Resource pulses increase the diversity of successful competitors in a multi-species stream fish assemblage

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Abstract. Food resources are often patchily distributed through space and time and are classified as resource pulses when hyperabundant. Resource pulses can benefit growth, reproduction, and abundance of various consumers. Yet, it is relatively unknown how such resources are partitioned among competing consumers and how this is influenced by the magnitude of the pulse. Here, we examined how the magnitude of a pulsed resource influences resource partitioning among diverse sizes and species of consumers in a natural setting over small spatial and temporal scales. We focused on salmon egg subsidies to stream fish consumers. We experimentally added different quantities of pink salmon eggs to five meter long experimental stream sections. Egg additions spanned three orders of magnitude from 6 to 3575 eggs. Stream fish (egg consumers) were captured and gastric lavaged at each experimental section to determine how many eggs each individual fish consumed. We modeled taxon-specific individual egg consumption as a function of egg availability, individual mass, community composition, number of competitors, and stream velocity using hurdle models in a Bayesian framework. We found that there were diminishing returns for increasing egg abundance increasing egg consumption (i.e., type II functional response) for individual size classes of fish, but that higher egg numbers were needed to benefit diverse consumers. Top models indicated that egg availability and individual fish characteristics (size and taxon) drove egg consumption, while community characteristics (species composition and number of competitors) were not supported. Our results suggest that resource pulses can provide rare opportunities for less dominant sizes and species of fish to consume abundant resources. The current paradigm in the stream fish literature suggests that stream fish communities are structured by dominance hierarchies; however, dominance hierarchies may be less influential where pulsed resources comprise a large portion of the resource base.

Key words: coho salmon; competition; functional response; resource pulse; salmon subsidy; sculpins; steelhead trout; stream fishes.

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INTRODUCTION

Consumers must cope with spatial and temporal variability in food resources (Weimerskirch et al. 2005, Armstrong and Schindler 2011). In extreme cases, resources come in pulses, defined by Yang et al. (2008) as uncommon events in which large quantities of a resource become available for a short period of time. Although infrequent, resource pulses can provide the majority of the energy and nutrient intake for animal consumers (Yang et al. 2008, 2010). For example, bank voles may acquire ~74% of their annual food intake from oak and hornbeam mast events (Selva

et al. 2012) that may only last ~4 weeks (Pucek et al. 1993). Resource pulses can also significantly alter the reproductive output and abundance of animal consumers (Yang et al. 2008, 2010); for example, female damselfish with access to coral propagules from a synchronized spawning event may produce larvae with 25% larger yolk sacs and 100% larger oil globules (McCormick 2003). While there is growing appreciation for the importance of resource pulses to consumers in a variety of ecosystems (Yang et al. 2010), it is less well understood how these resources are partitioned among competing consumers (Yang et al. 2008). It is possible that the magnitude of the resource pulse could temporarily alter competition; for instance, greater resource abundance could allow inferior competitors to acquire some portion of the resource pulse.

Salmon-bearing streams are a classic example of ecosystems that can experience resource pulses (Schindler et al. 2003, Moore et al. 2008, Walsh et al. 2020). Salmon spawn and die in streams annually, producing carcass tissues and eggs that are consumed by a variety of predators and scavengers (Naiman et al. 2002, Deacy et al. 2016) such as stream fishes (Lang et al. 2006, Bailey et al. 2019). Energy acquired during the brief salmon spawning period can dominate the annual energy budget for stream fish consumers (Scheuerell et al. 2007, Moore et al. 2008, Armstrong and Bond 2013); for example, through bioenergetic simulations, Moore et al. (2008) predicted that resident rainbow trout (*Oncorhynchus mykiss*) in their study would run an energetic deficit during the summer without salmon subsidies. Increased spawning salmon abundance can increase the growth (Rinella et al. 2012, Swain et al. 2014) and abundance (Nelson and Reynolds 2014, Swain and Reynolds 2015) of stream fishes, and alter their life histories (Bailey et al. 2018). The availability of this important food resource depends on stream fishes' ability to consume dislodged or unsuccessfully buried salmon eggs (Collins et al. 2016). Salmon eggs are energetically and nutritionally superior to benthic invertebrates (Cummins and Wuycheck 1971, Schindler et al. 2003), they are highly visible, and eggs do not have an escape response to predators. Indeed, when salmon eggs are at high abundances, stream fishes may eat little else (Moore et al. 2008, Armstrong et al. 2010). Salmon egg availability varies both seasonally and annually —the positive nonlinear effect of spawner abundance on available eggs, caused by nest superimposition at high spawner abundances, can magnify interannual variance in spawner abundance (Moore et al. 2008). Thus, salmon egg availability to stream consumers can be extremely variable and this variation may have consequences for egg consumption among competing stream fish.

Among drift-feeding stream fishes, competition is generally considered to be hierarchical, where larger individuals and certain species of fish express dominance and exclude others from territories or win direct contests for resources (Glova 1986, David et al. 2007, Sato and Watanabe 2014, Naman et al. 2019). During periods of regular (and low) resource availability, dominant individuals consume greater amounts of resources (Cutts et al. 1998, Taniguchi et al. 1998). However, although streams may be subject to long periods of low resource availability, most resources may be delivered in brief pulses such as synchronized aquatic insect emergences (Wesner et al. 2019), terrestrial insect dispersal/ outbreaks (Tyus and Minckley 1988), and stream fish spawning events (Armstrong and Bond 2013). The willingness to emigrate and territory sizes of stream fishes generally decrease as food availability increases, indicating that dominance hierarchies are weaker when more food is present (Slaney and Northcote 1974, Dill et al. 1981, Keeley 2000, Imre et al. 2004). Thus, while dominance hierarchies may structure drift-feeding stream fish behavior and foraging success most of the time, this paradigm may not be relevant during resource pulses, which can provide the bulk of the resources consumed by stream fishes.

