DISCUSSION / DISCUSSION

The importance of freshwater feeding in mature Pacific salmon: a reply to the comment by Armstrong on “Egg consumption in mature Pacific salmon (*Oncorhynchus* spp.)”[1]

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Abstract: Armstrong has questioned the biological relevance of the feeding observations that we presented in the study “Egg consumption in mature Pacific salmon (*Oncorhynchus* spp.)” (Can. J. Fish. Aquat. Sci. **66**(9): 1546–1553). Here we discuss his arguments and show that feeding can provide substantial energetic gains, which would, for example, allow feeding salmon to maintain body condition for up to an additional 23 days. Many consequences of feeding by mature Pacific salmon remain to be explored, but our study shows that these fish do feed in fresh water and that the benefits can be substantial.

Résumé : Armstrong a remis en question la pertinence biologique des observations d’alimentation que nous avons présentées dans « Egg consumption in mature Pacific salmon (*Oncorhynchus* spp.) » (J. Can. Sci. Haleut. Aquat. **66**(9): 1546–1553). Nous examinons ses arguments et démontrons que l’alimentation peut fournir des apports énergétiques substantiels, qui pourraient, par exemple, permettre aux saumons qui s’alimentent de maintenir leur condition corporelle jusqu’à 23 jours supplémentaires. Il reste de nombreuses conséquences de l’alimentation par les saumons du Pacifiques matures à explorer, mais notre étude montre que ces poissons s’alimentent de fait en eau douce et que les bénéfices peuvent être importants.

[Traduit par la Rédaction]

Sport fishermen have long known that mature Pacific salmon (*Oncorhynchus* spp.) will strike at objects that resemble eggs (e.g., Rutter 1903). However, because of the deeply entrenched belief that mature Pacific salmon cease feeding in fresh water, a number of fanciful explanations have been put forward in popular folklore to explain this behaviour. Mature salmon have at times been postulated to strike at eggs as a maladaptive vestige of oceanic feeding behaviour or as a way to eliminate potential competitors that their offspring might encounter as juveniles. Our study supports a far simpler explanation for this behaviour: Pacific salmon continue to feed because it provides them with nourishment (Garner et al. 2009).

Armstrong (2010) presents several arguments challenging the interpretation of our data. First, the author questions the choice of parameters we used in our energetic simulations. Second, the author suggests that the feeding rates we observed were insignificant compared with rates observed in other salmonids that feed on eggs. Third, the author questions whether the energy obtained from consuming eggs is biologically relevant. Fourth, the author questions the profitability of a feeding strategy in mature salmon. Below we outline our response to these points.

First, after further investigation of the energetic content of salmon eggs reported in Meka and Margraf (2007), we agree with Armstrong that this value is high. Examination of the methods used to determine energetic content in salmon eggs, which were described by Wetzel (1993), showed that the sample storage conditions were likely the source of the inflated values. Regardless, as we detail below, our conclusions are not affected when we instead use the conservative value of 9 $kJ \cdot g^{-1}$ suggested by Armstrong (2010). Furthermore, our values represent minimum estimates because our calculations of feeding rates were conservative. For example, the dead fish that we collected in the rivers likely underestimated feeding rates because of both loss of appetite

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during senescence and declining availability of eggs late in the breeding season. The fish that we sampled at hatcheries had been held in the hatchery environment for an indeterminate length of time and may have had reduced feeding opportunities without access to breeding areas.

