain and Stevenson (1999). Substrate size was measured along three transects at randomly generated distances from the rebar using a modified version of the Wolman Pebble Count (Bain and Stevenson 1999). At each transect the length of the intermediate axis of the substrate was measured 10 times at systematic intervals across the stream bed and then averaged across all transects.

## Video processing

Each video was 30 min long (the max length of recording given memory limitations); however, only the 15 min immediately following egg addition of each video was processed. We did not process the first 15 min of video because this occurred prior to egg addition when the rebar, camera, and scent cue were installed at a site. This period gave fish time to acclimate to the presence of the new objects in the environment and to locate the spawning cue. Additionally, the presence of a salmon egg cue would not be present without salmon spawning in a natural scenario, thus measuring rates of aggression prior to the addition of eggs was not sensible.

An aggressive behaviour between fishes was recorded when an approach, nip, push or chase behaviour was observed (Adams et al. 1995; Dunlop et al. 2014). We treated each aggressive interaction as a separate event because we could not track or identify individual fish. An approach was classified as a movement towards another fish in which the aggressive fish replaced the position of the aggressed fish. A nip involved physical contact using the mouth, usually directed at the aggressed fish's flank. A push involved physical contact when the aggressor charged the aggressed fish. A chase was recorded when the aggressor quickly and "purposefully" followed the aggressed fish and continued to follow the fleeing fish until passed its initial position. For each aggressive behaviour, the aggressor and aggressed species were identified and recorded. Aggressions were only recorded if all individuals involved were either close enough to the camera or remained in frame and moved close enough to the camera to get positive species identifications. Readers can refer to the supplementary material for example videos of aggressive interactions (see online resources 2–7).

Due to the inability to distinguish between some juvenile *Oncorhynchus mykiss* and juvenile *O. clarkii clarkii*, all questionable juvenile *O. mykiss* and/or *O. clarkii clarkii* were assumed to be *O. mykiss* because adult *O. mykiss* are typically numerically dominant and much larger than adult *O. clarkii clarkii* in the Keogh River (unpub. data). The relative sizes (smaller, larger or same size relative to the other individual involved in an interaction) of the aggressor and aggressed were also recorded and were based on visual estimations (with agreement among three observers). We estimated relative size because we only had one camera, there were no objects for scale or distance in the frame, and fish were constantly moving and changing position and/or orientation. Keogh River electrofishing data from the same time of year (unpublished) indicates that the mean fork lengths of juvenile *O. mykiss*, *O. kisutch*, *O. clarkii clarkii*, and *Cottus* spp. are 79.8 mm (SD 29.7), 56.9 mm (SD 8.9), 192.0 mm (SD 45.7), and 61.2 mm (SD 20.7) respectively. In the rare case that a single fish was aggressive to more than one other fish in the same motion, the behaviour was recorded as multiple individual aggressive acts. It was also noted if the aggressor consumed an egg within three seconds following an aggressive act because we were curious whether there was an immediate, tangible benefit to aggression. However, this was observed only 3 times out of 99 aggressions, thus we did not follow up with any analysis.

To characterize fish abundance by species, videos were paused at five intervals (1:00 min, 4:00 min, 7:00 min, 10:00 min and 12:00 min) and the abundance per fish species in those frames was recorded. Fish counts were subsequently averaged across the five intervals by species as well as by salmonids to provide measures of average fish abundance by site. This method of evaluating species abundances was not intended to represent all the fish within a 5 m site, but instead provide an estimate of the abundances of different species that were visible in the camera frame. Originally, video was recorded at 13 sites; however, three sites were removed from all analyses because ≤1 fish were observed at those sites through their respective videos. Individuals (count of one if it was an interspecific interaction or two for conspecific interactions) of a species were added to the total of the five interval counts for a site if an aggression involving the species occurred at that site but no individuals of that species were observed in the interval abundance counts.

## Analysis

For inferential statistics, we focused on pooled rates of salmonid aggression [i.e., all classes of aggression by any salmonid (*O. mykiss, O. kisutch, O. clarkii clarkia*) against any fish species] that occurred at a given site because we lacked sufficient observations of each class of aggression as well as the various combinations of species and relative sizes of fish that could be the aggressor or recipient of aggression. We also did not perform any inferential statistics on sculpins because they were rarely aggressors or the recipients of aggression.

