Environ Biol Fish (2012) 95:301–307
DOI 10.1007/s10641-012-9996-2

Chemosensory responses of juvenile Coho salmon, *Oncorhynchus kisutch*, Dolly Varden, *Salvelinus malma*, and sculpins (*Cottus* spp.) to eggs and other tissues from adult Pacific salmon

Thomas P. Quinn · Andrew H. Dittman · Hannah Barrett · Curry Cunningham · Morgan H. Bond

Received: 25 September 2011 / Accepted: 12 March 2012 / Published online: 22 March 2012

Abstract The carcasses of semelparous Pacific salmon (*Oncorhynchus* spp.) provide nutrients that enter aquatic ecosystems by various pathways, including direct consumption of tissue by fishes. Salmonids and other species frequently eat eggs and other tissues from dead salmon but the roles of vision and olfaction are unclear, as is the relative attraction to different tissues. Accordingly, we conducted a series of in situ experiments using minnow traps in two natural streams in Alaska to test the relative roles of chemosensory and visual cues in attraction of fishes to eggs from adult Pacific salmon, and then compared catch rates of traps baited with eggs, muscle, liver, and testis. Experiments indicated that chemical traces were necessary and sufficient to attract juvenile Dolly Varden (*Salvelinus malma*), coho salmon (*Oncorhynchus kisutch*), and sculpins (*Cottus* spp.) into traps. Combining both sites, 70 salmonids and 19 sculpins were trapped using visual and chemical cues, and 53 and 21, respectively, for traps with only chemical cues. Traps with only the sight of eggs caught no salmonids and only 5 sculpins, comparable to empty control traps. In addition, eggs were markedly more attractive than the other tissues, trapping 68 % of the salmonids and 69 % of the sculpins, compared to 14 % and 15 % for muscle tissue, 12 % and 11 % for liver, and 6 % and 5 % for the testis. Visual cues undoubtedly play a role in egg consumption in streams, but these experiments indicated a very important role of chemical traces in attracting fish to the vicinity of the eggs, and selective attraction of eggs over other salmon tissues.

Keywords Salmon eggs · Odors · Attraction · Salmonids · Sculpins · Marine derived nutrients

T. P. Quinn (✉) · H. Barrett · C. Cunningham · M. H. Bond
School of Aquatic and Fishery Sciences,
University of Washington,
Box 355020, Seattle, WA 98195, USA
e-mail: tquinn@u.washington.edu

A. H. Dittman
Environmental Physiology Program,
Northwest Fisheries Science Center, NOAA Fisheries,
2725 Montlake Boulevard East,
Seattle, WA 98112, USA

Introduction

Over the past two decades, a growing and diverse scientific literature has revealed the importance of nutrients from adult semelparous Pacific salmon, *Oncorhynchus* spp., for the terrestrial and aquatic ecosystems to which they return to spawn and die (Willson and Halupka 1995; Gende et al. 2002; Naiman et al. 2002). Fishes are among the diverse consumers, and Pacific salmon and trout, char (*Salvelinus* spp.) and grayling, *Thymallus arcticus*, feed heavily on eggs and other tissue from salmon, and these food sources are important for the growth and energetics of the consumers (Eastman 1996; Ellings 2003; Scheuerell et al. 2007; Moore et al. 2008; Denton et al. 2009; Garner et al. 2009; Armstrong et al. 2010; Denton et al. 2010). Freshwater sculpins, *Cottus aleuticus* and *C. cognatus*, also revealed a strong affinity for salmon eggs (Foote and Brown 1998), and attraction to the chemical cues emanating from eggs (Dittman et al. 1998; Mirza and Chivers 2002).

Salmon eggs are readily consumed, once the fish's gape is sufficiently large (Denton et al. 2009; Armstrong et al. 2010). Eggs are very high in energy density (Eastman 1996; Hendry and Berg 1999; Meka and Margraf 2007), their red-orange color makes them highly visible, and they are available as discrete units, unlike muscle and other tissues that might have to be bitten and torn from the carcass prior to consumption. Combined, these qualities make eggs an ideal food for stream-dwelling fishes. However, eggs are a comparatively small fraction of the available salmon tissue, about 20 % of the mass of females, and most of them are successfully buried by the female and thus unavailable as food for stream fishes. Only a fraction of the eggs will be mobilized by the digging of other females or by sediment transport, making them available as drift for stream fishes to consume (Moore et al. 2008). Different tissues (e.g., eggs, muscle, liver, fins) from salmon vary in energetic reward as food (Hendry and Berg 1999; Meka and Margraf 2007). Field experiments indicated that eggs were the primary tissue consumed by juvenile salmonids but other tissue was also eaten (Bilby et al. 1998), and larger (subadult and adult) salmonids shifted from eggs to flesh towards the end of the salmon spawning season (Eastman 1996), when eggs became more scarce and decomposing tissue more available.