Here, we performed an in situ field experiment in short stream segments to examine the following question: How does the magnitude of a pulsed resource influence resource partitioning among a diverse consumer community? Specifically, we experimentally created resource pulses of different magnitudes by adding quantities of salmon eggs spanning three orders of magnitude and measuring the functional responses of stream fish consumers that varied in size and species—juvenile steelhead trout (*O. mykiss*), coho salmon (*Oncorhynchus kisutch*), and sculpins (*Cottus* spp.). We hypothesized that higher

magnitude resource pulses would lead to broader sizes and species of consumers acquiring resources, and greater amounts of resources acquired per individual consumer. Specifically, we predicted that higher magnitude resource pulses would reduce the strength of dominance hierarchies, allowing smaller individuals and less competitive species to access resources and consume greater numbers of eggs.

MATERIALS AND METHODS

Study system

Pink salmon (*Oncorhynchus gorbuscha*) eggs were added to experimental reaches in the Keogh River (50°40′43.56″ N, 127°20′55.23″ W), British Columbia, Canada. The Keogh River is a small (31.2 km long with a watershed area of 130 km^2; Smith and Slaney 1980) coastal stream with low nutrient concentrations (Johnston et al. 1990) that drains into Johnstone Strait on the east coast of Vancouver Island, just south of the town of Port Hardy. Since 1972, salmonid monitoring has been ongoing and several habitat restoration projects have been completed at the Keogh River (Ward and Wightman 1989, Smith and Ward 2000, McCubbing and Ward 2002, Atlas et al. 2015, Bailey et al. 2018). Stream fish species that may prey on salmon eggs in the Keogh River include juvenile steelhead trout (*O. mykiss*), coho salmon (*O. kisutch*), cutthroat trout (*Oncorhynchus clarkii clarkii*), Dolly Varden char (*Salvelinus malma*), and sculpins *Cottus* spp. (*C. asper* and *C. aleuticus*). Estimated pink salmon spawner abundance has ranged from as few as ~75 to >800,000 fish over the last 40 yr (Bailey et al. 2018, Fisheries and Oceans Canada 2020), generating resource pulses that span many orders of magnitude.

Field experiment

Water-hardened pink salmon eggs were experimentally added to 5 m long sites in the Keogh River a three-week period from mid-August to the end of the first week of September. Eggs were sourced from mature female pink salmon staging at the mouth of the Keogh River, and egg treatments included six levels that ranged from 6 to 3575 eggs in logarithmic increments (6, 26, 72, 303, 865, 3575). Each egg treatment level was replicated six times for a total of 36 experimental units. These treatment levels were selected to approximate the range of eggs that stream fish might realistically encounter in the Keogh River from a year when extremely few pink salmon are spawning, to the peak of the largest pink salmon run ever recorded on the Keogh River (see Appendix S1 for calculations).

Site locations were determined by randomly selecting a habitat type (pool, riffle, or glide) and walking upstream until that habitat type was encountered (as characterized by Bain and Stevenson 1999, Fausti et al. 2004). This randomization method ensured that habitat was not confounded with egg treatment. Sites were placed within a 24-km stretch of river accessible to pink salmon, spaced a minimum of 20 m apart and a maximum of 11 km apart, and clustered around access points along the river. Site setup began with installing a seine net (1/4-inch mesh) across the downstream boundary of a site and anchoring it to the bottom by trapping the lead line with rocks. The upstream boundary of the site was then marked by a piece of rebar imbedded in the sediment through the thalweg of the stream. Next, a scent cue was installed at the upstream boundary of a site to simulate pink salmon spawning and to signal stream fishes that eggs may become available for consumption. The cue consisted of a weighted, sealed bag punched with small holes, and filled with water that eggs had soaked in for more than 24 h.

We left sites undisturbed for 15 min after adding the scent cue to allow fish to settle after the disturbance of setting up the net and rebar. Next, eggs were released all at once, underwater, and just above the substrate—akin to nest superimposition where eggs are released in a pulse. Thirty minutes after egg addition, three-pass electrofishing was used to capture as many fish from a site as possible. Captured fish were identified to species for salmonids or genus for sculpins, lightly anaesthetized, and then gastric lavage was used to sample their stomach contents. If a stomach sample contained salmon eggs, egg fragments, or egg casings, the contents were preserved in 95% ethanol for later enumeration. We waited 30 min after egg addition before electrofishing because we wanted to provide fish with enough time to find and consume eggs without allowing them to pass eggs into the lower gut where they would be inaccessible to gastric lavage. Based on our observations, eggs

did not drift out of the experimental reach (a few eggs were observed in the downstream net in only one of 36 sites). Fork length and mass of fish were measured after gastric lavage, at which time fish were placed in a flow-through recovery container in the stream before being released back into the site they were captured from.

We used a net at the downstream boundary of each site to ensure that the different experimental reaches operated as independent units. If we had allowed fish to move freely, we may have resampled the same fish from a previous site downstream. In addition, the downstream net enabled us to efficiently sample the fish community and prevent fish that had consumed eggs from leaving the experimental area during fish capture efforts.

We sampled a total of 36 sites and 1224 stream fish. Between one and six sites were sampled per day (depending on our supply of salmon eggs), and all experimentation was completed over the three weeks preceding when pink salmon typically arrive at the study reaches. Each site was only sampled once to minimize the impacts of electrofishing. Sites were sampled systematically from downstream to upstream to ensure that electrofishing never overlapped with the earliest migrating pink salmon spawners. Thus, all salmon eggs in the diets of the consumers were from the experimental treatments.

Eggs from stomach samples were counted back in the laboratory. When counting the number of eggs in a stomach sample, we only counted an outer egg casing as an egg when we found egg fragments in the stomach. When there were multiple egg casings, we examined the egg fragments in a stomach and approximated how many whole eggs worth of fragments there were and added that to the egg consumption count for a fish. Egg fragments and casings were common but not dominant. Using this method, we produced conservative estimates of egg consumption by stream fishes.

Analysis

We analyzed functional responses in separate models for each of the common predator taxa: steelhead trout, coho salmon, and sculpins. While cutthroat trout and Dolly Varden char were captured and did consume eggs, they were too rare to fit models for these species. We also omitted individuals from our models that were smaller than the smallest fish of each species recorded consuming an egg under the assumption that they were not capable of consuming eggs (50 mm *O. mykiss*, 45 mm *O. kisutch*, 56 mm *Cottus* spp.). For each of the common predator taxa, we tested a variety of potential covariates in a series of candidate models that were then competed to determine the top model.

