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Abstract: Routine hydraulic sampling of pink salmon eggs *Oncorhynchus gorbuscha* is the subject of a long-running dispute over impacts of the *Exxon Valdez* oil spill on embryo survival in Prince William Sound, Alaska, because relationships between the time of spawning, sensitivity of eggs to mechanical damage, and sample timing were unclear. Previous laboratory and hatchery studies demonstrate that resistance of eggs to mechanical damage increases with maturity, but natural populations require estimates of embryo age distributions and the ability to discriminate between sampler-induced and natural egg mortality. Resistance of naturally-spawned eggs to hydraulic shock, determined 6 times between late September and mid-November in a southeastern Alaska stream, increased sigmoidally from < 2% to 98%. In contrast, the number of eggs that died from natural causes was unrelated to sample time. Rapid removal of all eggs from the water allowed accurate discrimination between eggs shocked and killed by sampling and eggs dead prior to sampling. We caution that combining shocked and dead eggs into a single "dead" category does not accurately describe natural mortality, and recommend use of our method for future studies. Our study showed the rate of mortality resistance to the same hydraulic shock was slower in populations of naturally spawned, mixed-age eggs than in artificially cultured uniform-age eggs.

INTRODUCTION

Hydraulic pumping is typically used to assess salmon spawning success during freshwater incubation, and resulting data are often used in population dynamic models. In hydraulic pumping, a mixture of air and water is forcefully injected into streambed gravel through a handheld wand, dislodging and forcing eggs to the surface where they are trapped, along with gravel, in a net (McNeil 1964a). Live and dead eggs are removed from the gravel/water mixture and counted; the total number of live eggs is often used to predict adult run size. Accurate discrimination between eggs that were already dead from eggs that have been mechanically damaged ("shocked") by hydraulic pumping or removal from the gravel/water mixture is important in natural streams. Mechanical disturbance can cause embryo mortality 0–12 d (Jensen and Alderdice 1989; Jensen 1997) and possibly for the first 20 d (Collins et al. 2000) after fertilization because the delicate viteline membrane is the primary barrier between surrounding water and the yolk during this time period. If the membrane is ruptured, water penetrates the yolk, lipoproteins coagulate, and the embryo dies. Thus, hydraulic sampling should ideally occur after eggs become resistant to shock. However, the spawning period may be protracted (1.5–2 months; Dvinin 1952), and advancing winter can limit sampling options.

Hydraulic sampling was used in Prince William Sound (PWS), Alaska following the 1989 *Exxon Valdez* oil spill to assess the potential impact of spilled oil on the hundreds of pink salmon streams; the results are controversial. Bue et al. (1996, 1998) demonstrated higher levels of pink salmon *Oncorhynchus gorbuscha* embryo mortality in intertidal reaches of PWS streams exposed to *Exxon Valdez* oil. These observations were challenged by other investigators (Brannon and Maki 1996; Brannon et al. 2001) because relationships between time of spawning, egg sensitivity, and hydraulic sampling were unclear. Redd superimposition (disruption of redds by later-spawning fish; Dvinin 1952; McNeil 1964b; Heard 1991) is an important consequence of long spawning periods, and may cause up to 1/3 of spawned eggs to be displaced or damaged (Fukushima et al. 1998). Since displaced and damaged eggs die, average embryo development is controlled by later-

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spawning fish. Brannon et al. (2001) argue that higher embryo mortality in oiled streams was an artifact of sample timing because spawning was generally later in oiled than in non-oiled streams. This resulted in greater proportions of shock sensitive embryos in oiled than in non-oiled streams. However, embryo mortality was greater in oiled than in non-oiled streams in 1991, the only year in which the timing of spawning was accurately monitored (Rice et al. 2001), even when time of spawning was included as a covariate in analyses (Craig, et al. 2002). This controversy stimulated examination of resistance of naturally spawned pink salmon egg populations to mechanical damage.

