

Egg consumption in mature Pacific salmon (*Oncorhynchus* spp.)

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Abstract: For over a century, conventional wisdom has maintained that Pacific salmon (*Oncorhynchus* spp.) cease feeding when they return to freshwater rivers to spawn. Here, we overturn this belief by showing that multiple species of Pacific salmon consume eggs during spawning. Overall, 13% of stomachs contained eggs, and feeding rates were estimated at up to 14 eggs or 52 kJ per day. Feeding experiments revealed that mature salmon could digest eggs, as fed salmon maintained significantly higher body mass than unfed salmon. Such egg consumption presents a fundamental shift in our understanding of Pacific salmon ecology that may have important implications for migration and management models. Indeed, the energy from consumed eggs could allow salmon to migrate up to an additional 3.8 km upstream per day of feeding, or extend the duration of spawning activity by up to 12%. Furthermore, salmon stocks may have evolved local adaptations to their specific migration and spawning requirements that include nutrients from salmon eggs. Thus, successful salmon management efforts may need to preserve not only spawning habitat and migration corridors, but also feeding opportunities.

Résumé : Depuis plus d'un siècle, il est généralement convenu que les saumons du Pacifique (*Oncorhynchus* spp.) cessent de se nourrir lorsqu'ils retournent dans les rivières d'eau douce pour frayer. Nous infirmons cette croyance en montrant que plusieurs espèces de saumons du Pacifique consomment des œufs durant la fraie. Globalement, 13 % des estomacs contiennent des œufs et nous estimons les taux de consommation à 14 œufs ou 52 kJ par jour. Des expériences alimentaires montrent que les saumons matures sont capables de digérer les œufs, puisque les saumons alimentés maintiennent une masse corporelle significativement supérieure à celles des saumons qui jeûnent. Une telle consommation des œufs représente un changement fondamental dans notre compréhension de l'écologie des saumons du Pacifique, ce qui peut avoir des conséquences sur les modèles de migration et de gestion. En effet, l'énergie provenant de la consommation des œufs pourrait permettre aux saumons de migrer jusqu'à 3,8 km plus en amont par jour d'alimentation ou de prolonger leurs activités de fraie de jusqu'à 12 %. De plus, les stocks de saumons peuvent avoir développé des adaptations locales pour satisfaire leurs besoins spécifiques de migration et de fraie, ce qui inclut l'obtention de nutriments à partir des œufs de saumons. Ainsi, les efforts fructueux de gestion des saumons doivent peut-être préserver non seulement les habitats de fraie et les corridors de migration, mais aussi les occasions d'alimentation.

[Traduit par la Rédaction]

Introduction

Despite the enormous economic and cultural significance of anadromous salmonids, many stocks are suffering from dwindling returns or have been entirely extirpated (Parrish et al. 1998; Kareiva et al. 2000; Gustafson et al. 2007). These declines have been largely attributed to anthropogenic disturbances such as dams that prevent access to spawning areas (Levin and Tolimieri 2001) and commercial fisheries that harvest a million tonnes of salmonids annually (Food and Agriculture Organisation of the United Nations (FAO) 2007). These fisheries consist almost entirely of Pacific salmon (*Oncorhynchus* spp.), and as such, managing Pacific salmon stocks has become a key conservation priority. However, despite the clear importance of incorporating biological information into recovery planning, perhaps surprisingly,

some fundamental aspects of their ecology remain poorly understood.

Pacific salmon, like many other salmonids, are typically anadromous and therefore migrate between fresh and salt waters during their life span. These fishes begin life as eggs in the gravel of freshwater streams, which then emerge to feed for a few weeks to several years in the fresh water (Quinn 2005). The juveniles subsequently migrate to the ocean where they may continue to feed and grow for several years until they mature and return to their natal streams to spawn. The spawning migration is a period of extraordinary energetic requirement — salmon travel hundreds of kilometres in the ocean to reach their natal rivers and may then spend months in fresh water. Indeed, some stocks travel over 1000 km upstream and reach elevations that are 1000 m above sea level before they spawn (Quinn 2005).

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Salmon must survive this costly spawning migration, while simultaneously completing development of sexual characters and maintaining sufficient energy stores to complete spawning once they finish their migration.

Analyses of other anadromous salmonids suggest that feeding rates are significantly reduced when the adults return to freshwater rivers to spawn. For example, brown trout (*Salmo trutta*; Jonsson and Gravem 1985; Elliott 1997), white-spotted char (*Salvelinus leucomaenis*; Takami et al. 1996), Arctic char (*Salvelinus alpinus*; Rikardsen et al. 2003), and Atlantic salmon (*Salmo salar*; Johansen 2001) all feed less after returning to fresh water than they do in the ocean. The Pacific salmon are believed to show a similar pattern, and indeed for over 100 years, conventional wisdom has held that Pacific salmon cease feeding entirely when they return to freshwater rivers to spawn (Rutter 1903; Greene 1926). This belief persists despite a 50-year-old report indicating that limited feeding occurs in mature non-anadromous Chinook salmon (*Oncorhynchus tshawytscha*) (Bullivant 1959) and evidence that returning Masu salmon adults (*Oncorhynchus masou*) feed occasionally during migration (Higgs et al. 1995). Indeed, the belief that Pacific salmon cease feeding in fresh water has remained so deeply ingrained that it is frequently presented with no reference to supporting evidence (e.g., Brett 1995; Mesa and Magie 2006). The belief persists in part because the cessation of feeding is also thought to be associated with atrophy of the digestive tract, such that any ingested food would provide no nourishment (Rutter 1903). However, if these assumptions prove to be false and mature salmon do continue to feed in fresh water, then the ecology of Pacific salmon at this critical life stage will have been fundamentally misunderstood.