Species-specific individual egg consumption was modeled as a function of egg availability, individual fish characteristics, and fish community characteristics. Egg availability was measured as the number of eggs released at a site. For individual fish characteristics, we used ln(mass) and relative mass. We used the natural log of mass as a proxy for absolute competitive ability (a proxy for foraging efficiency and ability to win foraging contests) as well as a proxy for the maximum number of eggs an individual can consume (larger fish have greater internal volume to store food). In contrast, relative mass (the mass of an individual divided by the mass of the largest fish in a site, regardless of species) was used as proxy for the competitive ability of an individual relative to the largest competitor at a site. For community characteristics, we used site-level competitor abundance and site-level fish community composition. Competitor abundance indicates how many mouths an individual must compete with for food (i.e., more competitors are hypothesized to reduce the number of eggs consumed per individual) and was the sum of all fish captured at a site minus one. Community composition was summarized using a principle components analysis of site-level species abundances (PCA; Appendix S2). We used the first axis of the PCA which explained 94% of the variation in fish abundance by species at each site. We included community composition because there is evidence that even among closely related species such as salmonids, there are species-specific differences in competitive dominance (Young 2004, Thornton et al. 2017), and thus, sites with greater proportions of more dominant or less dominant species could reduce or increase individual egg consumption, respectively.

We examined stream velocity as potential variable. Stream velocity was measured by dropping a cork into the stream at the position of the rebar rod (that marked the upstream limit of a site) and timing how long it took to drift the length of a one-meter measuring stick. This measurement

was repeated five times at each site and averaged. This measurement occurred after fish sampling took place to avoid disturbing the fish. We used stream velocity rather than habitat type because stream velocity is related to habitat type and it was more likely that we would detect an effect from a quantitative variable than using a broad categorical variable. We hypothesized that higher stream velocities would reduce the probability of egg consumption and number of eggs consumed by fish.

We modeled egg consumption by stream fishes using hurdle models in a Bayesian framework with the BRMS package (BRMS translates R code to STAN; Bürkner 2017) in the statistical software R (R Core Team 2016). Hurdle models have two components; in this case, the first submodel determined the probability of an individual consuming at least one salmon egg (i.e., the occurrence of any eggs in a fish's stomach), and the second sub-model focused on the number of eggs in fish that consumed at least one egg. We used hurdle models rather than traditional functional responses because our data were zero-inflated, we hypothesized that different processes may influence the two components of the model, and only one response was measured for each individual fish (necessitating a random effects structure). We note that hurdle models can produce relationships between prey abundance and consumption rates that correspond with type I, II, or III functional responses.

The logistic component of the hurdle model modeled the presence or absence of eggs in an individual's diet, which can be conceptualized as the probability of a fish successfully accessing any eggs. This logistic component of hurdle models allowed us to test our hypothesis that increased egg availability increases the probability of egg consumption by less competitive stream fishes. Thus, ln(mass) and relative mass were potential covariates and represented the effect of body mass on competitive ability (foraging efficiency and ability to win direct contests).

The count portion of the hurdle model modeled the number of eggs consumed by fish that consumed at least one egg. Count component models were always offset by ln(mass) to account for size-limited food storage and relative size was used as a potential covariate to represent the competitive mechanism of fish size.

Using ln(mass) as an offset allowed us to estimate the variation in egg consumption that could be attributed to competitive ability (via relative mass) without being confounded by differences in stomach volume.

We included some of our covariates in all models for biological realism. Egg abundance (treated as a continuous variable) was included in all component models because there cannot be egg consumption without eggs. Site was set as a random effect in all component models to account for differences in habitat among sites and because egg treatments were applied at the site level, but responses were measured at the individual fish level. Stream velocity, number of competitors, and community composition were competed in some but not all models. Interactions among some of the covariates were tested (see Appendix S3 for candidate model lists). We were particularly interested in whether egg abundance and body size effects (ln(mass) or relative mass) interacted. If body size effects were positive at low egg abundance but declined with increasing egg abundance (in either the logistic or count component model), this would indicate that dominance hierarchies were strongly weakened by increasing resource availability. However, even if body size effects do not interact with egg availability, it is still possible to observe evidence of reduced hierarchical effects on egg consumption given that hurdle models are a product of independent logistic and count component models. We restricted the number of covariates in sculpin count models to two fixed effects due to low numbers of sculpins consuming eggs ($n = 29$).

In hurdle modeling, the combination of the best logistic component model and the best count component model combine to make the top hurdle model. Thus, candidate logistic generalized linear mixed effects models were competed first to determine the top logistic component model. The top logistic model was then set as the logistic component model in candidate hurdle models with different hypothesized count component models. To compare models, we used the post_prob() function in the BRMS package, which computes posterior model probabilities from marginal likelihoods to produce the relative probability of each candidate model against every other candidate model (probabilities of all models sum to one).

We followed modeling options recommended for BRMS (which translates R code to Stan; Bürkner 2017) and Stan (Stan Development Team 2019). Our logistic component models used the default logit link, while the count models were zero-truncated negative binomial models with a default log link. All covariates were standardized (centered and divided by one standard deviation; Schielzeth 2010) and assigned Gaussian priors with a mean of zero and standard deviation of 10. These weakly informative priors make the null assumption that none of the covariates have an effect but includes a standard deviation that is broad enough to detect effects of standardized variables should they exist (Gelman 2019). Each model was run using four chains with lengths of 3000 iterations where the first 1000 iterations were discarded as burn-in. We evaluated model convergence using the Gelman-Rubin diagnostic test on each candidate model to determine whether independent chains converged to a common posterior mode, with potential scale reduction factors (Rhat) <1.1 suggesting convergence.

Simulation model.—We simulated egg consumption across the total sampled Keogh River fish community to explore how egg resources are partitioned across multiple sizes and species of stream fishes. Using the top model posterior distribution for each fish taxon from the analysis described above, we made predictions across three levels of egg availability: 10, 100, and 1000 eggs. We used these egg quantities for ease of interpretation and set a maximum of 1000 eggs because predicted egg consumption changed little above that abundance. We predicted the egg consumption of every fish in our dataset 1000 times and calculated the average for each fish. Individuals not included in the above statistical analysis because they were too small to consume eggs were included here and their consumption was always set to zero. For sculpins, individual relative size was calculated relative to the largest fish in the entire dataset rather than the largest fish at the site level (following the top model), and thus, absolute mass is proportional to relative mass for sculpins in this simulation.