We used univariate regressions to test how salmon egg abundances, abundances of steelhead, coho, or pooled salmonids, stream velocity, substrate size, and egg depth affected the pooled rates of aggressive interactions. Egg abundances were natural log-transformed because treatments ranged from 6 to 3575 eggs in log increments, and taking the log of egg abundances normalized the data. We were restricted to univariate models due to low replication ($n = 10$ sites). The statistical approach was designed to standardize for variable fish abundances observed on video across sites because the number of aggressions observed should increase as the number of fishes observed increases. Thus, the number of salmonid aggressions observed at a site were divided by the average salmonid abundance. Exploratory analysis indicated no significant relationship between the salmonid abundance metric and the number of eggs added to a site, suggesting that fish were not more spatially aggregated at sites with larger egg abundances. We tested for an effect of coho, steelhead, and salmonid average abundance (Table 1) on pooled aggressions standardized by average salmonid abundance to determine whether aggressions were disproportionately caused by steelhead or coho (the only species consistently observed at most sites), and if rates of aggression scaled isometrically with increasing relative salmonid abundance.

All models were fit with linear models using the statistical programming language R (R core team and contributors worldwide 2017), and model assumptions were checked using diagnostic plots. All univariate models were competed using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002) and the top model was selected. Additionally, the 95% confidence intervals of all the parameter coefficients were checked to see if they crossed zero.

We also used descriptive statistics to summarize the rates of aggressive interactions among all species of fish we recorded and compared these interactions to a null behavioural expectation. Under null behaviour, we expected that a given individual observed in video is equally likely to make an aggressive action against any other individual observed at that site, regardless of species. For example, if we quantified the rate of aggressive actions by steelhead against any other species including steelhead, under the null behaviour assumption, we would expect that steelhead would make aggressive actions against their own species and other species in proportion to the relative average abundances of each species observed in video at a site.

$$\Pr_x(ij\ null) = \left(\tau_i\ \ \tau_x^{-1}\right)\left(\tau_j\ (\tau_x - 1)^{-1}\right) \tag{1}$$

$$\Pr_x(ij\ null, when\ j = i) = \left(\tau_i\ \ \tau_x^{-1}\right)\left((\tau_j - 1)\ (\tau_x - 1)^{-1}\right) \tag{2}$$

where $\tau$ is the count of either the aggressor species $i$, target species $j$, or the total number of individuals counted at any given site $x$. The proportion of observed aggressions was calculated as:

$$\Pr_x(ij\ observed) = \phi_{ij}\ \ \mathrm{T}_x^{-1} \tag{3}$$

where $\phi$ is the total number of aggressions of species $i$ on $j$ for a given site $x$ and T is the total number of all aggressions at that site. To determine if interactions occurred more or less than expected, the proportion of observed aggressive interactions was divided by the proportion of null expectation.

$$\theta = \Pr_x(ij\ observed)/\Pr_\mathrm{x}(ijnull)^{-1} \tag{4}$$

Thus, when $\theta$ was greater than one, species $i$ made more aggressions against species $j$ than would be expected based on their relative average abundances. When $\theta$ was less than one, species $i$ made less aggressions against species $j$ than was expected based on their relative average abundances. The output ($\theta$) of each conspecific and heterospecific interaction pair was then averaged across sites where these species pairs occurred. We also summarized the proportion of aggressive interactions by each combination of species and the relative size of the aggressor to the recipient of aggression.

## Results

*Oncorhynchus kisutch* and *O. mykiss* made up similar proportions of the observed average fish abundance across the 10 sites at 46% and 43%, respectively, whereas sculpin and adult *O. clarkii clarkii* accounted for only 4% and 7% of observed average fish abundance, respectively, across the sites (Table 1). The number of aggressive acts observed across the 10 sites ranged from 0 to 43 (mean = 9.9, SD = 11.8) and totalled 99 across the sites.

Pooled aggressive interactions as a function of natural log-transformed egg addition was the top AICc-selected model (Table 2), and the only model that outperformed the intercept-only model. As predicted, increasing egg abundance was associated with decreasing aggressive interactions among salmonids ($\beta$ = −0.052, 95% CI = −0.093 – -0.010, $R^2$ = 0.429; Fig. 2). In contrast, all other parameters tested had coefficients with 95% CIs that spanned zero (Table 2), suggesting no evidence of an effect on pooled aggression rates.