The return to fresh water is a critical period for anadromous salmon management programs because of the high energetic requirements of migration and the heightened vulnerability to anthropogenic disturbances. For example, hydroelectric dams and climate change have considerably altered the conditions experienced by migrating fishes (Rand et al. 2006; Battin et al. 2007; Waples et al. 2008). Consequently, modeling the bioenergetics of migration and spawning has received considerable attention (Gilhousen 1980; Crossin et al. 2004; Mesa and Magie 2006). In Pacific salmon, these models unequivocally assume that feeding stops when the fishes enter fresh water and thus that they have a fixed energy budget. Importantly, if Pacific salmon are not operating on a fixed energy budget, then these models may underestimate migration cost and overestimate the resilience of stocks to additional energetic stressors.

Here we document egg consumption in three species of Pacific salmon, thus overturning the conventional wisdom that feeding stops when these salmon mature. We provide four lines of evidence to document feeding behaviour in spawning Pacific salmon. First, we surveyed stomach contents of Pacific salmon from three rivers on eastern Vancouver Island, British Columbia. Second, detailed behavioural observations were taken during the breeding season on captive Chinook salmon in freshwater spawning channels. Third, feeding trials in Chinook salmon assessed the ability of mature fish to make use of energy from ingested eggs. Fourth, the stomach contents of fed salmon were sampled

over time to measure the clearance times for ingested eggs and to estimate feeding rates. We discuss the consequences of these results for salmon management programs.

Materials and methods

Fish survey

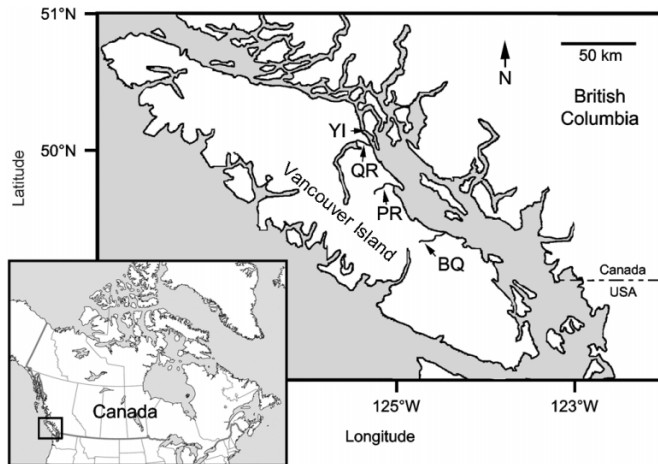
Feeding behaviour was examined in three species of Pacific salmon collected from four locations (Fig. 1). These rivers represent important native habitat for salmon, with each river home to Chinook salmon, chum salmon (*Oncorhynchus keta*), coho salmon (*Oncorhynchus kisutch*), and pink salmon (*Oncorhynchus gorbuscha*), as well as steelhead (*Oncorhynchus mykiss*) and cutthroat trout (*Oncorhynchus clarkii*). Our fourth sampling location was Yellow Island Aquaculture Ltd. (YIAL), which maintains a population of Chinook salmon and an experimental spawning channel facility that allowed us to perform detailed behavioural studies and to investigate egg metabolism. The YIAL population was founded with gametes from the Robertson Creek Hatchery on Vancouver Island and has been maintained since 1986.

Stomach content in wild salmon was examined during 9 October to 6 November 2007. The salmon were collected either after they had returned to the hatchery (residing on the natal rivers) or were collected directly from the river shortly after they had died. Body mass of each fish was measured with a hand scale (female body mass excluded the mass of her eggs). The stomachs were then dissected and the numbers of eggs or whole-egg casings in the stomach were counted, and any other items were noted. Prevalence of egg consumption was compared between species, sites, and sexes using a loglinear model, with partial chi-square values used to test the associations between all combinations of individual factors. The loglinear model was analyzed using an iterative backward elimination algorithm implemented in the model selection function of SPSS (ver. 17.0; SPSS Inc., Chicago, Illinois). Body mass was compared between fish that consumed or did not consume eggs using an analysis of variance (ANOVA) that also included species and sex as factors.

Genetic analysis was used to identify the species origin for a subset of the recovered eggs. DNA was extracted from the eggs using a proteinase K digestion followed by ethanol precipitation (Neff et al. 2000). To ensure there was no cross contamination of DNA from the eggs and the host stomach, the eggs were first washed with distilled water, and the outer membrane was excised and discarded. In addition, microsatellite genotypes of a subset of eggs ($n = 6$) were compared with the genotype of the individual that consumed them to confirm that the eggs were not being contaminated with host DNA. Species were identified by amplifying the major histocompatibility complex class II gene and using restriction enzymes to identify unique digestion patterns as described by Withler et al. (1997).