The objectives of our study were to determine how shock resistance of naturally spawned pink salmon eggs 1) changes over time, 2) relates to timing of spawning, and 3) can be used to provide accurate pre-disturbance estimates of egg mortality. Although several studies have examined shock induced mortalities of embryos in hatchery settings (Jensen 1997; Jensen and Alderdice 1989), few have been done in the wild. Collins et al. (2000) were the first to publish results of a study on the resistance of naturally spawned pink salmon embryos to shock, but they only sampled populations twice—about the time spawning ended, and a month later. Although their study showed that naturally spawned eggs become resistant to shock within one month, it did not define the rate at which this occurred.

METHODS

Study area

Lovers Cove Creek is located on eastern Baranof Island in southeastern Alaska (Figure 1). The stream encompasses an area of about 3.5 ha, has three primary channels that enter an extensive intertidal area approximately 458 m long (Hanavan and Skud 1954), and flows into Big Port Walter. About 60,000 pink salmon spawn in the intertidal portion of the stream each year. We restricted our observations to a relatively homogenous 100 m reach in the eastern branch of Lovers Cove Creek, including a straight 83 m intertidal section with fairly uniform gradient and gravel size (Martin 1973). Mean channel width was 15 m.

Hourly water temperature of Lovers Cove Creek was measured and recorded with a thermograph beginning October 19, 2000. Prior to that date, Lovers Cove Creek temperatures were regressed on daily Sashin Creek temperatures recorded at the Little Port Walter hatchery to estimate Lovers Cove Creek temperatures.

Run timing

Spawning time was determined by periodically counting spawners in the stream. Adults were counted in the study section of the stream about twice a week from August 29 to October 11, 2000. Two observers positioned about 20 m from the stream counted the fish at low tide, and the mean of their observations was used as the count for that day. The cumulative count of adults was used as the percent completion of spawning.

Resistance of naturally spawned eggs to mechanical damage

To determine how shock resistance changes over time, we periodically sampled during and after spawning. Most importantly, we needed to separate naturally dead eggs (dead prior to sampling) from eggs damaged or killed during the sampling. We classified eggs as dead only if they died naturally in the stream prior to sampling, distinct from eggs killed by the sampling process.

The 100-m study section of Lovers Cove Creek was divided into 25 transects, each perpendicular to stream flow, and marked on the banks with metal stakes. Three or four transects were randomly selected and sampled without replacement during one of six 2–3 d sampling periods between September 27 and November 15, 2000. This was done so that sampling did not influence results obtained from transects sampled at later dates. For each transect sampled, a line was fastened across the stream, and gravel was excavated within 1.5 m upstream of the line with a 1-m long by 3.8 cm diameter stainless steel probe discharging a 170 L/min air-water mixture. A cylindrical basket (0.1 m^2) with a 1 mm mesh collection bag surrounded the probe. Our sampling equipment was similar to that used in PWS following the *Exxon Valdez* oil spill. We used one of the same probes from PWS, but our sampling cylinder was 0.086 m^2 smaller than that used in PWS, and we used a Honda model WP20X pump instead of a Tanaka model TCP381 or Homelite model SLS water pump (Craig et al. 1995). Each 0.1 m^2 area was pumped for 1 min and dislodged eggs were transferred immediately to a plastic tray. Eggs from consecutive pumpings along a transect were combined to form samples of at least 100 eggs, and pumping continued until a minimum of 5 samples were obtained for each transect. Eight to 35 pumpings per transect were necessary to obtain sufficient numbers of eggs. A total of 2,415–4,756 eggs were collected during each sample period. We were careful to not walk on adjacent transects to avoid damaging incubating eggs. Our sampling procedures differed from those used in routine field sampling in PWS because we pumped for a set time and immediately sorted eggs after pumping. During PWS field sampling, pumping and egg sorting times varied depending on the number of eggs in a sample.

Eggs were sorted from the gravel and debris, removed from the water, and placed on a screen (1 mm mesh size) for classification and counting after each pumping. Eggs were classified by color as live without visible eye pigmentation (pink), live with pigmented eyes (pink), dead (white), or dying from shock (changing from pink to white). Removal of eggs from water slowed the characteristic change from pink to white that occurs in shocked eggs as proteins coagulate, and ensured that shocked eggs were not confused with eggs that were already dead prior to sampling. Serendipitous observation in a concurrent experiment, Carls et al. (2004) demonstrated that removal from water arrests color change. After initial classification, to ensure that mildly shocked eggs were not misidentified as live eggs, remaining pink-colored eggs were gently placed in water for about 10 minutes to allow continued whitening of mildly shocked eggs. Empty chorions were not counted because of the uncertainty of their origin.

