Spatial and temporal variation in dissolved oxygen in natural egg pockets of chum salmon, in Kennedy Creek, Washington

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The effects of dissolved oxygen (DO) on incubating salmonid embryos have been studied extensively in the laboratory but there is little information on levels experienced by salmon embryos in complex natural channels. We monitored 33 natural egg pockets of chum salmon Oncorhynchus keta, from shortly after spawning until emergence, and found that DO levels varied considerably among and within egg pockets over time. Egg pocket DO levels varied from 2–10 mg l⁻¹ at the time of spawning and generally declined during incubation but the declines did not occur in all pockets and were not always steady. Much of the variability may be attributed to local channel topography. Pool tailouts had the highest and least variable DO levels whereas levels in lateral bars were generally lower and more variable. Levels in glides and riffles tended to be intermediate between those in pool tailouts and lateral bars. In spite of the variation in DO levels and habitats used by chum salmon, DO levels were not correlated with egg pocket sediment composition (per cent of the sample <1.0 or 4.0 mm diameter) or with the egg pocket’s depth.

Key words: chum salmon; incubation; dissolved oxygen; fine sediment.

INTRODUCTION

Among salmonid fishes, a large but highly variable fraction of the life-time mortality takes place between the time fertilized eggs are deposited in the gravel and when they emerge as fry several months later. Under conditions of high spawner density, redd superimposition by other females can reduce survival to emergence (STE) (McNeil, 1964). Otherwise, the major factors affecting survival during this period are displacement by high stream flows that scour the stream bed (McNeil, 1964; Thorne & Ames, 1987), suffocation of the developing embryos due to inadequate circulation of intragravel water (Everest et al., 1987), and entombment of hatched and fully formed fry in the gravel bed (Bjornn, 1969). The latter two mortality agents are considered to be closely associated with high concentrations of fine sediment in stream beds.

Fine sediment is a natural component of stream beds but land-use practices that disturb vegetative cover often cause erosion that delivers sand and silt to stream courses. Natural background rates and sediment delivery processes vary considerably over forested landscapes but logging operations frequently result in elevated rates of sediment delivery to streams (e.g. Platts et al., 1989). Some of the most compelling evidence that forest practices harm salmonid fishes comes from studies of fine sediment and STE (Scrivener & Brownlee, 1989).

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Relationships between fine sediment concentration and STE often vary greatly (Chapman, 1988). Moreover, the relationships are apparently extraordinarily steep (e.g. Tagart, 1984). That is, slight changes in fine sediment concentration seem to produce large changes in embryo mortality. In most of the STE studies, the precise mechanism of mortality is never identified. Dissolved oxygen (DO) is often implicated because it can vary with stream bed porosity and apparent velocity, both of which are inversely related to fine sediment concentrations (Coble, 1961; Tagart, 1984), and because decreased DO levels have been associated with logging operations (Ringler & Hall, 1975; Woods, 1980).

The DO requirements and effects of hypoxial stress on salmonid embryos and larvae have been studied extensively in the laboratory and artificial channels (Wickett, 1954; Alderdice et al., 1958; Silver et al., 1963; Shumway et al., 1964; Koski, 1975). DO levels vary within salmonid spawning areas (e.g. McNeil, 1962; Turnpenny & Williams, 1980) and positive correlations have been reported between DO and STE for rainbow trout *Oncorhynchus mykiss* (Walbaum) embryos in a groundwater-fed stream (Sowden & Power, 1985), and for embryos buried experimentally in natural stream beds (Atlantic salmon *Salmo salar* L., Lacroix, 1985; brown trout *S. trutta* L., Maret et al., 1993). However, optimization of STE by selection of sites with large gravel and high circulation rates may conflict with the probability of scour in such sites (Holtby & Healey, 1986). Construction of egg pockets deep below the surface of the stream bed might protect the embryos from scour but expose them to lower DO levels.