Food resources from salmon such as eggs and tissue are only available during the periods when salmon are spawning, and in discrete locations. Salmonids may make within-season movements to exploit food resources associated with salmon spawning, and grow faster than those not taking advantage of these resources (Ruff et al. 2011). The spatial and temporal heterogeneity of eggs may select for the development of acute sensory systems enabling fish to detect these resources when they are available. Salmonids are typically thought to rely primarily on visual cues for foraging (e.g., Mazur and Beauchamp 2003) but chemical cues may also be important for locating prey items (Hara 2006). To determine the relative attractiveness of salmon carcass tissues to juvenile salmonids, and the sensory systems involved in attraction, we used field experiments to test 1) whether juvenile salmonids were attracted to eggs based on visual or chemosensory cues, and 2) whether other tissues were as attractive as eggs. Most long-distance chemosensory-directed behaviors of fishes are thought to involve olfaction (Kleerekoper 1969), and Pavlov and Kasumyan (1990) reviewed the involvement of sensory systems in feeding and concluded that chemosensory attraction to prey items over 1.0 m away generally involved olfaction. However, we did not attempt to determine the relative roles of olfaction and gustation in determining responses to food items.

Methods

Field experiments were carried out in July and August at two locations, Chignik River, on the Alaskan Peninsula (56° 16" N, 158° 50' W) and Whitefish Creek (59° 16" N, 158° 40' W), a tributary of Lake Aleknagik in the Wood River system of Bristol Bay. These areas were chosen chiefly for logistic reasons but each has spawning sockeye salmon, *O. nerka*, and the Chignik River also has Chinook salmon, *O. tshawytscha*. Both sites are populated by juvenile coho salmon, *O. kisutch*, and Dolly Varden, *S. malma*; Dolly Varden are more numerous in the Chignik River whereas coho salmon are more numerous in Whitefish Creek. In addition, sculpins (*Cottus aleuticus* and *C. cognatus*) were present at the both sites, and rainbow trout (*O. mykiss*) were present in Whitefish Creek. These sculpin species could not be reliably distinguished without sacrificing the fish so the species were combined. All experiments were conducted by placing eggs or other tissue in containers within standard conical Gee minnow traps (Portt et al. 2006), 40 cm long with a 2.5 cm opening at each end, deployed in slow moving water within the stream. These traps are effective for salmonids of this size (Bryant 2000).

Attraction to eggs

The first experiment was designed to determine whether attraction to eggs was based on visual or chemosensory information. Each of four treatments was replicated four times at Chignik: 1) eggs in a transparent “zip-lock” bag, so they could be seen but not smelled, 2) eggs in a transparent “zip-lock” bag with 160 round holes, 2 mm in diameter, so they could be seen and smelled, 3) eggs in a “zip-lock” bag that had been made opaque by wrapping it in black electrical tape but with 160 round 2 mm holes so the eggs could be smelled but not seen, and 4) a control with no odors or bag at all. These studies did not address which chemosensory systems (e.g., taste, olfaction) might be involved in attraction to eggs but we use “odor” to describe any chemosensory cues emanating from eggs. For these experiments, eggs were collected from a sockeye salmon and frozen at – 20 °C. Each day, eggs were thawed and placed in the bags as needed.

The experiment at the Chignik River was conducted at a single site, within about 1 m of the bank in flowing water about 0.7 m deep. To initiate a trial, 15 g +/− 0.5 g of eggs in the zip-lock bag were placed in the trap, which was lowered into the water. After 5 min the trap was retrieved and the fish were identified, counted, and released. The trap was left out of the water for a 10 min recovery period, during which the fish dispersed from the immediate vicinity of the testing location. Each treatment was tested once each day, on different days, and the order was rotated among trials to control for the possibility that the order of presentation affected the results.