There were substantial differences in patterns of aggressive interactions among and within species. On average, *O. kisutch* aggressions towards other *O. kisutch* occurred the most compared to the null expectation, followed by adult *O. clarkii clarkii* towards *O. mykiss*, *O. mykiss* towards *O. mykiss*, and adult *O. clarkii clarkii* towards *O. kisutch* (Figs. 3 and 4). Interspecific interactions between *O. kisutch* and *O. mykiss* were close to the null expectation (SE exceeded 1). Interactions with *Cottus*

**Table 2** AICc table of competing models ranked from most-supported to least supported including parameter effect estimates and 95% confidence intervals

| Parameter | K | AICc | ΔAICc | AICc Wt | Cumulative Wt | Log likelihood | Effect estimate | Lower 95% CI | Upper 95% CI |
|---|---|---|---|---|---|---|---|---|---|
| ln(no. eggs) | 3 | −4.45 | 0.00 | 0.44 | 0.44 | 7.23 | −0.05 | −0.09 | −0.01 |
| Intercept | 2 | −3.13 | 1.32 | 0.23 | 0.66 | 4.42 | 0.28 | 0.17 | 0.38 |
| Substrate size | 3 | −2.17 | 2.28 | 0.14 | 0.80 | 6.09 | −1.60 | −3.37 | 0.17 |
| Velocity (m/s) | 3 | −0.72 | 3.73 | 0.07 | 0.87 | 5.36 | −0.26 | −0.66 | 0.14 |
| No. steelhead | 3 | 0.10 | 4.55 | 0.04 | 0.92 | 4.95 | −0.05 | −0.16 | 0.06 |
| No. coho | 3 | 0.90 | 5.35 | 0.03 | 0.95 | 4.55 | 0.01 | −0.04 | 0.06 |
| Egg depth | 3 | 1.08 | 5.53 | 0.03 | 0.97 | 4.46 | 0.17 | −1.14 | 1.48 |
| No. salmonids | 3 | 1.15 | 5.60 | 0.03 | 1.00 | 4.42 | 0.00 | −0.05 | 0.05 |

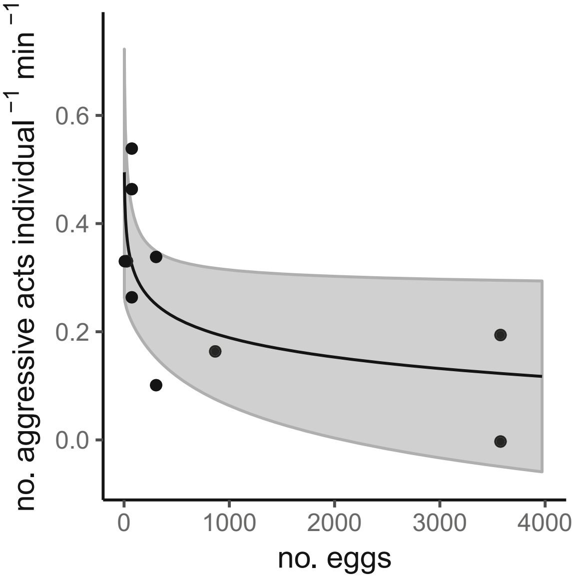

**Fig. 2** Relationship between the mean number of aggressive acts per salmonid per minute and the number of salmon eggs added to a site. Points represent the data, the black line shows the mean model prediction, and the gray area around the mean illustrates the 95% confidence interval