Second in the comment, Armstrong (2010) highlights that several other species of salmonids that feed on salmon eggs have considerably higher feeding rates than were observed in our study of Pacific salmon (e.g., Scheuerell et al. 2007; Denton et al. 2009; Armstrong et al. 2010). However, all of the studies Armstrong details focus on stream resident fishes that were not reproductively active and were thus able to devote their time entirely to foraging. The rations that we observed are in fact quite comparable to other migratory salmonids that feed opportunistically during migration and spawning. For example, two studies of mature sea-run brown trout (*Salmo trutta*) showed that about 25% of individuals continued to feed when they were in freshwater locations without access to marine prey (Harris 1971; Elliott 1997). In mature Atlantic salmon (*Salmo salar*), stomach contents showed that 30% of the fish continued to feed after returning to fresh water (Johansen 2001), whereas in white-spotted charr (*Salvelinus leucomaenis*), only 9% of the fish fed during upstream migration (Takami et al. 1996). Our finding of egg consumption by 13% of the Pacific salmon that we sampled is thus within the range of previously observed values in migratory salmon, while the 27% prevalence that we observed in Quinsam River coho salmon (*Oncorhynchus kisutch*) is in the upper end of that range. It is also interesting that all of the species we studied were semelparous, whereas the other studies on migratory salmon looked at iteroparous species, which suggests that reproductive strategy does not directly dictate feeding rates. While we do not contest that migratory salmon rely extensively on energy accumulated prior to migration to complete spawning, our study and these others on migratory salmonids clearly suggest that these fishes also use opportunistic feeding in fresh water to support the costs of migration and breeding.

Third, we argue that consuming eggs can provide mature Pacific salmon with biologically relevant amounts of energy. Of course, as pointed out by Armstrong (2010), an average fish in our study, which weighed about 5 kg and fed at a rate of 1 egg per day, would achieve only modest energetic gains. However, this calculation ignores the variation in our data, not to mention it includes populations where our data suggest that feeding was both uncommon and likely to be less important. If we examine the variation in our data more closely, our most actively feeding fish was a coho salmon jack that weighed only 0.37 kg and had 159 eggs in his stomach. Using the energetic model and parameters applied by Armstrong (from Hanson et al. 1997), the energy from the eggs present in this fish's stomach would be sufficient to sustain his body mass for more than 23 days. Moreover, 71% of the coho salmon jacks that we observed feeding consumed eggs at a rate that was more than double that needed to maintain their body mass (n = 7, body mass = 0.34–074 kg). The energetic gains associated with egg consumption in Pacific salmon may thus be particularly important for precocial males (also see Maekawa and Hino 1987; Blanchfield and Ridgway 1999). On the other hand, one of our most surprising findings was that large individuals were no less likely to feed than their smaller counterparts. Indeed, we observed the highest feeding prevalence in nonprecociously maturing female coho salmon from the Quinsam River, in which 40% of the sampled females had consumed eggs. Importantly, female salmon may continue to feed in fresh water not only to offset the relatively higher costs of breeding that they incur (Hendry and Berg 1999), but to obtain physiologically important resources, including carotenoids and dietary protein (Ketola 1982; Blount et al. 2000; Garner et al. 2010). Regardless of the exact benefits associated with consuming eggs, such feeding can offer biologically important benefits to mature Pacific salmon.

Fourth, Armstrong (2010) argued that the benefits of feeding would be outweighed by, for example, the energetic cost of feeding, increased exposure to predators, and interference with mating opportunities. Our behavioural observations instead suggest that individuals that consumed eggs on the breeding ground fed opportunistically and at low cost. Eggs were captured when suspended in the water column near where salmon were already defending a spawning territory. Feeding in this manner never required an individual to swim more than 3 m and would prevent mating only for a few seconds. In the case of individuals that we observed with large numbers of eggs in their stomachs (i.e., up to 159 eggs), they were instead using an intensive feeding strategy that may have incurred costs by both forgoing spawning opportunities and risking injury from larger fish defending their nests. However, for actively feeding individuals the costs of foraging could be balanced by substantial energetic gains such as the resources to maintain body condition for 23 days as we calculated above. We postulate that mature Pacific salmon adjust their foraging behaviour in response to their individual energetic state, which will ultimately determine the value of incurring the costs associated with an active feeding strategy.

Overall, we agree with Armstrong (2010) that many consequences of feeding behaviour for the breeding energetics of Pacific salmon remain to be explored. For example, we observed considerable differences in feeding behaviour among populations over even a small geographic scale, so it is still too early to make widespread generalizations about freshwater feeding patterns across systems. Nevertheless, our study fundamentally alters the understanding of the breeding ecology of Pacific salmon by shifting the burden of proof. Where once it was acceptable to dismiss freshwater feeding by mature Pacific salmon out of hand, there is surprisingly little data to support this belief. Our study instead shows that Pacific salmon do feed in fresh water and that the energetic and physiological benefits may be substantial.

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