During 5 October to 15 November 2006, an examination of spawning behaviour was conducted using Chinook salmon at YIAL. Mature males ($n = 110$, age = 2–4 years, mass = 0.17–5.23 kg) and mature females ($n = 81$, age = 3–5 years, mass = 1.03–4.90 kg) were transferred from sea water to six freshwater spawning channels, each 15 × 3.5 m in area with

Fig. 1. Sampling locations in British Columbia, Canada, used for stomach content analysis of three species of Pacific salmon (*Oncorhynchus* spp.). Locations: BQ, Big Qualicum River; PR, Puntledge River; QR, Quinsam River; YI, Yellow Island Aquaculture.



a water depth of 1 m. Behaviour was then observed continuously during daylight by two observers stationed in 5 m high towers overlooking the channels. A previous study of this population has shown typical patterns of sexual selection, with both competition and mate choice operating (Neff et al. 2008). When each fish died, it was collected from the channels and the mass and stomach content were examined as described above.

Feeding trials

Trials were conducted from 17 October to 16 November 2007 to determine if mature fish could successfully digest eggs and if energy from eggs contributed to spermatogenesis or body condition. Thirty-two mature male Chinook salmon from YIAL (mean mass = 0.57 kg, range = 0.44–0.76 kg) were transferred to four outdoor freshwater tanks (3000 L), with each tank divided evenly into two sections by a rigid screen (four fish per section, eight fish per tank). These tanks were covered by netting to exclude predators but were otherwise subject to natural patterns of light and precipitation. Tanks received a freshwater flow of approximately 10 L·min⁻¹, with a temperature of 7.5 ± 2.0 °C. Fish were allowed two days to acclimate and then were anaesthetized with buffered MS-222 (tricaine methanesulfonate) so that they could be uniquely marked by clipping the adipose or left pelvic fin, mass and fork length could be measured, and milt could be collected before returning them to the divided tanks. To avoid diluting milt with water, the area around the genital pore was dried prior to milt collection, and care was taken to avoid expressing milt accidentally during handling. Milt was collected by applying pressure to the abdomen until it was no longer readily expressed, with all collections performed by the same individual to ensure consistency. Milt samples were collected in a preweighed Styrofoam cup to measure the total mass of available milt. Spermatocrit was determined as the percentage by volume of sperm cells in the homogenized milt and was measured in triplicate using a standard protocol (Liljedal et al. 1999); approximately 60 µL of milt was drawn into a capillary tube and then centrifuged for 5 min before measuring the percentage of

packed cells. Following these initial measurements, half of each tank was fed unfertilized Chinook salmon eggs twice daily (approximately 50 eggs per fish per day), whereas the other half received no eggs. At the start of the trials, fed and unfed fish did not differ in body mass, fork length, milt mass, or spermatocrit (*t* tests, all *P* > 0.62). Every seven days, fish were anaesthetized to measure body mass and collect milt. Dead fish were removed daily and noted to compare survival between groups. After 28 days, feeding was stopped and measurements were concluded, although surviving fish were maintained in fresh water for an additional two days to quantify survival.

Daily change in body mass was calculated as the natural log of final body mass (the mass on day 28 or the mass at death for fish that lived less than 28 days) minus the natural log of body mass at the start of the trials, then divided by the number of days in fresh water, and expressed as a percentage. The daily change in body mass was compared between fed and unfed fish using an ANOVA that included diet and tank as factors. To control for differences in milt production between fed and unfed fish, we also calculated daily change in body mass after adding the mass of milt collected from each fish back to their final body masses and analyzed these data as described above. Differences in spermatocrit and the mass of milt were compared between fed and unfed fish using an ANOVA that included diet, tank, and sampling date (7, 14, 21, 28 days) as factors. A log-rank survival analysis was used to compare survival between fed and unfed fish.

Egg retention

To evaluate gastric evacuation rate, force-feeding trials were performed using YIAL Chinook salmon from 10 to 17 November 2007. Mature fish (*n* = 108, mean mass = 1.49 kg, range = 0.26–4.00 kg) were transferred to fresh water for at least 24 h and then anaesthetized with buffered MS-222 so that 10 unfertilized, water-hardened eggs could be fed to each fish. Eggs were fed by using a rubber tube to bypass the throat sphincter, with a piston inside the tube injecting the eggs into the stomach. Fed fish were subsequently held in groups of 20 or fewer in 3000 L tanks. Tanks were located indoors with a 16 h light – 8 h dark cycle, freshwater flow of approximately 10 L·min⁻¹, and a temperature of 7.5 ± 1.0 °C. Fish were sacrificed at 0, 8, 24, 48, 96, or 168 h after the force feeding, and the stomach was removed to count the number of eggs and egg casings. Five fish were excluded from these analyses because their stomachs still contained food pellets from saltwater feeding, which could increase the retention time of fed eggs. The percentage of eggs remaining at each sampling period were fit to an exponential model of gastric evacuation (Elliott 1972). The instantaneous rate of gastric evacuation derived from this equation was then used to estimate the daily feeding rate for individuals collected in the survey of spawning fish, using daily feeding rate = 24 × stomach content × rate of gastric evacuation (Eggers 1979; Bromley 1994). We converted these estimates to energy consumption rates assuming an average egg mass of 0.29 g, which was an average of the values for Chinook, chum, and coho salmon native to Vancouver Island (Beacham and Murray 1993). For these estimates, we used a previously reported energy

density of salmon eggs (18.7 kJ·g⁻¹; 95% digestible) (Meka and Margraf 2007) and assumed that 30% of the available energy was lost through faeces (Brett 1995). Energy consumption rates were converted into a river migration distance and a duration of spawning activity using an average of the previously presented migration costs (4.56 kJ·kg⁻¹·km⁻¹) and spawning costs (145 kJ·kg⁻¹·day⁻¹) for Pacific salmon (Brett 1995). The average mass of feeding fish used in this calculation came from the individuals collected in our study and ranged from 2.18 kg in female coho salmon from the Puntledge River to 9.48 kg in male Chinook salmon from the Quinsam River.