The experiment was repeated at Whitefish Creek but four sites were used at a time. Traps were placed in ca. 0.5–0.8 m deep areas on the outer side of a stream bends about 30 m apart. Catch rates in pilot experiments were lower than those at Chignik so the traps were left in the water for 30 min before being checked and redeployed after a 5 min recovery period. On each of five testing days, each of the four treatments was tested four times, once in each of the four sites, for a total of 20 trials for each treatment. The treatments were rotated among sites within each testing day, and the order in which sites received the treatments was rotated among days. Thus each treatment was equally distributed with respect to the trial sites and the order in which it was tested at each site to avoid any bias.

Attraction to different salmon tissues

Based on the results of this experiment (attraction to eggs, but only if odors were present) we conducted a second experiment, to determine whether the fish were attracted specifically to eggs or whether this was a general attraction to tissues from adult salmon. The experiment consisted of four treatments, each with 15 g +/− 0.5 g of salmon tissue as in the previous experiment: 1) sockeye salmon eggs, 2) skeletal muscle from the side of the fish, above the lateral line, 3) liver, and 4) testis. Tissues were placed in transparent “zip-lock” bags with 2 mm holes as in the first experiment. With the exception of the sockeye salmon eggs, the tissues were taken from a male Chinook salmon at the Chignik River site. As in the previous experiments at Chignik, the trials were conducted sequentially at a single location, with the order of the treatments rotated among trials and a 10 min recovery period between trials. Thus each treatment was tested four times, in each of two complete sets of trials.

A similar experiment to determine the relative attractiveness of different salmon tissues was conducted at Whitefish Creek. In these trials, five traps were set in sequence, one for each of the five treatments, in five different locations in the stream, with a 5 min recovery period between trials. As with the other experiment at Whitefish Creek, the traps were left for 30 min before being checked, and the fish identified and released. The five treatments were eggs, muscle, liver, testis (15 g each, all from sockeye salmon), and a control treatment with an empty trap. Each treatment was run five times in each of the five locations for a total of 25 replicates of each treatment at Whitefish Creek.

Results

Attraction to eggs

In 16 trials at the Chignik River site, 59 Dolly Varden and 24 coho salmon were caught and the species showed similar patterns (Table 1). Trials without odors (control and visual signal only) caught virtually no fish (Dolly Varden = 0, coho salmon = 4) whereas trials with chemosensory signals present caught many more fish (59 Dolly Varden and 20 coho salmon). ANOVA on the catches (species combined) indicated that the two treatments with odors (with and without visual signals) caught similar numbers of fish, and significantly more than the treatments without odors (visual only and control), which did not differ from

Table 1 Catches of juvenile Dolly Varden, coho salmon, and sculpins in the Chignik River and Whitefish Creek, in traps baited with sockeye salmon eggs that could be seen and smelled (Visual + Odors), smelled but not seen (Odors only), seen but not smelled (Visual only), and unbaited control traps

	Dolly Varden		Coho salmon		Sculpins	
	Chignik	Whitefish	Chignik	Whitefish	Chignik	Whitefish
Visual + odors	34	9	9	18	1	18
Odors only	25	7	11	10	4	17
Visual only	0	0	0	0	2	3
Control	0	0	4	0	0	4

each other ($F_{3,12}$=8.68, P<0.0025). Too few sculpins (7) were caught for analysis.

At Whitefish Creek, coho salmon were the most abundant salmonid species caught (28), more numerous than Dolly Varden (16), and rainbow trout (11), but 42 sculpins were caught (Table 1). ANOVA indicated that there was significant variation among treatments in catches of coho salmon ($F_{3,76}$=4.75, P= 0.004), sculpins ($F_{3,76}$=3.04, P=0.034), and salmonids (coho salmon, Dolly Varden and rainbow trout combined: $F_{3,76}$=4.53, P=0.006). No salmonids were caught in any of the trials without egg odors (visual and control) and at least one salmonid was caught on about half the trials with odors present (10 of 20 with odors only and 9 of 20 with visual cues and odors). The numbers of sculpins were similarly low in control and visual treatments compared to the two treatments with odors.