Controlled studies have indicated the effects of DO concentrations at different developmental stages but only information from natural field settings can reveal the range and temporal patterns of DO concentrations experienced by wild salmon embryos. Specifically, female salmon might avoid areas of low DO when selecting redd sites, DO levels might vary among habitat types within the stream, and DO levels might change over the incubation period. Moreover, DO levels may co-vary with gravel composition and depth of the egg pocket. Because this information has seldom been collected from the immediate environment of embryos in the field, we studied the temporal and spatial variability of DO in undisturbed chum salmon *Oncorhynchus keta* (Walbaum) egg pockets in a complex natural channel. Our study was designed to address the following null hypotheses: (1) egg pocket DO levels do not differ from saturation at the time of egg deposition; (2) DO levels remain constant during the embryonic incubation period; (3) DO levels do not vary among habitat types within the area of the stream used by spawning salmon; (4) DO levels do not vary with gravel composition, and (5) DO levels do not vary with egg pocket depth.

**MATERIALS AND METHODS**

**STUDY SITE**

Kennedy Creek is a third-order drainage, flowing about 16 km into Totten Inlet in southern Puget Sound (Fig. 1). The creek's headwaters consist of numerous high-gradient first- and second-order channels draining steep hillslopes flowing into a large, flat valley created by glacio-fluvial erosion and deposition. The valley gradually narrows into a bedrock canyon near river km 44, where the stream flows over a large falls and through a narrow canyon that prevents upstream migration of anadromous salmonids. Below the
FIG. 1. Location map of Kennedy Creek, Washington. Studies of chum salmon incubation were conducted 1 to 2 km from the creek’s mouth.

gorge, the stream flows through a narrow V-shaped valley for about 1.5 km where the channel is occasionally restricted by bedrock outcrops, then gradually becomes more sinuous and less constricted. The study sites were located in a reach between river km 1–2 that is moderately confined by valley walls and is slightly incised into highly erodible deposits.

The climate is maritime with relatively wet, mild winters. Annual precipitation averages 147 cm, mostly as rain from October through April. Discharge ranges from a mean low flow of 0.1 m$^3$ s$^{-1}$ in August to a mean high flow of 4.8 m$^3$ s$^{-1}$ in January, with a mean annual discharge of 1.7 m$^3$ s$^{-1}$. The highest peak flow recorded between 1960 and 1979 (the period of record for the U.S. Geological Survey gaging station) was 39.1 m$^3$ s$^{-1}$ and the mean annual peak flow (recurrence interval 2.33 years) is approximately 22.9 m$^3$ s$^{-1}$ (Williams et al., 1985).

Most forests in the watershed were harvested earlier in the century and now consist of second-growth stands of Douglas fir *Pseudotsuga menziesii* in well-drained sites and red alder *Alnus rubra* in wetter sites. Harvest of second-growth timber in the basin is under way and a dense system of roads is in place. Four study reaches were selected based on differences in general physical criteria. Two were structurally simple reaches, having relatively smooth, gradually changing long profiles, relatively narrow bank-full channel widths, low lateral bar relief, and little large woody debris. The other two reaches were more complex, having abruptly changing long profiles, relatively wide bank-full channel widths, high lateral bar relief, and large quantities of large woody debris.

**SAMPLE COLLECTION AND ANALYSIS**

We observed pairs of chum salmon until they spawned, and inserted a 15-cm plastic tent peg attached to a sampling tube into the centre of the egg pocket before the female began to cover the eggs. The last 6–8 cm of this tube was perforated and covered by a fine mesh stainless steel screen. As soon as the sampling tube was inserted, the location of the pocket was surveyed with reference to two or three benchmarks located away from the active channel. These procedures took 7–10 min, after which the female returned (within 5–10 min) and began normal redd covering. The sampling tube trailed back over the
TABLE 1. Dissolved oxygen concentrations in mg l$^{-1}$ (s.d.) in chum salmon egg pockets in four types of habitats (number of egg pockets in parentheses) at the time of fertilization and at the approximate dates of hatching and emergence from the gravel, estimated on the basis of the thermal regime during the winter.