Results

Body mass in wild fish was highest in Chinook salmon (males, 0.9–14.2 kg; females, 3.9–11.1 kg), followed by chum salmon (males, 2.3–8.4 kg; females, 2.5–4.9 kg) and coho salmon (males, 0.3–6.7 kg; females, 1.1–3.9 kg). The surveys of stomach contents showed that egg consumption occurred in all three rivers in British Columbia, but the proportion of fish that fed on eggs differed significantly among rivers (loglinear model: $\chi^2 = 34.3$, $df = 2$, $P < 0.001$; Table 1), as well as among species ($\chi^2 = 21.0$, $df = 2$, $P < 0.001$), with the highest frequency in coho salmon (21.2%) and lower levels in chum (7.1%) and Chinook (9.8%) salmon. There was, however, no difference in the prevalence of egg consumption between live fish collected at the hatcheries (16%) and dead fish collected directly from the rivers (10%) ($\chi^2 = 1.98$, $df = 1$, $P = 0.16$). Although occurring in both sexes, egg consumption was more frequent in females (20.7%) than in males (11.8%) ($\chi^2 = 8.50$, $df = 1$, $P = 0.004$). All higher-order interactions included in the model had no significant effect on the frequency of egg consumption (all $P > 0.77$). There was no significant difference in body mass between salmon that consumed eggs (mean = 4.2 kg, range = 0.3–12.9 kg) and salmon that did not consume eggs (mean = 4.7 kg, range = 0.3–14.2 kg) after controlling for differences based on sex and species (ANOVA, $F_{[1,463]} = 2.75$, $P = 0.098$). Qualitative observations during sampling suggested that digestive atrophy (thickening and hardening of the stomach) was uncommon in salmon from these rivers, as most salmon had non-occluded stomachs with thin, flexible walls.

Genetic identification determined the species origin for a subset of the recovered eggs. For 12 eggs recovered from five Chinook salmon stomachs, all of the eggs were identified as being from Chinook salmon. For 20 eggs recovered from 11 coho salmon stomachs, 18 coho salmon eggs and two Chinook salmon eggs were identified. Alternative food items were not observed in the stomach of any fish, although a small percentage of the sampled stomachs did contain stones (1.1%), wood or leaves (1.1%), plastic (0.2%), or tapeworms (1.3%).

Stomach content analysis of Chinook salmon in freshwater spawning channels similarly identified egg consumption (Table 1), whereas the behavioural observations of these fish revealed a typical feeding pattern. Egg cannibalism was observed a combined six times in two males and one female. For each observed incidence of egg cannibalism, a female was digging in an area of previous egg depo-

sition and forced eggs upwards into the water column, at which point another fish ate them. The cannibal was always close (less than 3 m) to the area where the digging occurred and responded rapidly to the sight of the egg, capturing it before the egg settled back to the gravel. For the single female that we observed cannibalizing an egg, the event occurred in the territory of a female who was immediately adjacent and upstream to her own territory, several days after the cannibal had deposited eggs in her own nest. Although a similar pattern was seen for each of the six observed feeding events, these events account for only a small proportion of the 128 eggs recovered from the stomachs of channel fish. Thus, egg consumption may also involve other less conspicuous behaviours.

Feeding trials in Chinook salmon showed that mature fish could make use of energy from ingested eggs. Average body mass remained close to constant, with only a modest 0.8% decline in fish fed eggs for four weeks, whereas body mass declined by a more significant 19.3% in unfed fish (ANOVA, $F_{[1,27]} = 24.8$, $P < 0.001$; Fig. 2a). The change in mass did not differ among tanks (ANOVA, $F_{[3,27]} = 0.98$, $P = 0.42$). Spermatocrit declined significantly over time (ANOVA, $F_{[3,85]} = 3.84$, $P = 0.012$) but did not differ between fed and unfed fish (ANOVA, $F_{[1,85]} = 1.34$, $P = 0.25$; Fig. 2b) or between tanks (ANOVA, $F_{[3,85]} = 1.39$, $P = 0.25$). Significantly more milt was collected from unfed fish than from fed fish (ANOVA, $F_{[3,84]} = 19.5$, $P < 0.001$; Fig. 2c). The mass of milt that was collected increased significantly over time (ANOVA, $F_{[3,84]} = 5.32$, $P = 0.002$) and also differed among tanks (ANOVA, $F_{[3,84]} = 2.86$, $P = 0.042$). The difference in body mass was not driven by these differences in milt retention, as unfed fish still lost significantly more mass than fed fish (ANOVA, $F_{[1,26]} = 18.5$, $P < 0.001$) when the mass of expelled milt was added to final body mass. The fed fish had a longer median survival in fresh water compared with the unfed fish (29.0 days vs. 21.5 days), but the difference was not significant (survival analysis, $\chi^2 = 0.48$, $df = 1$, $P = 0.49$; Fig. 2d).