RESULTS

Across all egg treatments and sites, we captured a total of 234 juvenile steelhead trout, 423 juvenile coho salmon, 541 sculpins, 20 cutthroat trout, and six Dolly Varden char. The proportion of fish from each taxon that consumed at least one egg was 0.56, 0.42, 0.06, 0.55, and 0.33, respectively. Per gram of fish, steelhead trout, coho salmon, sculpins, cutthroat trout, and Dolly Varden char consumed 0.57, 0.33, 0.04, 0.35, and 0.12 eggs, respectively. Per site, there was an average of 6.6 steelhead trout (range 0–20), 12.5 coho salmon (range 2–46), 50.9 sculpins (range 0–221), 0.5 cutthroat trout (range 0–3), and 0.2 Dolly Varden char (range 0–2).

Top models

For steelhead trout, coho salmon, and sculpins, all top candidate logistic component models included a measure of individual mass (relative mass for sculpins and natural log of absolute mass for the Salmonids), and egg abundance (included in all candidate models; Appendix S3). Similarly, the top count component model for each taxon contained egg abundance (included in all candidate models) and an offset of individual absolute mass (included in all candidate models; Appendix S3). Top models never included interaction terms and candidate models including interactions never exceeded a relative model probability of 5% (Tables 1, 2). Neither species composition nor number of competitors at the site level (community-level factors) appeared in the top model for any taxon, and candidate models that included these terms never exceeded a relative model probability of 8% (Tables 1, 2). Similarly, candidate models that included stream velocity never exceeded a relative model probability of 5% (Tables 1, 2).

Overall, fish size and egg abundance had consistently large and positive effects on egg consumption. As predicted, increased egg availability increased the number of eggs consumed across fish taxa (Tables 1, 2, Figs. 1, 2). Egg availability had strong mean standardized effects in the logistic component models (range across taxa was 1.45–1.98; Table 3), supporting our hypothesis that higher abundances of eggs would enable more individuals, including those less dominant, to access eggs. The mean effect of egg abundance was also positive in the count component models, albeit weaker and less certain (range across taxa 0.19–0.52; Table 3). Fish size (individual mass or relative mass) had

Table 1. Top logistic component models for steelhead trout, coho salmon, and sculpins.

Species and model rank	Candidate logistic model	Relative model probability	Cumulative probability
Steelhead trout			
1	egg abundance + ln(mass) + (1|site)	0.76	0.76
2	egg abundance + relative mass + ln(mass) + (1|site)	0.18	0.94
3	egg abundance + ln(mass) + egg abundance:ln(mass) + (1|site)	0.02	0.96
4	egg abundance + relative mass + ln(mass) + relative mass:ln(mass) + (1|site)	0.02	0.98
5	egg abundance + ln(mass) + no. competitors + (1|site)	0.02	1.00
Coho salmon			
1	egg abundance + ln(mass) + (1|site)	0.83	0.83
2	egg abundance + relative mass + ln(mass) + (1|site)	0.12	0.95
3	egg abundance + ln(mass) + no. competitors + (1|site)	0.02	0.97
4	egg abundance + relative mass + ln(mass) + relative mass:ln(mass) + (1|site)	0.02	0.98
5	egg abundance + ln(mass) + egg abundance:ln(mass) + (1|site)	0.01	1.00
Sculpins			
1	egg abundance + relative mass + (1|site)	0.37	0.37
2	egg abundance + (1|site)	0.30	0.68
3	egg abundance + no. competitors + (1|site)	0.08	0.76
4	egg abundance + relative mass + no. competitors + (1|site)	0.05	0.81
5	egg abundance + relative mass + egg abundance:relative mass + (1|site)	0.05	0.86
6	egg abundance + stream velocity + (1|site)	0.05	0.91
7	egg abundance + ln(mass) + (1|site)	0.04	0.94
8	egg abundance + (1 + egg abundance|site)	0.02	0.97
9	egg abundance + relative mass + ln(mass) + (1|site)	0.01	0.98
10	egg abundance + ln(mass) + no. competitors + (1|site)	0.01	0.99
11	egg abundance + relative mass + no. competitors + egg abundance:relative mass + (1|site)	0.01	1.00

positive mean standardized effects across logistic component models (range across taxa 1.25–2.53; Table 3), supporting our hypothesis that larger fish were competitively dominant over smaller fish. As expected, the offset of the natural log of individual mass explained much of the variation in the number of eggs consumed in the count component models (Fig. 1b, d, f) because this variable controlled for differences in stomach volume.

Steelhead trout.—Larger steelhead trout presented with higher salmon egg abundances were not only more likely to consume at least one egg, but also generally consumed greater quantities of eggs (Table 3, Fig. 1a, b). In the top hurdle model, an average juvenile steelhead (4.4 g) was predicted to eat 1.7 eggs on average (95% CI 1.3–2.2) at mean egg abundance (266 eggs added) and 3.2 eggs (95% CI 2.4–4.0) at high egg abundance (2224 eggs; mean + 1 SD; predictions are for all steelhead regardless of whether they consumed eggs). With respect to individual size, at mean egg abundance (266 eggs added), a 4.4-g

steelhead was predicted to consume 1.7 eggs (95% CI 1.3–2.2), whereas an 11.1-g (mean + 1 SD) steelhead was predicted to consume 5.7 eggs (95% CI 4.1–7.4; Fig. 2a).

Coho salmon.—Larger coho salmon presented with higher salmon egg abundances were also more likely to consume at least one egg and consumed greater quantities of eggs (Table 3, Fig. 1c, d). In the top hurdle model, an average juvenile coho (1.9 g) was predicted to eat 0.5 eggs on average (95% CI 0.1–1.1) at mean egg abundance (250 eggs added) and 1.4 eggs (95% CI 0.5–2.1) at high egg abundance (1633 eggs; mean + 1 SD; predictions are for all coho regardless of whether they consumed eggs). With respect to individual size, at mean egg abundance (250 eggs added), a 1.9-g coho was predicted to consume 0.5 eggs (95% CI 0.1–1.1), whereas a 3.0-g (mean + 1 SD) coho was predicted to consume 1.2 eggs (95% CI 0.4–2.0; Fig. 2b).