<table>
<thead>
<tr>
<th>Developmental stages</th>
<th>Habitat type</th>
<th>Pool tailout (11)</th>
<th>Glide (10)</th>
<th>Riffle (8)</th>
<th>Lateral bar (4)</th>
<th>Total (33)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fertilization</td>
<td></td>
<td>8.6 (1.2)</td>
<td>6.7 (2.9)</td>
<td>9.0 (1.5)</td>
<td>7.7 (2.2)</td>
<td>8.0 (2.1)</td>
</tr>
<tr>
<td>Hatching</td>
<td></td>
<td>9.8 (0.8)</td>
<td>8.7 (3.0)</td>
<td>7.6 (2.9)</td>
<td>8.2 (1.3)</td>
<td>8.7 (2.3)</td>
</tr>
<tr>
<td>Emergence</td>
<td></td>
<td>7.6 (2.6)</td>
<td>6.0 (3.4)</td>
<td>5.6 (3.4)</td>
<td>3.6 (2.9)</td>
<td>6.2 (3.2)</td>
</tr>
</tbody>
</table>

tailspill of the redd and allowed us to withdraw water samples from the egg pocket without further disturbance. The female later constructed additional egg pockets in succession and redds were completed within the normal time span of about 1 day. At this time we also categorized the habitat as pool tailout, glide, riffle or lateral bar.

Sampling tubes were inserted into 41 egg pockets and water samples were withdrawn every 7–14 days. We first evacuated a volume sufficient to empty the tube to the egg pocket, then withdrew 60 ml for a temperature measurement, and finally withdrew 125 ml into a sample bottle, fixed it chemically, and analysed the DO in the laboratory by idiometric titration. The water extraction was done slowly (over about 5 min) to minimize alteration of the intragrain flow pattern. Temperatures were taken so that we could compute DO saturation and estimate the embryos’ developmental stage, using data obtained from Kennedy Creek chum salmon (Tom Burns, Washington Department of Fish and Wildlife, Olympia, Washington, pers. comm.). We standardized our analysis of DO to ‘days since fertilization’ rather than calendar date because the DO requirements change with the stage of embryonic development and our egg pockets were constructed over a period of several weeks (31 October to 5 December 1991).

In late March, after we estimated that all embryos would have emerged from the gravel, we sampled the particle size distribution in the egg pockets by inserting tri-tube freeze core probes into the egg pocket, introducing liquid carbon dioxide into the hollow tubes, and withdrawing the frozen core of gravel from the streambed (Everest et al., 1980). The cores were then laid across sampling boxes and melted off the probes. The boxes were arranged to collect sediment from each of four strata: the undisturbed sediments underlying the egg pocket, the egg pocket itself, the bridging layer (the layer of particles deposited by initial covering actions of the female), and the rest of the cover material up to and including the surface layers of gravel. Sediments from all strata were packaged individually for processing. In the laboratory, sediment samples were dried to a constant weight and shaken mechanically through 21 standard sieves representing a $\log_{2}(\text{particle size diameter})$ gradation from $-6$ (64 mm) to $4$ (0.063 mm). This sieve series conforms to standard particle size determination methods used in sedimentology studies and facilitates comparisons with the Wentworth (1922) particle size scale. All 22 size fractions, including the pan silts, were weighed to the nearest 0.1 g.

RESULTS

We obtained complete records (samples collected from 1–5 days after egg pocket construction to the estimated date of emergence in the last 2 weeks of March) for 33 of the 41 egg pockets (Table I). The other eight sampling tubes were displaced by stream bed scour or by other females constructing redds later in the spawning period. DO levels in the egg pockets varied considerably at the time of spawning (range: 2.9 to 10.9 mg l$^{-1}$; Fig. 2). This variation in DO did
distribution of dissolved oxygen (DO) in 33 chum salmon egg pockets at three developmental stages. (a) Spawning; (b) hatching; (c) emergence.

not result primarily from differences in water temperature, as the per cent saturation also varied (27–92%).