These feeding trials were also used to estimate feeding rates by comparing the change in mass between the fed and unfed fish. Unfed fish lost an average of 0.763% body mass per day, whereas fed fish lost an average of 0.029% body mass per day, indicating that feeding provided a daily benefit equivalent to 0.734% body mass to the fed fish. Assuming a standard energy content for body mass of 6 kJ·g wet mass⁻¹ as in other salmonids (Meka and Margraf 2007) and an average observed mass of 565 g for fed fish, this represents an average energy gain of 25 kJ·day⁻¹ in the fed fish. As salmon eggs contain approximately 18.7 kJ·g wet mass⁻¹, with 95% of that energy digestible (Meka and Margraf 2007), and assuming that 30% of the available energy is lost through faeces (Brett 1995), this suggests that the fed fish were consuming on average 2.0 g of eggs per day, which at an average egg mass of 0.27 g measured at YIAL, represents an average feeding rate of 7 eggs·day⁻¹. This estimate is consistent with estimates from feeding fish derived from the natural-stream stomach surveys (see below).

Measuring the clearance time for ingested eggs revealed that 85% of the eggs were cleared within two days of ingestion (Fig. 3). Based on these data, we calculated the rate of gastric evacuation and, as in Eggers (1979), used this rate in

Table 1. Numbers of Pacific salmon (*Oncorhynchus* spp.) consuming eggs and the estimated mean feeding rates for these fish.

Species	Location	Sex	Stomach content			Feeding rate (eggs·day ⁻¹)	
			Present	Absent	%	All fish	Feeding fish
Chum	Big Qualicum River	Female	0	11	0.0	0.00	—
		Male	3	28	9.7	0.13	1.37
Coho	Puntledge River	Female	1	38	2.6	0.03	1.03
		Male	1	31	3.1	0.03	1.03
	Quinsam River	Female	25	37	40.3	1.69	4.19
		Male	24	84	22.2	3.20	14.38
Chinook	Big Qualicum River	Male	0	26	0.0	0.00	—
	Quinsam River	Female	13	63	17.1	0.36	2.13
		Male	5	77	6.1	0.11	1.85
	Yellow Island channels	Female	0	76	0.0	0.00	—
		Male	14	93	13.1	1.21	9.24
Total			86	564	13.2	0.96	7.24

Fig. 2. Changes in (a) body mass, (b) spermatocrit, (c) total milt mass, and (d) survival in fed and unfed Chinook salmon (*Oncorhynchus tshawytscha*). Fish were repeatedly sampled every 7 days during the 28-day feeding period, with survival measurements continuing for an additional 2 days after feeding stopped. Changes in body mass were calculated on day 28, or at the time of death for fish that survived less than 28 days. Spermatocrit was measured as the percentage of sperm cells by volume in the milt. Means are presented with ± 1 standard error (SE) for fed fish (solid symbols and solid bars) and unfed fish (open symbols and open bars). Survival is reported as the proportion of fed fish (broken line) and unfed fish (solid line) that were alive on each day. Significant differences between fed and unfed fish are indicated with asterisks.

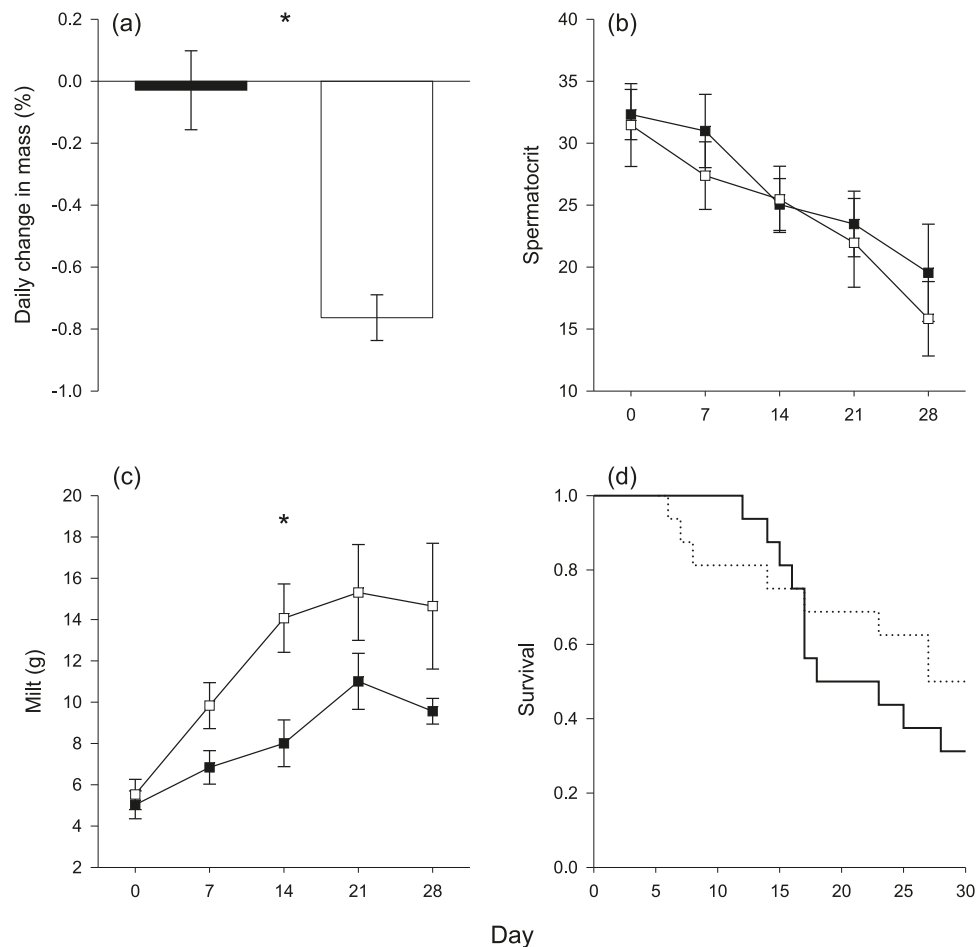
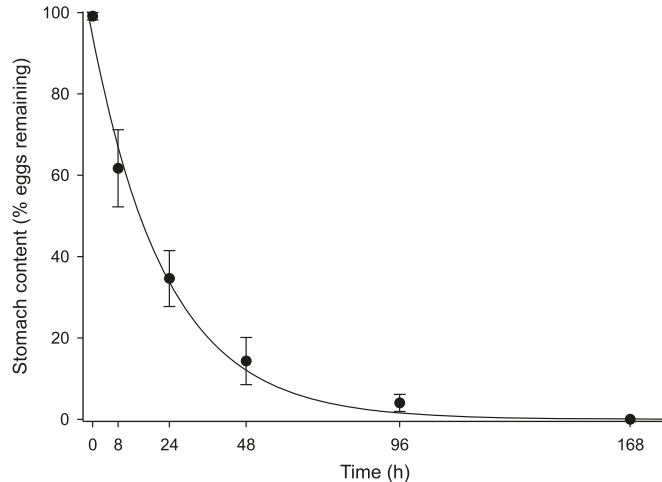