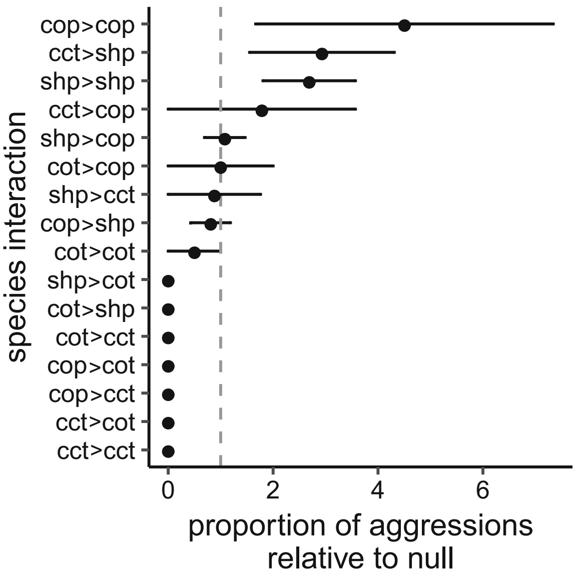

**Fig. 3** Mean proportion of observed species-specific aggressive interactions (± SE), relative to the null expectation ($\theta$, see Eq. 4). The dotted vertical line is at $x = 1$, which indicates an equal proportion of observed interactions to the null expectation; values above 1 indicate higher than the null expectation and values below are less than the null expectation. cot = *Cottus spp.*, cop = *O. kisutch*, shp = *O. mykiss*, cct = *O. clarkii clarkii*. Closing angle brackets in the y-axis pairs indicate aggressor (open side) and the recipient of aggression (closed side). Values of 0 indicate that this aggressive interaction was not observed

spp. always occurred less than or equal to the null and the only salmonid interaction that did not occur was adult *O. clarkii clarkii* towards adult *O. clarkii clarkii*.

Each species differed in the frequency of aggressions associated with the relative size between aggressor and aggressed. Conspecific *O. kisutch* aggressions occurred the most between individuals of the same size, whereas conspecific *O. mykiss* aggressions occurred almost equally from larger individuals and those of the same size (Table 3). Aggressions of *O. kisutch* on *O. mykiss* occurred the most when the *O. kisutch* was larger (41.2%) rather than when they were the same size or smaller (both 29.4%). *O. mykiss* were almost always larger than *O. kisutch* when they attacked (96.3%). Adult *O. clarkii clarkii* were always larger than the fish they attacked.

## Discussion

This study demonstrates that the rate of aggressive interactions in stream fishes decrease as pink salmon egg availability increases. These results suggest that a breakdown in competitive interactions among stream fishes can temporarily occur when resources are superabundant. This study's findings are similar to results from several ex situ studies on intraspecific aggression for food among *O. kisutch* and *O. mykiss* (Slaney and Northcote 1974; Mason 1976; Moutou et al. 1998; Noble et al. 2007), where aggressive interaction rates decreased with increasing food availability. This study also contrasts with the results of Keenleyside and Yamamoto (1962) and Glova (1986), where the addition of food coincided with the greatest rates of intra- and interspecific aggression among salmonids. Glova (1986) did not manipulate the amounts of food added in the experiment, and Keenleyside and Yamamoto (1962) manipulated the number of times fish were fed per day rather than the amount fish were fed at a given feeding event. However, if these methods are viewed in the context of stomach fullness in the presence and absence of food, they may fit with the results from this study. If fish have relatively empty stomachs but there is no food to compete for, then fish will likely conserve energy and forgo aggression. When fish are presented with food, they may become more aggressive because there is food to compete for (e.g., Glova 1986), and as the amount of food increases, stomach fullness and thus the drive to