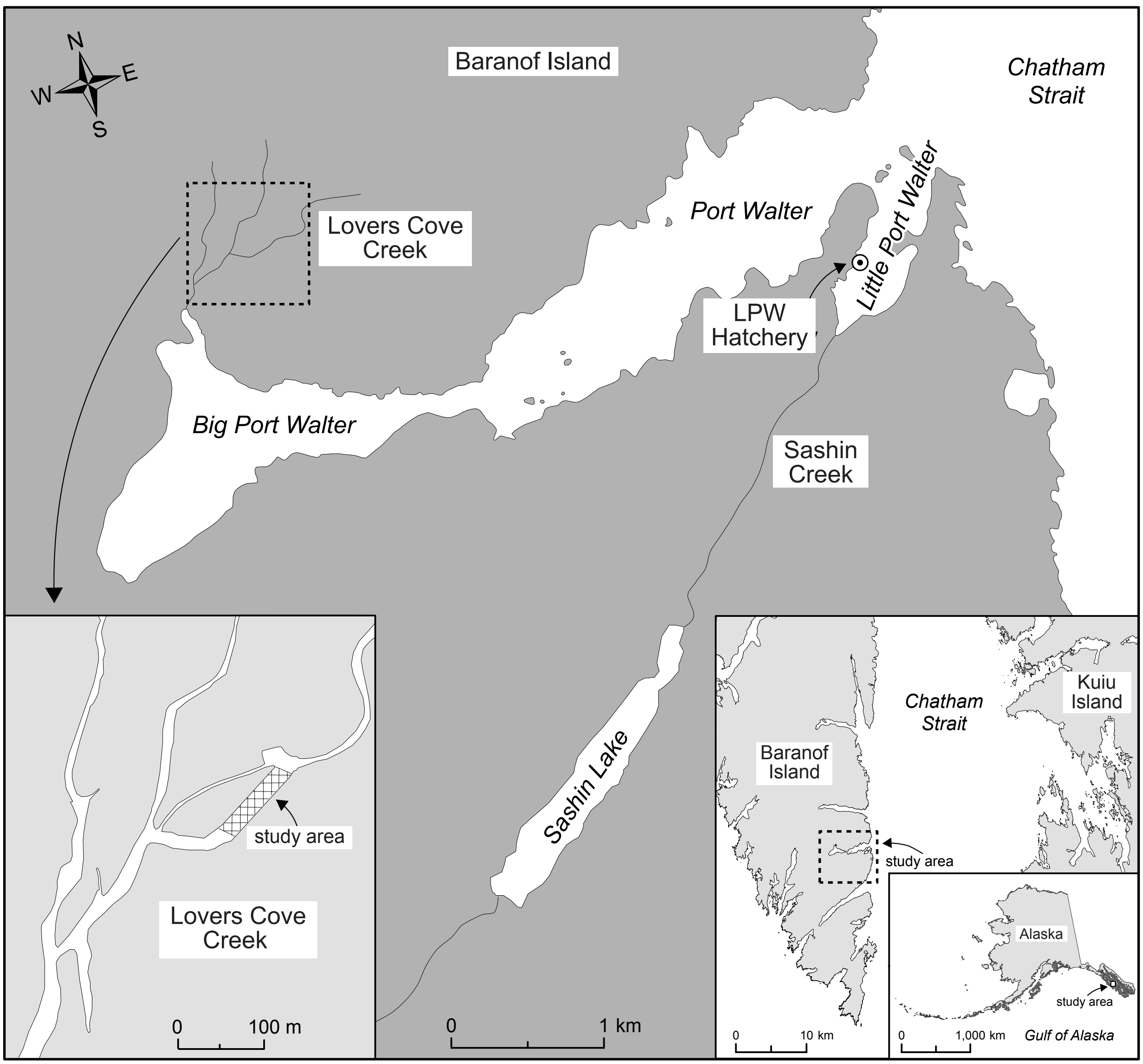

Figure 1. Lovers Cove Creek study area in southeastern Alaska.