In addition to the variation in initial DO levels among egg pockets, there was considerable temporal variation in DO within egg pockets (Table I; Fig. 2). DO levels at emergence were generally lower than those at fertilization but some egg pockets experienced little change and others fluctuated but did not decline. Wilcoxon signed rank tests did not detect a change in DO between spawning and hatching (means: 8.0 v. 8.7 mg l⁻¹; P=0.10), but did detect a decrease between spawning and emergence and between hatching and emergence (Table I; P<0.01 in both cases). In general, DO appeared to fluctuate more in the early part of the incubation period than later (Fig. 3).

Analysis of temporal trends in DO levels was complicated by variation among study reaches and habitat types. A Kruskal–Wallis test (non-parametric one-way ANOVA) indicated differences in DO levels among study reaches in DO at hatching and emergence (P<0.05, for both cases), but not at the time of spawning (P=0.27). The reaches, however, differed in the proportions of egg pockets in the different habitat types, and DO patterns seemed to differ among habitats. The range in DO levels in individual egg pockets over time (Fig. 4) made it difficult to define reach-specific patterns. When we examined the ranges of DOs experienced in individual egg pockets, two modes were apparent; one group of egg pockets had little fluctuation in DO whereas levels in the other group varied considerably. The distribution of these ranges in DO tended to vary among habitat types (Table I). Pool tailouts tended to have high DO levels.
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FIG. 3. Temporal trends in dissolved oxygen (DO) in individual chum salmon egg pockets from different reaches of the study site (designated A, B, C and D in the figure).

FIG. 4. Percentage frequency distribution of the maximum range of dissolved oxygen (DO) experienced during the entire incubation period in 33 individual chum salmon egg pockets.

that changed little whereas riffle DO levels were initially high but decreased more. DO levels in glides were lower and more variable than those in riffles and pool tailouts at fertilization and also varied at emergence date. We measured
Dissolved Oxygen in Chum Salmon Egg Pockets

Fig. 5. Relationship between fine sediment (per cent material <4·0 mm diameter, by dry weight) and dissolved oxygen (DO) in chum salmon egg pockets at the time of hatching. Two mg l\(^{-1}\) is the level of dissolved oxygen below which chum salmon survival to emergence drops rapidly (Koski, 1975).

Table II. Proportion of fine sediment (S.D.) collected by freeze-cores in 33 chum salmon egg pockets in four types of habitats (number of egg pockets in parentheses) at the approximate date of emergence from the gravel, estimated on the basis of the thermal regime during the winter.

<table>
<thead>
<tr>
<th>Fine sediment</th>
<th>Pool tailout (11)</th>
<th>Glide (10)</th>
<th>Riffle (8)</th>
<th>Lateral bar (4)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Per cent &lt;1·0 mm</td>
<td>6·8 (2·6)</td>
<td>7·3 (2·2)</td>
<td>7·7 (4·1)</td>
<td>8·1 (2·4)</td>
</tr>
<tr>
<td>Per cent &lt;4·0 mm</td>
<td>14·2 (3·7)</td>
<td>16·2 (5·1)</td>
<td>14·9 (6·1)</td>
<td>17·2 (4·6)</td>
</tr>
</tbody>
</table>

Only four lateral bar egg pockets but three of them experienced DO levels that changed by 7–9 mg l\(^{-1}\) during incubation.

We did not detect any correlation between DO levels and the proportion of the gravel less than either 1·0 or 4·0 mm (e.g. Fig. 5). The average per cent fines <1·0 and 4·0 mm in the 33 egg pockets were 7·3% (S.D. 2·8%) and 15·4% (S.D. = 4·8), respectively (Table II). Small sample sizes precluded a statistically rigorous evaluation of sediment composition by habitat type but some variation was noted. The level of fines generally increased from pool tailout to lateral bar locations (Table II). Variation in gravel composition and DO within habitat type obscured any relationship that might have existed between per cent of fine material and DO levels.