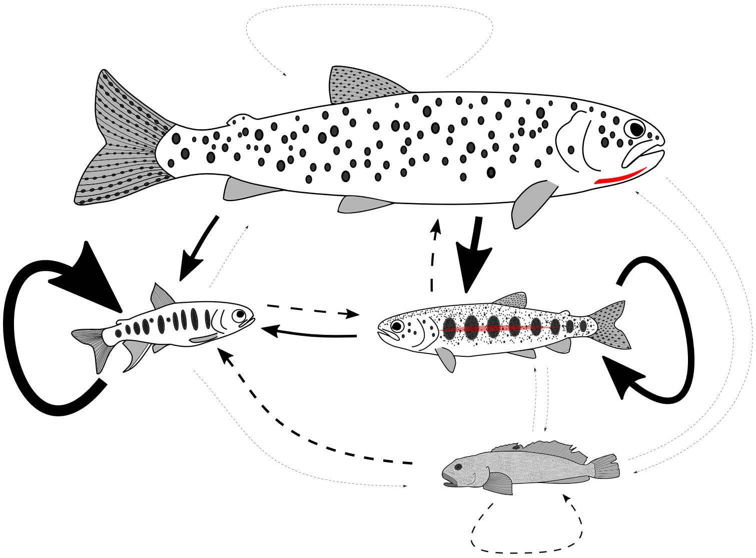

**Fig. 4** Illustration of intra- and interspecies aggression in the presence of drifting salmon eggs. Line and dash widths are scaled to represent the frequency of interactions relative to the null expectation ($\theta$, see Eq. 4, see Fig. 3). Arrows point from the aggressor to the recipient—for example, *O. clarkii clarkii* tended to be aggressive towards *O. kisutch* parr, but *O. kisutch* parr were not aggressive towards *O. clarkii clarkii*. Dashed lines represent interactions that occurred less often than the null expectation whereas solid lines represent interactions that happened as often as the null or more than the null expectation. Starting at the top and then proceeding clockwise: *O. clarkii clarkii*, *O. mykiss* parr, *Cottus spp.*, and *O. kisutch* parr. Images are scaled relative to the mean size of each species in the Keogh River

compete for food likely decreases (e.g., the results of this study; Noble et al. 2007).

Collectively, this body of research suggests that aggression rates may be higher when food is present compared to when food is absent, with rates of aggression initially declining rapidly as food availability increases and decelerating as food availability reaches saturation. The results of this study suggest that increased food availability may not only provide more food but also have indirect short-term benefits of decreasing the damage and energetic costs of aggressive behaviour in natural systems, which has been connected to increased growth rates and survival in experiments (Cutts et al. 1998; Moutou et al. 1998). Mechanistically, saturating a habitat with a pulse of high-value food can result in stream fish consuming up to and in some cases greater amounts of food than their daily maximum consumption rates ($C_{\max}$; e.g., Furey et al. 2015). This leads to high energetic demand for digestion, leaving little remaining aerobic scope available (Norin and Clark 2017) for energetically-demanding behaviours such as aggression.

Aggressive interactions within and among species appeared non-random, suggesting strong hierarchical patterns of dominance within and across species. This study's results parallel prior research that identify high rates of aggression from larger fish and between fish with high niche overlap (Nakano 1995; Harwood et al. 2002; Young 2004; Kaspersson et al. 2010). Adult *Oncorhynchus*

**Table 3** Percent of interactions within species pairs where the aggressor species was larger, smaller, or the same size as the recipient species. cot = *Cottus spp.*, cop = *O. kisutch*, shp = *O. mykiss*, cct = *O. clarkii clarkii*. Closing angle brackets in the x-axis pairs indicate aggressor (open side) and the recipient of aggression (closed side)

| Relative size | cop > cop | cop > shp | shp > shp | shp > cop | cct > cop | cct > shp |
|---|---|---|---|---|---|---|
| Larger | 17.8 | 41.2 | 47.7 | 96.3 | 100 | 100 |
| Same | 79 | 29.4 | 45.5 | 3.7 | 0 | 0 |
| Smaller | 3.2 | 29.4 | 6.8 | 0 | 0 | 0 |

*clarkii clarkii*, which were consistently the largest individuals, were more aggressive towards the two other salmonid species than null expectations. Adult *O. clarkii clarkii* were also rarely the recipients of aggressive attacks, suggesting that they are at the top of the dominance hierarchy in this system. Conspecific aggressions within the two smaller salmonids, juvenile *O. kisutch* and *O. mykiss*, occurred more frequently than the null expectation. However, the interspecific interactions between *O. kisutch* and *O. mykiss* were near the null expectation. These interspecific aggressions tended to come from larger individuals, particularly in the case of *O. mykiss* attacking *O. kisutch* (96.3% of all *O. mykiss* on *O. kisutch* interactions). Thus, there appeared to be size- and species-structured patterns of interference competition.

As predicted, the benthic fish present in Keogh River fish community (*Cottus* spp.) had the fewest number of interactions with any species, and even their conspecific interactions were below the null expectation. *Cottus* spp. are typical benthic ambush predators (Baltz et al. 1982) and territorial; larger *C. bairdi* will exclude smaller individuals from prime habitat (Rashleigh and Grossman 2005) and there is some evidence that interference competition driven by *C. perplexus* density reduces their feeding rates (Preston et al. 2018). Hence, we would have expected to observe levels of intraspecific competition that scaled with the relative average abundance of *Cottus* spp. However, *Cottus* spp. were observed few times, so it is possible that our results are the product of our small sample size. Overall, our study helps provide insight into the patterns of dominance across and within species in this stream fish community (Figs. 3 and 4).