Shock resistance in known-age eggs

To compare shock resistance of naturally spawned eggs to those of known age, gametes from Lovers Cove Creek pink salmon (3 females, 2 males) were artificially crossed, incubated in the nearby Little Port Walter hatchery, and periodically tested for shock resistance. Tests were conducted four times: October 19, October 25, November 6, and November 15. The first test was 1 d after fertilization, and the fourth was 28 d after fertilization. For each test, about 200 eggs were placed within a 10 cm diameter by 2 cm high aluminum ring in a simulated redd consisting of a 208 L barrel filled with 80 cm of Lovers Cove Creek gravel. The ring was covered with eight $0.05 \times 2 \times 10$ cm pieces of plastic to protect the eggs as they were covered with approximately 20–25 cm of additional gravel from Lovers Cove Creek (20–25 cm redd depths are typical for well-populated spawning grounds; Heard 1991). Before hydraulic sampling, water was added so that the gravel surface was covered with about 20 cm of water. Eggs were then pumped with the same equipment and procedures used to collect naturally spawned eggs from Lovers Cove Creek.

Data analysis

For each day of tests, the percentages of all live (uneyed and eyed), shocked, and dead (excluding those dying from shock) eggs were calculated. Shock resistance, percentage of eyed eggs, and percentage of dead eggs with time were described by logistical regression using maximum likelihood fitting (SAS GENMOD procedure, SAS 1999) and corrected for overdispersion (Williams 1982). The binomial model is used with log odds assumed to be linearly related to time. Overdispersion is a phenomenon that sometimes occurs in data that are modeled with the binomial distribution. If the estimate of dispersion after fitting, as measured by the deviance divided by the degrees of freedom, is not near 1, then the data are either overdispersed (dispersion >1) or underdispersed (dispersion < 1). Uncorrected dispersion ranged from 2.0 to 3.5 in our data. A simple way to model this situation is to allow the variance functions of these distributions to have a multiplicative overdispersion factor: $V(\mu) = \varphi\mu(1-\mu)$, where $V(\mu)$ is the variance of the mean, μ is the mean, and φ is the overdispersion factor. In our data set, estimates corrected for dispersion were highly similar to uncorrected estimates and the conclusions reached were the same. Times when half (or 90%) of the embryos became resistant to shock (or became eyed) were estimated from the logistic equations and are reported as time ± SD.

RESULTS

Run timing

Pink salmon spawning in Lovers Cove Creek began about September 1 and ended 40 d later (October 11; Figure 2). There were 2 abundance peaks in the run, September 5 (294 fish) and October 5 (393 fish), and a total of 1,085 adult pink salmon were counted. Spawning ended on October 11, 2000. Mean daily water temperature in the creek during spawning was 7.2°C.

Resistance of naturally spawned eggs to mechanical damage

Resistance of eggs to hydraulic shock in Lovers Cove Creek increased sigmoidally over time (Figure 3a). The percentage of shock resistant eggs (all live eggs) increased from about 4% to 98% between September 27 and November 17 (14 d before to 37 d after spawning ended) and was significantly related to time ($r^2 = 0.85$; $P < 0.001$). When spawning ended on October 11, an estimated 23% of the eggs were resistant to shock. Twelve days after spawning ended, the upper end of the sensitivity period predicted by Jensen (1997), just over half (55%) of the eggs were resistant to shock. Twenty days after spawning ended, the end of the sensitivity period predicted by Collins et al. (2000), 76% of the eggs were resistant to shock. Resistance to hydraulic shock did not reach 90% until 28 d after all spawning ended.