Fig. 3. Proportion of a standard meal remaining over time in Chinook salmon (*Oncorhynchus tshawytscha*) that were force-fed 10 eggs. Mean proportions of eggs remaining in the stomach are reported with ± 1 standard error (SE). The line is from a regression modelling exponential evacuation of stomach contents and has the equation: stomach content = $94.22 \cdot e^{-0.0428(\text{time})}$ ($r^2 = 0.59$, $n = 108$, $P < 0.001$).



combination with the number of eggs recovered in the survey of spawning fish to estimate daily feeding rates (Table 1). Mean feeding rates ranged from 0 to 1.7 eggs·day⁻¹ in female salmon and from 1 to 4 eggs·day⁻¹ in females that were observed feeding. These feeding rates correspond to a mean energy gain of 0–6.1 kJ·day⁻¹ in female salmon and 3.7–15.1 kJ·day⁻¹ in females that were observed feeding. Mean feeding rates ranged from 0 to 3.2 eggs·day⁻¹ in male salmon and from 1 to 14 eggs·day⁻¹ in males that were observed feeding. These feeding rates correspond to a mean energy gain of 0–11.5 kJ·day⁻¹ in male salmon and 3.7–51.9 kJ·day⁻¹ in males that were observed feeding.

Discussion

Egg consumption appears to be common in spawning Pacific salmon. Pacific salmon are thus consistent with a number of other salmonids that also consume eggs during spawning, including brook trout (*Salvelinus fontinalis*) (White 1930; Greeley 1932; Blanchfield and Ridgway 1999), Miyabe char (*Salvelinus malma miyabei*) (Maekawa and Hino 1987), Atlantic salmon (Jones and King 1950), and rainbow trout (Greeley 1932). In our study, we identified egg consumption in all three rivers and in each of the three species that we examined. Overall, we recovered eggs in 13% of the stomachs that we sampled, and prevalence was highest in coho salmon from the Quinsam River at 27%. These estimates are conservative as force-feeding experiments in Chinook salmon revealed that 85% of ingested eggs were cleared from the stomach within two days. Thus, we would detect only eggs consumed within about two days and may miss eggs consumed more sporadically during the spawning season. Therefore, the prevalence of egg consumption is likely a minimum estimate for our sample populations.

Mature salmon can benefit from consuming eggs. We showed that fed salmon could use the energy from ingested

eggs to maintain higher body mass than unfed fish. This increased mass may enable feeding fish to maintain high levels of activity associated with spawning behaviour (Brett 1995). Surprisingly, fed fish produced less milt than unfed fish, which suggests that feeding did not contribute to sperm production. Survival was also not significantly higher in fed fish than unfed fish, but our study maintained fish in a benign environment relative to spawning grounds where energetic limitations may have a greater impact on survival. Regardless of the exact benefits of egg consumption, the reduced rate of body mass loss in the fed fish clearly supports the ability of mature salmon to digest eggs.

Here we have demonstrated a serious error in the understanding of Pacific salmon breeding ecology — feeding does not stop upon the return to fresh water. Thus, the ubiquitous assumption of a fixed energy budget is false and may result in an underestimate of the actual cost of migration and spawning. Given that Pacific salmon stocks show high natal philopatry, it is also possible that many stocks have evolved local adaptations to their specific migration and spawning requirements that include nutrients from salmon eggs. Such a dependence on supplemental energy from freshwater feeding could explain why some stocks fail to recover even when released from fishing pressure, as lower abundances of salmon may remove feeding opportunities that some stocks depend on to successfully complete migration and spawning. Indeed, using the energy gains that we estimated for feeding salmon and previous estimates of the energetic costs of migration and spawning in Pacific salmon (Brett 1995), the females that we examined could migrate an additional 0.25–1.15 km per day of feeding or extend the duration of spawning activity by 0.7%–3.6%. Similarly, the males that we examined could migrate an additional 0.15–3.83 km per day of feeding or extend the duration of spawning activity by 0.4%–12%. Pacific salmon may require this supplemental energy for successful migration and spawning.