Attraction to different salmon tissues

As in the first experiment, the trials with different salmon tissues as bait in the Chignik River caught more Dolly Varden (406) than coho salmon (65; Table 2). The Dolly Varden showed a strong attraction to the eggs relative to other tissues (Table 2; ANOVA $F_{3,28}$=7.72, P<0.001). The other tissues did not differ in the number of Dolly Varden caught (t-tests, P> 0.742 in all pairwise comparisons). Fewer coho salmon were caught and catches did not differ significantly among tissue types ($F_{3,28}$=2.50, P=0.08), though order was similar to that seen in Dolly Varden (eggs=26, muscle=22, liver=15, testis=2). In addition, 61 sculpins were caught, primarily in the traps containing eggs (Table 2).

The experiment at Whitefish Creek caught only 4 Dolly Varden (all in trials with eggs) and no rainbow trout so the data on these species were not examined any further. The coho salmon entered the traps with eggs significantly more frequently than any of the other treatments, including control (empty) traps ($F_{4,120}$=18.23, P<0.0001; Table 2). Other than eggs, none of the tissue-baited traps was more attractive than empty traps (F $_{3,100}$=0.48, P>0.70). As with the coho salmon, the sculpins were more frequently caught in traps with eggs than any of the other treatments ($F_{4,120}$=6.51, P<0.001), and the other traps, including controls, had similar catches.

The overall catch rates were much lower at Whitefish Creek compared to the Chignik River, and we were concerned that uneven distribution of catches might have biased the ANOVA results. We therefore

Table 2 Catches of juvenile Dolly Varden, coho salmon, and sculpins in traps baited with eggs, muscle, liver, and testis from adult salmon in trials in the Chignik River and Whitefish Creek. Control trials were not conducted (NC) in the Chignik River

	Dolly Varden		Coho salmon		Sculpins	
	Chignik	Whitefish	Chignik	Whitefish	Chignik	Whitefish
Eggs	270	4	26	87	38	51
Muscle	53	0	22	5	12	8
Liver	49	0	15	3	6	8
Testis	34	0	2	1	5	2
Control	NC	0	NC	2	NC	4

conducted χ^2 tests using the presence or absence of fish in each trial as the response data (i.e., in how many of the 25 trials in each treatment was at least one coho salmon or one sculpin trapped). These tests indicated a significant difference among the five treatments for both species in the number of trials in which fish were captured (coho; χ^2=48.68, df=4, p<0.001, sculpins; χ^2= 32.92, p<0.001). Excluding data from traps containing eggs, there was no significant difference in catches of coho salmon (χ^2=1.69, df=3. p>0.50) or sculpins (χ^2= 4.17, df=3, p>0.20).

Discussion

The growth of juvenile salmonids is enhanced by consumption of energy-rich salmon eggs (Bilby et al. 1998; Denton et al. 2009; Armstrong et al. 2010), thus we predicted that they would have sensory mechanisms to detect and orient to eggs. Our first experiment indicated that odors were necessary and sufficient to attract juvenile salmonids (coho salmon and Dolly Varden), and also sculpins, into traps. Trials with visible eggs releasing no chemical signals caught no salmonids, and trials with odors alone were nearly as successful as those with odors and the sight of eggs (53 vs. 70 salmonids, combining both species and sites). Fishermen routinely catch adult Dolly Varden and rainbow trout (*O. mykiss*) using orange and pink plastic beads that imitate eggs, so drift-feeding fish can identify eggs based on visual information alone. However, in those situations the fish must capture the egg (or bead) before it drifts by, and odors are probably not used for prey detection.

We did not determine the chemoreceptor system used to detect eggs (i.e., olfaction, taste, solitary chemosensory cells) but we hypothesize that this behavior is olfaction-based, based on the general reliance of fishes on olfaction at larger spatial scales (see reviews by Kleerekoper 1969; Pavlov and Kasumyan 1990). In our studies, salmonids were not apparent in the immediate vicinity prior to placement of the traps, and fish were observed moving to the traps from considerable distances. However, definitive demonstration that eggs are detected by the olfactory system would require sensory-ablation studies or physiological testing of the olfactory and other chemoreceptor systems.

The recent literature on olfaction and foraging has been dominated by consideration of the "evolutionary arms race" and exchange of information between prey and predator (reviewed by Ferrari et al. 2010). The attraction of predators to eggs is therefore an interesting special case, as the prey (egg) cannot detect the predator, initiate any escape behavior, or communicate the threat to conspecifics. Moreover, there are challenges to locating prey based on odors in a fast-flowing environment (Weissburg and Zimmer-Faust 1993). The odors of eggs may be a "sign-stimulus" that elicits positive rheotaxis, and the fish move upstream until they can see the eggs.