Percentages of maturing eggs, as determined by the presence of pigmented eyes, increased in parallel to shock resistance ($r^2 = 0.84$; $P < 0.001$), although shock resistance preceded eye pigmentation (Figure 3a). For example, half the eggs were resistant to shock

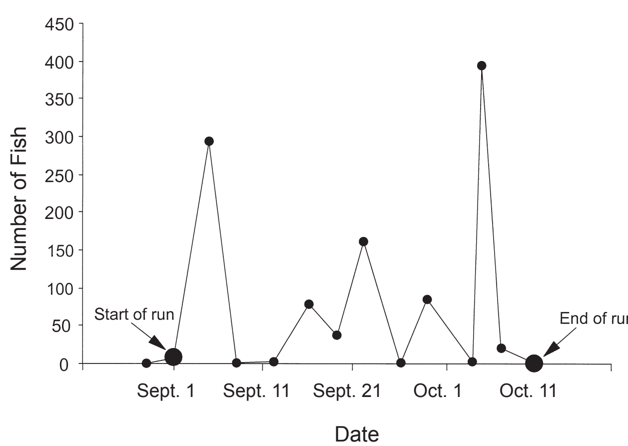

Figure 2. Run timing: number of adult pink salmon counted periodically in a 100 m study section of Lovers Cove Creek, Alaska in 2000.

on October 21 (10 d after spawning ended), but half of the eggs did not have pigmented eyes until October 31 (20 d after spawning ended).

Dead eggs

The percentage of eggs that were dead prior to sampling in Lovers Cove Creek was not related to sampling date ($r^2 = 0.04$; $P = 0.72$) and varied widely by transect (Figure 3b). Mean percent dead eggs varied greatly among days (12–59%), as well as among transects (7–95%).

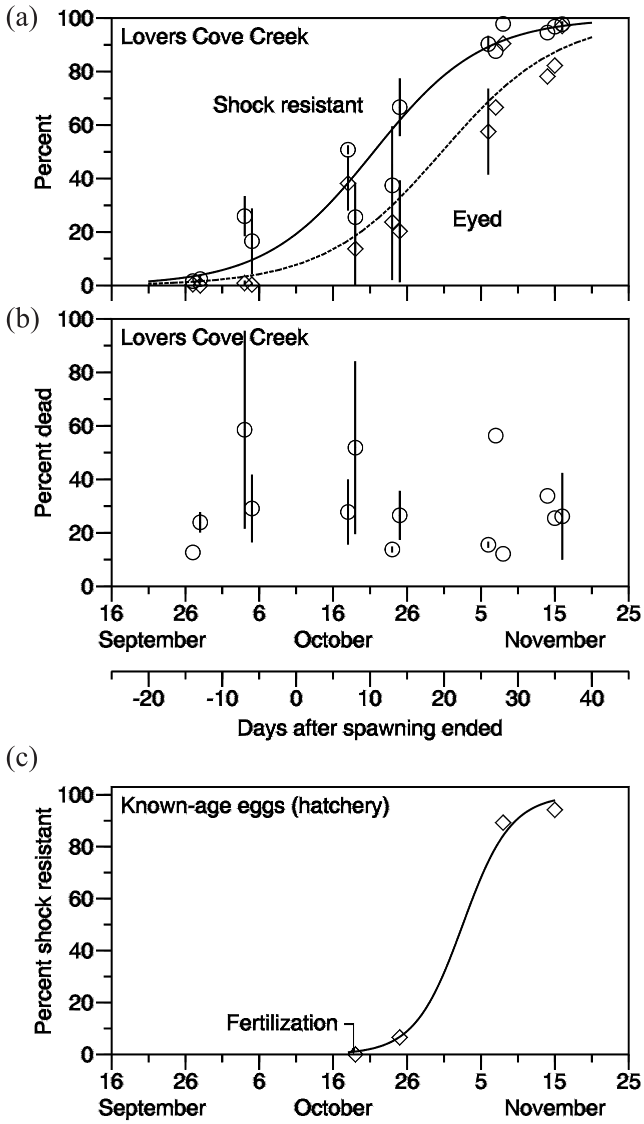

Figure 3.(a) Mean percentages of pink salmon eggs from Lovers Cove Creek that survived hydraulic shock (circles) and mean percentages of live eggs that were eyed (diamonds). Error bars are ± 1 SE; $n = 1$ where error bars are absent. Regression curve for shock resistence shown by solid line and for eyed eggs by dashed line. (b) Mean percentages of pink salmon from Lovers Cove Creek that were already dead prior to sampling. (c) Percentages of known-age pink salmon eggs that survived hydraulic shock after being pumped from an artificial redd.