Pacific salmon stocks may need to be managed within an integrated framework. We found that 10% of the ingested eggs in coho salmon, which typically migrate and spawn shortly after the other salmon (Quinn 2005), were from Chinook salmon. This 10% represents about 5 kJ·day⁻¹ and suggests that some species may depend on nutrients acquired from the eggs of previously arriving fish to complete their own maturation. Thus, salmon conservation efforts may need to preserve not only spawning habitat and migration corridors, but also feeding opportunities.

In conclusion, our observations of egg consumption provide a novel insight into the freshwater ecology of the Pacific salmon. These data are in direct contradiction to the fixed energy budget universally assumed for spawning Pacific salmon. These findings also suggest interesting new directions for study, as the benefits of feeding for spawning fish, the prevalence of egg consumption prior to reaching the spawning grounds, and the temporal and geographic patterns of egg consumption remain to be determined.

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References

- Battin, J., Wiley, M.W., Ruckelshaus, M.H., Palmer, R.N., Korb, E., Bartz, K.K., and Imaki, H. 2007. Projected impacts of climate change on salmon habitat restoration. *Proc. Natl. Acad. Sci. U.S.A.* **104**(16): 6720–6725. doi:10.1073/pnas.0701685104. PMID:17412830.
- Beacham, T.D., and Murray, C.B. 1993. Fecundity and egg size variation in North American Pacific salmon (*Oncorhynchus*). *J. Fish Biol.* **42**(4): 485–508. doi:10.1111/j.1095-8649.1993.tb00354.x.
- Blanchfield, P.J., and Ridgway, M.S. 1999. The cost of peripheral males in a brook trout mating system. *Anim. Behav.* **57**(3): 537–544. doi:10.1006/anbe.1998.1014. PMID:10196043.
- Brett, J.R. 1995. Energetics. *In* *Physiological ecology of Pacific salmon*. Edited by C. Groot, L. Margolis, and W.C. Clarke. University of British Columbia Press, Vancouver, B.C. pp. 3–68.
- Bromley, P.J. 1994. The role of gastric evacuation experiments in quantifying the feeding rates of predatory fish. *Rev. Fish Biol. Fish.* **4**(1): 36–66. doi:10.1007/BF00043260.
- Bullivant, J.S. 1959. Stomach contents of spawning quinnat salmon. *Nature (London)*, **184**: 71. doi:10.1038/184071a0.
- Crossin, G.T., Hinch, S.G., Farrell, A.P., Higgs, D.A., Lotto, A.G., Oakes, J.D., and Healey, M.C. 2004. Energetics and morphology of sockeye salmon: effects of upriver migratory distance and elevation. *J. Fish Biol.* **65**(3): 788–810. doi:10.1111/j.0022-1112.2004.00486.x.
- Eggers, D.M. 1979. Comment on some recent methods for estimating food consumption by fish. *J. Fish. Res. Board Can.* **36**: 1018–1019.
- Elliott, J.M. 1972. Rates of gastric evacuation in brown trout, *Salmo trutta* L. *Freshw. Biol.* **2**(1): 1–18. doi:10.1111/j.1365-2427.1972.tb01575.x.
- Elliott, J.M. 1997. Stomach contents of adult sea trout caught in six English rivers. *J. Fish Biol.* **50**: 1129–1132. doi:10.1111/j.1095-8649.1997.tb01638.x.
- Food and Agriculture Organisation of the United Nations. 2007. Capture production 1950–2005. FAO Fisheries Information and Statistics Service, Rome, Italy.
- Gilhousen, P. 1980. Energy sources and expenditures in Fraser river sockeye salmon during their spawning migration. International Pacific Salmon Fisheries Commission, Bulletin XXII, New Westminster, B.C.
- Greeley, J.R. 1932. The spawning habits of brook, brown and rainbow trout and the problem of egg predators. *Trans. Am. Fish. Soc.* **62**(1): 239–248. doi:10.1577/1548-8659(1932)62[239:TSHOBB]2.0.CO;2.
- Greene, C.W. 1926. The physiology of the spawning migration. *Physiol. Rev.* **6**: 201–241.
- Gustafson, R.G., Waples, R.S., Myers, J.M., Weitkamp, L.A., Bryant, G.J., Johnson, O.W., and Hard, J.J. 2007. Pacific salmon extinctions: quantifying lost and remaining diversity. *Conserv. Biol.* **21**(4): 1009–1020. doi:10.1111/j.1523-1739.2007.00693.x. PMID:17650251.
- Higgs, D.A., Macdonald, J.S., Levings, C.D., and Dosanjh, B.S. 1995. Nutrition and feeding habits in relation to life history stage. *In* *Physiological ecology of Pacific salmon*. Edited by C. Groot, L. Margolis, and W.C. Clarke. UBC Press, Vancouver, British Columbia. pp. 159–315.