Sculpins.—Larger sculpins relative to other stream fishes at their site presented with higher

Table 2. Top count component models for steelhead trout, coho salmon, and sculpins.

Species and model rank	Candidate count model	Relative model probability	Cumulative probability
Steelhead trout			
1	egg abundance + (1|site) + offset(ln(mass))	0.91	0.91
2	egg abundance + (1 + egg abundance|site) + offset(ln(mass))	0.05	0.96
3	egg abundance + relative mass + (1|site) + offset(ln(mass))	0.02	0.98
4	egg abundance + no. competitors + (1|site) + offset(ln(mass))	0.01	0.99
5	egg abundance + stream velocity + (1|site) + offset(ln(mass))	0.01	1.00
Coho salmon			
1	egg abundance + (1|site) + offset(ln(mass))	0.86	0.86
2	egg abundance + relative mass + (1|site) + offset(ln(mass))	0.08	0.94
3	egg abundance + (1 + egg abundance|site) + offset(ln(mass))	0.02	0.96
4	egg abundance + no. competitors + (1|site) + offset(ln(mass))	0.02	0.98
5	egg abundance + relative mass + egg abundance:relative mass + (1|site) + offset(ln(mass))	0.01	0.99
6	egg abundance + stream velocity + (1|site) + offset(ln(mass))	0.01	1.00
Sculpins			
1	egg abundance + (1|site) + offset(ln(mass))	0.75	0.77
2	egg abundance + relative mass + (1|site) + offset(ln(mass))	0.16	0.92
3	egg abundance + no. competitors + (1|site) + offset(ln(mass))	0.06	0.98
4	egg abundance + stream velocity + (1|site) + offset(ln(mass))	0.02	1.00

salmon egg abundances were more likely to consume at least one egg and consumed greater quantities of eggs (Table 3, Fig. 1e, f). In the top hurdle model, an average sculpin (5.8 g and 25% of the mass of the largest fish in a site) was predicted to eat 0.1 eggs on average (95% CI 0.0–0.2) at mean egg abundance (108 eggs) and 0.4 eggs (95% CI 0.1–1.3) at high egg abundance (1110 eggs; mean + 1 SD; predictions are for all sculpins regardless of whether they consumed eggs). With respect to relative size, at mean egg abundance (108 eggs) a 5.8-g sculpin with 25% relative mass was predicted to consume 0.1 eggs (95% CI 0.0–0.2), whereas an 11.3-g sculpin with 50% relative mass (mean + 1 SD) was predicted to consume 0.2 eggs (95% CI 0.0–0.7; Fig. 2c).

Simulation model

Incorporating the results of our top model fits into a simulation model revealed that across egg abundances, simulated steelhead consumed the most eggs (Fig. 3). At low egg abundance, 30% of steelhead consumed eggs at an average of 0.73 eggs per individual, and at high egg abundance, 96% of steelhead consumed eggs at an average of 5.3 eggs per individual. However, as egg abundance increased, coho and sculpins were increasingly able to eat eggs (Fig. 3). At low egg

abundance, only 2% of coho and 5% of sculpins consumed eggs at an average of 0.03 and 0.05 eggs per individual, respectively. At high abundance, 96% of coho consumed eggs averaging 1.8 eggs per individual, while 53% of sculpins consumed eggs averaging 0.53 eggs per individual. Relative to their size, coho consumed the most eggs (0.45 eggs/g), followed by steelhead (0.41 eggs/g) and then sculpins (0.12 eggs/g). Across species, small fish (e.g., <4.0 g) that were unlikely to access eggs at low egg abundance (1.6% consumed eggs) could access eggs at higher abundances (69.7% consumed eggs). Thus, higher magnitude resource pulses benefited a broader diversity of fish consumers.