In addition to the experiments revealing the importance of chemical traces, our experiments also indicated that eggs were especially attractive compared to other salmon tissues. In the Chignik River trials, Dolly Varden were much more strongly attracted to eggs than to the other tissues. Compared to the Dolly Varden, the coho salmon attraction to eggs was more similar to the muscle and liver, and fewer were caught in traps baited with testis relative to the other tissues. The experiments at Whitefish Creek caught too few Dolly Varden for analysis but the coho salmon were strongly attracted to traps with eggs and similarly low catch rates occurred with the other tissues. Combining the data from both sites, the traps with eggs caught 387 salmonids: 4.8 times more than with muscle (80), 5.8 times more than with liver (67), and 10.4 times more than with testis (37). The sculpins trapped also showed preferential attraction to the traps with eggs over the other tissues.

The coho salmon results at the two sites differed somewhat but the overall conclusion was clear; salmonids were strongly attracted to eggs. Based on gape-limitation experiments (Armstrong et al. 2010), virtually all the salmonids were large enough to eat eggs (i.e., >60 mm) and the great majority were >70 mm long. These fish were more attracted to the energy-rich and easily consumed eggs than the other tissues. It seems likely that the eggs were more attractive rather than merely more detectable, but these possibilities cannot be distinguished by our results. We did not systematically vary the in-stream age of the salmon whose tissues were used as bait, thus their energy content might have differed, depending on the stage of senescence (Gende et al. 2004). We also did not allow the tissue to decay in the stream, and such partially decayed tissue might be more detectable or attractive.

As has been noted elsewhere (Finelli et al. 2000), detection of odors for foraging in flowing media poses certain challenges. During periods of heavy spawning by salmon, the waters of the streams are presumably rich in odors from eggs and other salmon tissues. Densities of at least one adult salmon per m^2 are not uncommon in streams with sockeye, chum (*O. keta*) and pink salmon (*O. gorbuscha*), and in the absence of fishing such densities would take place even more frequently. During periods of high salmon density and high odor concentrations, olfactory adaptation might occur, limiting its utility for egg detection. At such times, vision might be the primary sensory system for egg detection. However, our experiments were conducted prior to or at the very beginning of the spawning season in the sites, so odor concentrations were much lower than would occur later in the season. Olfaction may function primarily for long distance detection of spawning salmon, allowing egg consumers to locate concentrations of spawning salmon.

Notwithstanding the possible saturation of a stream with egg odors, salmon eggs are remarkably easy to consume, as they drift freely (being only slightly negatively buoyant), are brightly colored, and have no capacity for evasive action. They fit conveniently into the mouths of small fish, and are highly nutritious [ca. 18 694 J g^{-1} for eggs vs. 4900 for prey fish, 2700 for salmon carcass muscle tissue, and 2000 for invertebrates; (Meka and Margraf 2007)]. Other types of tissue (e.g., muscle, liver, and testis) are less readily consumable by small fish because they would have to be torn from larger pieces. Salmonid eggs are not only consumed by other species of salmonids (Johnson and Ringler 1979; Eastman 1996; Scheuerell et al. 2007; Denton et al. 2009) and cottids (Foote and Brown 1998; Mirza and Chivers 2002) but also round gobies, *Neogobius melanostomus* (Fitzsimons et al. 2006), the cyprinid fallfish, *Semotilus corporalis* (Johnson et al. 2009), and likely others as well. Recently spawned eggs are also cannibalized by conspecifics (Greeley 1932; Aymes et al. 2010, and references therein). Eggs and larval animals are notably edible (Orians and Jantzen 1974), and the combination of chemical traces and color make salmonid eggs especially vulnerable when they are outside the protection of the egg pocket. Consumption of eggs plays a large role in the ecology of fishes that are sympatric with spawning salmon, especially when the salmon are at high densities (Moore et al. 2008).

Acknowledgments We thank Conrad Gowell, Jennifer Griffiths, and Lindsey Cipiela for assistance with the Chignik River trials, Brian Quinn, and the students in the Aquatic Ecological Research in Alaska class for the Whitefish Creek trials, and Darran May for assistance preparing sampling supplies. Comments by Ray Hilborn and Daniel Schindler on earlier versions of the text are appreciated.

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