Shock resistance in known-age eggs

Shock resistance in known-age eggs increased more rapidly than in naturally spawned eggs (Figure 3c). Percentages of eggs resistant to shock increased from 0–93% between 1 and 28 d after fertilization. Only about 35% of the eggs were resistant to hydraulic shock 12 d after fertilization, but 21 d after fertilization, 87% were resistant. Resistance to hydraulic shock reached 93%, 28 d after fertilization.

DISCUSSION

Results of this study demonstrate that resistance of naturally spawned pink salmon eggs to hydraulic shock increases sigmoidally over time, but changes more slowly than in a population of uniform-aged eggs. Pink salmon egg susceptibility to mechanical damage has previously been thoroughly studied with known-age eggs (e.g., Jensen 1997), but the application of these results to wild populations requires an understanding of egg age distributions and field testing. We can compare our results to only one other field study published on this topic (Collins et al. 2000), but results of this study show the need to discriminate between natural eggs that died prior to sampling and mortality caused by sampling. This information can help interpret pink salmon egg mortality data collected after the *Exxon Valdez* oil spill, a topic that has proven controversial because the relationship between time of spawning and hydraulic sampling was unknown in most years (e.g., Bue et al. 1998; Brannon et al. 2001; Rice et al. 2001).

An important difference between naturally spawned egg populations and those used in the laboratory assessment of shock resistance is that there are eggs of various ages in wild populations, whereas eggs are of similar age in laboratory populations. The expected effect is that average resistance to shock will increase more slowly in egg samples from wild populations than would be predicted from laboratory studies using uniform-age eggs. This is just what we observed in our study. Adults spawned over a 40 d period, and the rate of egg resistance to shock increased more slowly in the wild population than in uniform-age embryos subjected to the same hydraulic shock.

Redd superimposition by later spawning pink salmon probably also contributes to the slower increase in resistance to hydraulic shock observed in wild populations. This is because later spawning salmon displace and kill eggs already in the gravel, which increases the proportion of immature eggs. For example, 54% of the spawning was completed 3 weeks prior to October 17. At observed water temperatures of approximately 7°C those eggs should have matured to the eyed stage, yet only 12% of sampled eggs were eyed on this date. Half the laboratory eggs were resistant to shock within 16 d after fertilization, but only 32% of wild eggs were resistant 12 d after 75% of spawning was complete. Effects of superimposition likely vary spatially and temporally, cannot be predicted with high precision, and will also vary according to population differences in run timing.

Our results are similar to those of Collins et al. (2000), but we sampled more frequently and thus were able to more clearly define the rate at which shock resistance developed. Collins et al. (2000) reported that shock resistance of pink salmon eggs in PWS increased from about 58% at the end of spawning to 98% about one month later. We observed a lower percentage of shock resistant eggs (23%) at the end of spawning. This could have been due to differences in the timing of spawning, superimposition, or hydraulic energy between study sites. However, a month after spawning 92% of the eggs at our study site were resistant to shock, similar to estimates by Collins et al. (2000). Although Collins et al. (2000) predicted naturally spawned eggs would become shock resistant in about 20 d, our data indicate about 25% of eggs can still be damaged by hydraulic pumping at this time. Most, but not all eggs eventually become immune to shock. In our study, only 2% were susceptible to shock 36 d after spawning ended, a result reasonably consistent with Collins et al. (2000; 2% susceptible 20–29 d after spawning) given the potential differences between streams, salmon behavior, and sampling procedures.

Discriminating between eggs killed by sampling and eggs already dead is crucial in accurately determining pre-sampling mortalities in a stream. For example, after the *Exxon Valdez* oil spill, field sampling was done to determine whether pink salmon eggs were killed by oil exposure in intertidal reaches of streams. Unfortunately, the difficulty in discriminating eggs killed by sampling led to controversy over the results. Brannon et al. (2001) alleged that oil-related mortalities reported by Bue et al. (1996) were really due to differences in timing of spawning between oiled and reference streams that led to lesser percentages of shock resistant eggs in oiled streams. Bue et al. (1998) and Craig et al. (2002) addressed these concerns in two ways by: (1) incubating eggs from oiled and reference streams together in hatchery incubators thereby eliminating the issue of shocking or run timing and (2) including time of spawning as a covariate in the analysis for 1991, the only year for which spawning timing data was available. These studies and corrections, together with other corroborative field and laboratory studies confirmed that oil caused mortality (Carls et al. 2003; Marty et al. 1997; Heintz et al. 1999; Rice et al. 2001). This controversy clearly illustrates the importance of distinguishing eggs that were killed by sampling from those already dead.