Discussion

We discovered that resource abundance and individual-level traits (species identity and body size) had greater effects on resource consumption by an assemblage of fish predators than community-level characteristics. Specifically, egg abundance, species identity, and individual size were influential drivers of stream fishes foraging on salmon eggs. In contrast to predictions based on the typical paradigm that stream fish are consistently structured by interspecific competition, we
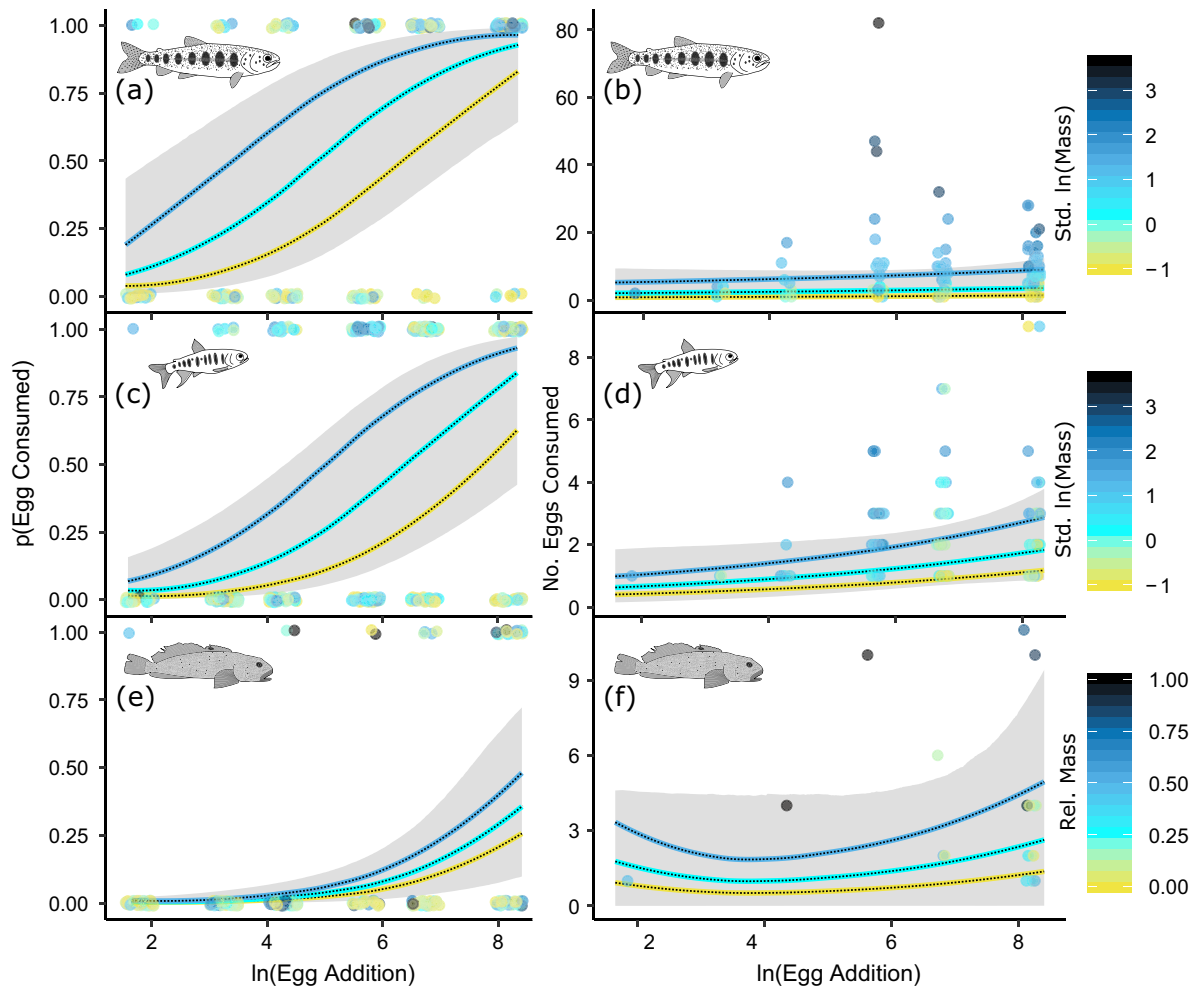
Fig. 1. Data and mean predictions with 95% credible intervals for the (a, c, e) logistic and (b, d, f) count components of (a, b) steelhead trout, (c, d) coho salmon, and (e, f) sculpin hurdle models. Gray-shaded areas represent the combined 95% credible intervals of the three lines shown in each plot. Yellow, cyan, and blue lines represent mean − 1 SD ln(mass), mean ln(mass), and mean + 1 SD ln(mass), respectively, for (a) steelhead trout and (b) coho salmon. For (c) sculpins, yellow, cyan, and blue lines represent mean − 1 SD relative mass, mean relative mass, and mean + 1 SD relative mass, respectively. Points are colored according to the mass or relative mass of the individual fish, and represent (a, c, e) no eggs consumed or one or more eggs consumed, or (b, d, f) the number of eggs consumed if a fish consumed one or more eggs.

found that community composition and the number of competitors had little apparent effect on egg consumption, at least at the spatial and temporal scale of this field experiment. Fish consumers became saturated at high egg densities following the shape of a type II functional response curve. And while none of our top models included interactions between resource availability and metrics of body size, the product of

the logistic and count component models suggests that increased egg availability enabled subordinate fishes to consume more eggs. Ultimately, high resource abundance resulted in a greater number of sizes and species of stream fishes consuming salmon eggs.

Extremely high densities of salmon eggs saturated stream fish predators, with consumption rates following the shape of a type II functional
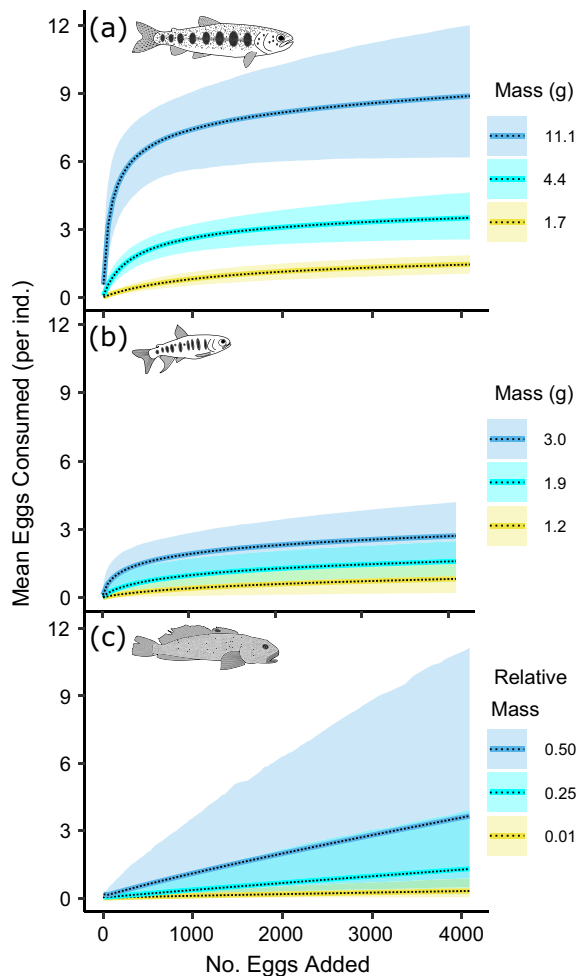
Fig. 2. Hurdle model mean predictions and 95% credible intervals of egg consumption by (a) steelhead trout, (b) coho salmon, and (c) sculpins given 30 min to consume eggs across a range of egg availabilities. Yellow, cyan, and blue lines represent mean − 1 SD ln (mass), mean ln(mass), and mean + 1 SD ln(mass), respectively, for (a) steelhead trout and (b) coho salmon. For (c) sculpins, yellow, cyan, and blue lines represent mean − 1 SD relative mass, mean relative mass, and mean + 1 SD relative mass, respectively.