When there are fewer eggs in the stream, juvenile salmonids exhibited more energetically-costly (Metcalfe 1986) and harmful aggressive behaviours (Cutts et al. 1998; Moutou et al. 1998) to consume presumably fewer available eggs. Conversely, greater amounts of eggs in the stream were associated with fewer aggressive behaviours, and fish presumably consumed more eggs for a lower energetic cost. Thus, reducing the total number of aggressive behaviours may disproportionately benefit smaller salmonid individuals in the community that tend to be the recipients of aggression. This suggests that larger pulses of food not only increase the amount of food that fishes get to consume, but also increases the efficiency of energy transfer to all sizes of salmonids. Given that salmon egg subsidies can contribute most of the energy used for growth in a stream fish community over a year (Scheuerell et al. 2007; Armstrong and Bond 2013), and assuming that interference competition regulates foraging success and energy budgets, we speculate that dominance hierarchies could be weakened by large salmon runs, and strengthened or maintained by weak salmon runs.

This simple experiment uncovers how spawning salmon can temporarily affect competitive behaviour in stream fishes in a natural environment, but it has important limitations. All the results of this study are limited to what was observed in a single camera and could be strengthened by further observations, greater replication, and a quantification of the number of eggs consumed per species-species combination at the different levels of experimental egg addition. The 15° camera angle captured many salmonids but few *Cottus* spp. likely because *Cottus* spp. are benthic, thus *Cottus* spp. lying behind gravel and cobble further from the camera would have been hidden from view. Like Ebner et al. (2009), we recommend the use of horizontal cameras, but in combination with vertical cameras to capture benthic and mid-water aquatic species in complex habitats.

Given covariation between size and species identification of *O. clarkii clarkii* and *O. mykiss*, it was not possible to separate size effects from species effects for *O. clarkii clarkii* and *O. mykiss.* Typically, the dominance hierarchy among hetero- and conspecific salmonids is driven by body size (e.g., Usio and Nakano 1998) because individuals occupy the same or similar niche space. However, size-driven hierarchies among species can break down if environmental conditions such as temperature change to favour smaller species (Baltz et al. 1982; Taniguchi et al. 1998). Given that water temperatures averaged 15.3 °C (SD 1.0; well below lethal limits for *Oncorhynchus* spp.; Brett 1952; Richter and Kolmes 2005), it is unlikely that dominance hierarchies were affected by temperature in this study.

Finally, this study focuses on the short-term effects of pulsed prey resources on competitive behaviour, which may not be applicable to longer-term processes. On one hand, prey availability is naturally patchy and stochastic (Armstrong and Schindler 2011); streams experience aquatic insect hatches, terrestrial insect inputs through dispersal or wind events, and salmon spawning events, all of which can be spatially and/or temporally variable (Baxter et al. 2005; Moore et al. 2015; Wesner et al. 2019). On the other hand, streams experience ambient levels of constant invertebrate drift that are more stable and representative of average prey availability through time and space (Brittain and Eikeland 1988). During resource pulses, stream fishes likely clump near the source of the pulse and display aggression dynamics like stream fishes in this study which clumped just downstream of the scent cue and point of egg addition. However, this study does not represent regular periods, where stream fishes likely maintain their normal territories, and thus display different aggression dynamics.

## Conclusion

This study furthers the understanding of how salmon egg pulses affect stream fish communities. As salmon egg abundance increased, aggressive interaction rates per fish decreased. This demonstrates that pulsed resource superabundance can result in a temporary breakdown in interference competition. Given that smaller fish appear to have the most to gain from temporary breakdowns in interference competition, large pulses of food may serve to reduce the strength of dominance hierarchies in stream fish communities.

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**Compliance with ethical standard** All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the Canadian Animal Care Committee (CACC) and Simon Fraser University.

**Conflict of interest** The authors declare that they have no conflict of interest.

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