Modification of egg handling techniques developed during this study has improved the ability of investigators to identify eggs killed by sampling. How eggs are handled after they are collected affects the speed at which shock symptoms appear. If eggs remain in fresh water after sampling, shocked eggs change from pink to opaque white in less than 10 minutes and become difficult to distinguish from eggs that were already dead. In past studies, hydraulically sampled eggs remained in a water-gravel mixture for extended periods in order to collect large numbers of eggs, therefore non-sampling mortality could have been overestimated. Our modification limits pumping to short time intervals (1 min), after which all eggs are quickly removed from water. This prevents water from entering shock-damaged eggs, thus eggs remain pink and clearly distinguishable from eggs that were dead prior to sampling. To determine egg mortalities due to shocking, remaining eggs can be placed in water after the dead ones are counted and removed. Shocked eggs will absorb water and will whiten in a few minutes.

Further evidence that our improved sampling techniques successfully allowed discrimination between shocked and dead eggs is provided by our time series of data. Percentages of naturally dead eggs in Lovers Cove Creek varied among sampling periods but were not related to time, whereas percentages of shocked eggs decreased with time. Although daily variance in natural mortality was occasionally high, this was probably due to dead eggs sampled from gravel with poor incubation conditions, a measure of spatial rather than temporal variability. When calculated by sampling period (1–3 d), mean percentages of dead eggs (20–36%) in Lovers Cove Creek were similar to those reported by Collins et al. (2000; 21%). This was in sharp contrast to the percentages of eggs killed by sampling, which decreased predictably from nearly all to almost none.

CONCLUSIONS

Ideally, pink salmon eggs should be allowed to incubate for one month before hydraulic sampling takes place so that most embryos become resistant to mechanical shock. Our improved sampling technique, however, provides clear distinction between eggs killed by sampling shock and those that were already dead by allowing greater latitude in sample timing, thus alleviating problems posed by differences in run timing and egg maturity within and between streams. In all cases, observers should be very intentional in discriminating between eggs killed by sampling shock and those that were already dead. Combining live and shocked eggs into a single "live" category provides an accurate description of pre-sampling conditions, but combining shocked and dead eggs into a single "dead" category overestimates the number of dead eggs present prior to sampling.

LITERATURE CITED

Brannon, E. L., and A. W. Maki. 1996. The *Exxon Valdez* oil spill: Analysis of impacts on the Prince William Sound pink salmon. Reviews in Fisheries Science 4:289–337.

Brannon, E. L., K. C. M. Collins, L. L. Moulton, and K. R. Parker. 2001. Resolving allegations of oil damage to incubating pink salmon eggs in Prince William Sound. Canadian Journal of Fisheries and Aquatic Sciences 58:1070–1076.

Bue, B. G., S. Sharr, S. D. Moffitt, and A. Craig. 1996. Effects of the *Exxon Valdez* oil spill on pink salmon embryos and preemergent fry. American Fisheries Society Symposium 18:619–627.

Bue, B. G., S. Sharr, and J. E. Seeb. 1998. Evidence of damage to pink salmon populations inhabiting Prince William Sound, Alaska, two generations after the *Exxon Valdez* oil spill. Transactions of the American Fisheries Society 127:35–43.

Carls, M. G., R. E. Thomas, and J. F. Thedinga. 2004. Observer classification of live, mechanically damaged, and dead pink salmon eggs. Transactions of the American Fisheries Society 133:245–251.

Carls, M. G., R. E. Thomas, and S. D. Rice. 2003. Mechanism for transport of oil-contaminated water into pink salmon redds. Marine Ecology Progress Series 248:245–255.