response (Holling 1959). Not surprisingly, larger fish consumed more eggs than their smaller counterparts. Stream fish communities are typically structured by species-influenced dominance hierarchies (Glova 1986, David et al. 2007, Naman et al. 2019). Indeed, Bailey et al. (2019) observed size- and species-specific patterns of competitive interactions in video analysis from a

subset of this study. Yet here we found that the community composition per se did not influence individual consumption rates. This lack of a statistical effect of community composition may be due to the lack of manipulation of the fish community in this study, or relatively weak species interactions. The different consumers had different patterns of consumption as a function of egg density, implying they had different competitive abilities. Coho consumed more eggs relative to their size than steelhead or sculpins (Fig. 3). This aligns with earlier studies (Glova 1986, Young 2004) that showed that coho are dominant or quasi-dominant over sympatric trout of equal size. However, in this system, juvenile coho were generally smaller than most steelhead trout. In contrast, sculpins ate relatively fewer eggs than the drift-feeding salmonids. Sculpins are benthic predators that can consume salmon eggs directly from salmon nests by moving through interstitial spaces in the substrate (Foote and Brown 1998). This mode of foraging likely reduces the rate of interactions between sculpins and salmonids, and is supported by Bailey et al. (2019) who observed that sculpins rarely interacted with salmonids during egg experiments. Collectively, these findings showcase the functional relationships between the abundance of a pulsed resource (salmon eggs) and their consumption by a community of consumers (stream fishes).

Resource pulses of eggs allowed smaller, less dominant fishes to access, and consume salmon eggs. This aligns with the work of Sato and Watanabe (2014), who found that only the largest of their three subsidy treatments allowed subdominant fish access to that subsidy. Here, we have expanded on that result by showing that this relationship is upheld in a multi-species system across a much wider range of subsidization and fish size variation. As we predicted, large dominant salmonids were more likely to consume eggs than smaller fishes at very low salmon egg availability (Fig. 1), indicating that they were more effective competitors. At higher egg availabilities, hurdle model prediction slopes of total eggs consumed by large and small fish became approximately parallel (Fig 2), suggesting that fish at the tops of their respective dominance hierarchies were either satiated or unable to monopolize the salmon eggs. Underwater video analysis from a subset of this study found

Table 3. Top logistic and count component model results for steelhead trout, coho salmon, and sculpins.

| | | Model variable effects† | | | | | |
| | | ln(egg abundance) | | | mass‡ | | |
Taxon	Component model	Mean	Lower 95% CI	Upper 95% CI	Mean	Lower 95% CI	Upper 95% CI
steelhead	logistic	1.98	1.40	2.67	1.46	0.96	2.04
trout	count	0.19	−0.07	0.48	N/A	N/A	N/A
coho	logistic	1.45	0.91	2.11	1.25	0.89	1.62
salmon	count	0.32	0.07	0.62	N/A	N/A	N/A
sculpins	logistic	1.72	0.96	2.65	2.53	0.72	4.49
	count	0.52	−1.30	1.69	N/A	N/A	N/A

† Variable effect units are natural log odds for logistic models, and natural log of eggs consumed for count models given a one standard deviation increase in the variable of interest.

‡ For steelhead trout and coho salmon, mass is the natural logarithm of the absolute mass of an individual fish in grams; for sculpins, mass is the mass of an individual sculpin divided by the mass of the largest fish at a given site.

that increasing egg availability reduced the frequency of interference competition behaviors among stream fishes (Bailey et al. 2019), suggesting that dominance hierarchies were indeed eroded by increasing egg availability. Overall, while stream fish communities are generally considered to be highly size-structured competitive hierarchies (Nakano 1995, David et al. 2007, Naman et al. 2019), this paradigm may shift during resource pulses. More generally, resource pulses may be particularly important for species and sizes of consumer that would normally be competitively subordinate.

There are several caveats to this study that should be discussed. First, we did not allow fish to enter a treatment segment from further downstream. Fish consumers may track spawning salmon to access the resource subsidy (Foote and Brown 1998, Armstrong et al. 2013, Sergeant et al. 2015); thus, we needed to use a stop net in order to keep the experimental reaches independent and facilitate fish capture. The second caveat is that we did not examine egg consumption over the days or weeks that salmon spawning runs usually last; our experiments ran for 30 min from the point of egg addition to the beginning of fish extraction. Given more time to forage, individuals may have found and consumed more eggs, but more time would also allow digestion to take place which could have skewed our results. Thus, our study focused on the immediate benefits to fish consumers (e.g., consumption rates), not seasonal (e.g., growth), nor longer-term impacts (e.g., survival or life histories). Third, we did not assess the mass of

alternative food items, that is, fish and invertebrates. However, anecdotally we note that only one large steelhead in our study had consumed another fish, and all other fishes examined in our study consumed only a few small invertebrates. Therefore, it is unlikely that egg consumption was significantly affected by alternative prey sources in our study. Finally, we did not bury eggs in the gravel like salmon do, which sculpins may be uniquely able to access via interstitial spaces (Foote and Brown 1998). Thus, our interpretation of the functional responses of sculpins to salmon eggs is focused on eggs released into the water column, such as when eggs are uncovered by nest superimposition. Overall, we suggest that our study provides novel insights into the short-term impacts of different levels of egg subsidies to fish consumers and that scaling up these findings remains a research frontier.