- Johansen, M. 2001. Evidence of freshwater feeding by adult salmon in the Tana River, northern Norway. *J. Fish Biol.* **59**(5): 1405–1407. doi:10.1111/j.1095-8649.2001.tb00201.x.
- Jones, J.W., and King, G.M. 1950. Further experimental observations on the spawning behaviour of the Atlantic salmon (*Salmo salar* Linn.). *Proc. Zool. Soc. Lond.* **120**: 217–223.
- Jonsson, B., and Gravem, F.R. 1985. Use of space and food by resident and migrant brown trout, *Salmo trutta*. *Environ. Biol. Fishes.* **14**(4): 281–293. doi:10.1007/BF00002633.
- Kareiva, P., Marvier, M., and McClure, M. 2000. Recovery and management options for spring/summer chinook salmon in the Columbia River basin. *Science (Washington, D.C.)*, **290**(5493): 977–979. doi:10.1126/science.290.5493.977. PMID:11062128.
- Levin, P.S., and Tolimieri, N. 2001. Differences in the impacts of dams on the dynamics of salmon populations. *Anim. Conserv.* **4**: 291–299. doi:10.1017/S1367943001001342.
- Liljedal, S., Folstad, I., and Skarstein, F. 1999. Secondary sex traits, parasites, immunity and ejaculate quality in the Arctic charr. *Proc. R. Soc. B Biol. Sci.* **266**: 1893–1898. doi:10.1098/rspb.1999.0863.
- Maekawa, K., and Hino, T. 1987. Effect of cannibalism on alternative life histories in charr. *Evolution*, **41**(5): 1120–1123. doi:10.2307/2409196.
- Meka, J.M., and Margraf, F.J. 2007. Using a bioenergetic model to assess growth reduction from catch-and-release fishing and hooking injury in rainbow trout, *Oncorhynchus mykiss*. *Fish. Manag. Ecol.* **14**(2): 131–139. doi:10.1111/j.1365-2400.2007.00533.x.
- Mesa, M.G., and Magie, C.D. 2006. Evaluation of energy expenditure in adult spring Chinook salmon migrating upstream in the Columbia River Basin: an assessment based on sequential proximate analysis. *River Res. Appl.* **22**(10): 1085–1095. doi:10.1002/tra.955.
- Neff, B.D., Fu, P., and Gross, M.R. 2000. Microsatellite multiplexing in fish. *Trans. Am. Fish. Soc.* **129**(2): 584–593. doi:10.1577/1548-8659(2000)129<0584:MMIF>2.0.CO;2.
- Neff, B.D., Garner, S.R., Heath, J.W., and Heath, D.D. 2008. The MHC and non-random mating in a captive population of Chinook salmon. *Heredity*, **101**(2): 175–185. doi:10.1038/hdy.2008.43. PMID:18506203.
- Parrish, D.L., Behnke, R.J., Gephart, S.R., McCormick, S.D., and Reeves, G.H. 1998. Why aren't there more Atlantic salmon (*Salmo salar*)? *Can. J. Fish. Aquat. Sci.* **55**(Suppl. 1): s281–s287. doi:10.1139/cjfas-55-S1-281.
- Quinn, T.P. 2005. The behaviour and ecology of Pacific salmon and trout. University of Washington Press, Seattle, Washington.
- Rand, P.S., Hinch, S.G., Morrison, J., Foreman, M.G.G., MacNutt, M.J., Macdonald, J.S., Healey, M.C., Farrell, A.P., and Higgs, D.A. 2006. Effects of river discharge, temperature, and future climates on energetics and mortality of adult migrating Fraser River sockeye salmon. *Trans. Am. Fish. Soc.* **135**(3): 655–667. doi:10.1577/T05-023.1.
- Rikardsen, A.H., Amundsen, P.A., and Bodin, P.J. 2003. Growth and diet of anadromous Arctic charr after their return to freshwater. *Ecol. Freshwat. Fish.* **12**(1): 74–80. doi:10.1034/j.1600-0633.2003.00001.x.
- Rutter, C. 1903. Natural history of the Quinnat salmon. A report of investigations in the Sacramento River, 1896–1901. *Bull. U.S. Fish. Comm.* **22**: 65–141.
- Takami, T., Murakami, Y., and Mori, M. 1996. Growth and feeding habits of anadromous white-spotted charr (*Salvelinus leucoma-*

- nis*) in southwestern Hokkaido, Japan. *Sci. Rep. Hokkaido Fish Hatchery*, **50**: 37–44.
- Waples, R.S., Zabel, R.W., Scheuerell, M.D., and Sanderson, B.L. 2008. Evolutionary responses by native species to major anthropogenic changes to their ecosystems: Pacific salmon in the Columbia River hydropower system. *Mol. Ecol.* **17**(1): 84–96. doi:10.1111/j.1365-294X.2007.03510.x. PMID:18268786.
- White, H.C. 1930. Some observations on the eastern brook trout (*S. fontinalis*) of Prince Edward Island. *Trans. Am. Fish. Soc.* **60**(1): 101–108. doi:10.1577/1548-8659(1930)60[101:SOOTEB]2.0.CO;2.
- Withler, R.E., Beacham, T.D., Ming, T.J., and Miller, K.M. 1997. Species identification of Pacific salmon by means of a major histocompatibility complex gene. *N. Am. J. Fish. Manage.* **17**(4): 929–938. doi:10.1577/1548-8675(1997)017<0929:SIOPSB>2.3.CO;2.