Collins, K. M., E. L. Brannon, L. L. Moulton, M. A. Cronin, and K. R. Parker. 2000. Hydraulic sampling protocol to estimate natural embryo mortality of pink salmon. Transactions of the American Fisheries Society 129:827–834.

Craig, A. K., S. Sharr, and S. D. Moffitt. 1995. A compilation of historical preemergent fry and egg deposition survey data from Prince William Sound, 1961–1995. Alaska Department of Fish and Game, Division of Commercial Fisheries Management and Development, Regional Information Report No. 2A95-49. Juneau, AK.

Craig A. K., T. M. Willette, D. G. Evans, and B. G. Bue. 2002. Injury to pink salmon embryos in Prince William Sound–Field monitoring. Restoration Report 98191A-1 *Exxon Valdez* Oil Spill Final Report. Alaska Department of Fish and Game, Anchorage.

Dvinin, P. A. 1952. The salmon of south Sakhalin. Izvestiia Tikhookeanskovo Nauchno-Issledovatelskovo Instituta Rybnovo Khoziaistva i Okeanografii 37:69–108. (Translated from Russian; Fisheries Research Board of Canada Translation Service 120).

Fukushima, M., T. J. Quinn, and W. W. Smoker. 1998. Estimation of eggs lost from superimposed pink salmon (*Oncorhynchus gorbuscha*) redds. Canadian Journal of Fisheries Aquatic and Sciences 55:618–625.

Hanavan, M. G., and B. E. Skud. 1954. Intertidal spawning of pink salmon. Fishery Bulletin 56:167–185.

Heard, W. R. 1991. Life history of pink salmon (*Oncorhynchus gorbuscha*). Pages 121–230 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. Department of Fisheries and Oceans, Biological Sciences Branch, Pacific Biological Station, Nanaimo, British Columbia, Canada. University of British Columbia Press, Vancouver, British Columbia.

Heintz, R. A., J. W. Short, and S. D. Rice. 1999. Sensitivity of fish embryos to weathered crude oil: Part II. Incubating downstream from weathered *Exxon Valdez* crude oil caused increased mortality of pink salmon (*Oncorhynchus gorbuscha*) embryos. Environmental Toxicology and Chemistry 18:494–503.

Jensen, J. O. T. 1997. Mechanical shock sensitivity in salmonid eggs. Pages 1–3 *in* C. Clark, editor. Aquaculture Update 78. Pacific Biological Station, Nanaimo, British Columbia.

Jensen, J. O., and D. F. Alderdice. 1989. Comparison of mechanical shock sensitivity of eggs of five Pacific salmon (*Oncorhynchus*) species and steelhead trout (*Salmo gairdneri*). Aquaculture 78: 163–181.

Martin, R. M. 1973. Hydraulic modification of intragravel streambed flow as a means of improving egg-to-fry survival. MS thesis. Humbolt State University.

Marty, G. D., J. W. Short, D. M. Dambach, N. H. Willits, R. A. Heintz, S. D. Rice, J. J. Stegeman, and D. E. Hinton. 1997. Ascites, premature emergence, increased gonadal cell apoptosis, and cytochrome P4501A induction in pink salmon larvae continuously exposed to oil-contaminated gravel during development. Canadian Journal of Zoology 75: 989–1007.

McNeil, W. J. 1964a. A method of measuring mortality of pink salmon eggs and larvae. U.S. Fish and Wildlife Service Fishery Bulletin 63:575–588.

McNeil, W. J. 1964b. Redd superimposition and egg capacity of pink salmon spawning beds. Journal of the Fisheries Research Board Canada 21:1385–1396.

Rice S. D., R. E. Thomas, M. G. Carls, R. A. Heintz, A. C. Wertheimer, M. L. Murphy, J. W. Short, and A. Moles. 2001. Impacts to pink salmon following the *Exxon Valdez* oil spill: persistence, toxicity, sensitivity, and controversy. Reviews in Fisheries Science 9(3):165–211.

SAS. 1999. SAS OnLineDoc Version 8. SAS Institute Inc. Cary, NC.

Williams, D. A. 1982. Extra-binomial variation in logistic linear models. Applied Statistics 31:144–148.