The diversity of fish consumers that benefit from salmon subsidies will be influenced by variability in salmon spawning abundance, which in turn is influenced by environmental variability as well as human management actions such as harvest rates of fisheries. Thus, our study adds to the growing body of research that illuminates the potential trade-offs between harvest and the ecosystem benefits that salmon provide (Levi et al. 2012). Increasing the number of eggs (a high quality, energy-dense food) a stream fish consumes can increase resident fish growth and survival (Bentley et al. 2012, Bailey et al. 2018). Our results indicate that there were diminishing returns for increasing egg abundance increasing egg consumption (i.e., type II
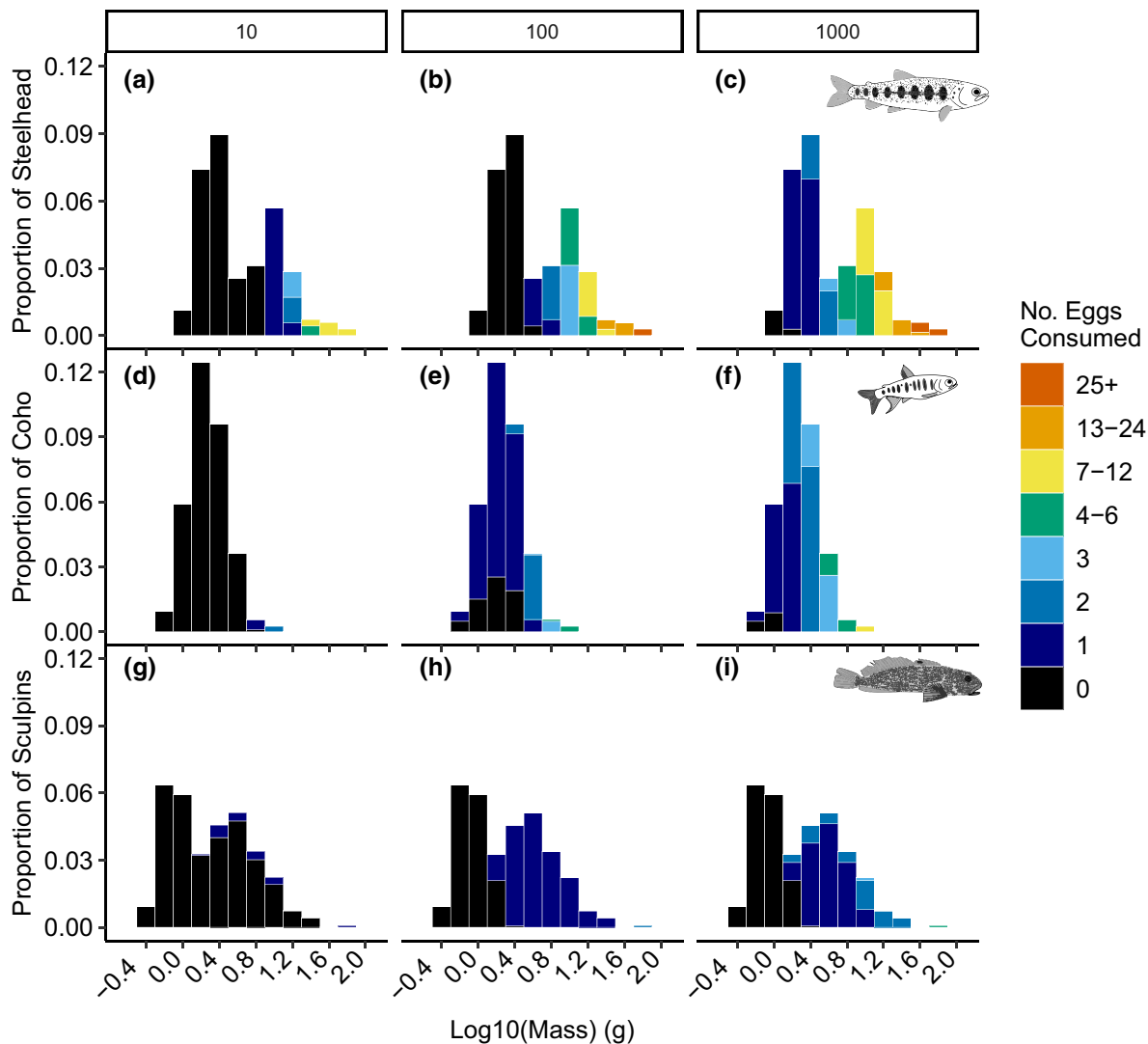
Fig. 3. Histograms of the average of 1000 times bootstrapped individual-level egg consumption predictions for (a, b, c) steelhead trout, (d, e, f) coho salmon, and (g, h, i) sculpins under three different egg availability scenarios: (a, d, g) 10 eggs, (b, e, h) 100 eggs, and (c, f, i) 1000 eggs. Predictions were made for every steelhead trout, coho salmon, and sculpin in the dataset to represent the range of sizes observed. Individuals not included in the analysis because they were too small to consume eggs are included here, but their response is always set to zero. For sculpins, individual relative size was calculated relative to the largest fish in the entire dataset rather than the largest fish at the site level, and thus, absolute mass is proportional to relative mass for the purposes of this simulation.

functional response) for individual size classes of fish, but that higher egg numbers were needed to benefit diverse consumers. This aligns with the synthesis of Walsh et al. (2020) who showed that ecological relationships between freshwater fish and salmon density tend to be asymptotic, and require extremely high salmon densities (7.3 kg/m^2) to reach 90% of their asymptote. Moore et al. (2008) found that the relationship between salmon spawning density and the number of salmon eggs available for consumption is positively exponential and linked to nest superimposition by female salmon. Thus, even modest increases in salmon returns could have large impacts on egg consumption by diverse stream fish consumers.

Resource pulses have been hypothesized to provide opportunities for consumers to maximize their energy acquisition (Yang et al. 2008, Armstrong and Schindler 2011). Such resource pulses often take the form of subsidies, where prey resources cross ecosystem boundaries and thus can reach disproportionately high abundances. Past studies have experimentally manipulated resource subsidies to stream fishes to show that subsidies can drive a many-fold increase in the growth rate of consumers (Wipfli et al. 2003, Uno and Power 2015, Collins et al. 2016) and reduce hierarchical effects among two size classes within a consumer species (Sato and Watanabe 2014, Naman et al. 2019). Subsidies can also temporarily alter trophic cascades (Sato and Watanabe 2014, Collins et al. 2016), although this may depend on the timing of subsidies (Sato et al. 2016), and generate apparent competition over longer time scales (Marcarelli et al. 2020). Here, we provide rare, in situ empirical evidence of pulse-level resources increasing the diversity of sizes and species of consumers that benefit from a single subsidy. Collectively, our results combined with the studies mentioned above suggest that resource subsidies may promote the persistence of subdominant individuals and species, potentially facilitating a diversity of species and size structures. However, human activities can decrease the magnitude of these resource pulses and results from our study suggest that this loss will decrease the diversity of the benefactors. For example, many resource pulses are driven by migratory animals (Bauer and Hoye 2014), such as salmon in our study system, yet migratory animal populations are rapidly diminishing (Wilcove and Wikelski 2008). We suggest that decreases in the magnitude of resource pulses will not only decrease resources to individual consumers, but also reduce the number of species and sizes of consumers that can benefit.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3211/full