We hypothesized that DO might decrease with depth of the egg pocket, under the assumption that surface water with relatively high DO levels might not
penetrate deep into the gravel bed. The mean depths of the 33 egg pocket ceilings, measured in autumn and spring, were 22.0 and 19.0 cm, respectively (s.d. = 8.6 and 10.6 cm, respectively) but the median depths were slightly less (20.4 cm in autumn and 17.1 in spring). Our results, however, did not support the prediction. There was no correlation between DO and egg pocket depth at the dates of fertilization, hatching or emergence ($r^2 = 0.03$, $0.08$ and $0.10$, respectively, $P > 0.05$ in all cases). We explored further the relationship between water source (surface or ground) and DO by subtracting surface from subsurface water temperatures. We assumed that greater differences in temperature (absolute values) would indicate greater separation of water sources, hence greater contribution of ground water to the egg pocket environment. The surface water ranged from 10.8°C on 1 November to a low of 6.2°C on 19 December, then warmed to 9.5°C when the last measurements were taken on 4 March. The water in the egg pockets was generally warmer than the surface water during most of the period of record. We observed temperature differences up to 2.5°C but most differences were within 1.0°C, perhaps because the creek did not get very cold. There was a negative relationship between temperature difference and DO (i.e. lower DO when surface and subsurface temperatures were more different) but temperature difference explained relatively little of the overall variation ($r^2 = 0.04$, $P < 0.001$). The mean temperature differences between surface and egg pocket readings were similar among habitat types (lateral bars: 0.57°C, glides: 0.67°C, pool tailouts: 0.68°C, riffles: 0.79°C, ANOVA $F = 1.81$, $P = 0.14$).

**DISCUSSION**

Our data present a unique window into natural chum salmon egg pockets and advance our understanding of the DO levels experienced by wild salmon embryos. Our first null hypothesis, that egg pocket DO levels would not differ from saturation at the time of egg deposition, was strongly rejected. This not only confirmed the finding of other studies that DO levels vary considerably in natural streams (McNeil, 1962; Lacroix, 1985; Leman, 1993) but, more importantly, indicated that female salmon were either unable to detect the low DO levels or were unable to avoid them (see also Sowden & Power, 1985). It is very likely that they could distinguish between saturated surface water and the low DO levels that characterized some pockets (Davis, 1975; Fast, 1987) but perhaps they were unable actually to sample the intragravel water that bathed the egg pocket. Alternatively, they may have detected the low DO but not avoided it, because there was so much competition for space [in 1991–1992 approximately 5000 chum salmon spawned per km in the 4.4 km accessible length of Kennedy Creek (Washington Department of Fish and Wildlife, unpublished data)], or because the levels were not sufficiently low to trigger avoidance.

Our second null hypothesis, that DO levels would remain constant, was also falsified. There was both a general reduction in DO from fertilization to emergence and substantial fluctuations in many egg pockets. The reductions in DO might have resulted from the respiration of the alevins themselves, or from the decay of dead embryos. The fluctuations and increases from
fertilization to hatching might reflect changes in the water sources irrigating the pockets. The interchange between surface and subsurface water, as indicated by the similarity between temperatures in the creek and the egg pocket, was correlated with DO but explained little of the overall variation. Whatever the reasons for the variation, our results indicated that single measurements of DO levels may not represent accurately conditions at a given location, supporting similar findings by Sowden & Power (1985) in a groundwater-fed stream.

Our third null hypothesis, that DO levels would not vary among habitat types within the area of the stream used by spawning salmon, was rejected generally, although there was a great deal of variation among egg pockets within habitats. McNeil (1962) described a highly variable intragravel oxygen environment for pink *O. gorbuscha* (Walbaum) and chum salmon spawning streams in Alaska. Spatial and temporal variability in McNeil's (1962) study appeared to be related to both broad scale interannual environmental controls and fine scale in-channel conditions. More recently, Leman (1993) described the spawning sites of chum salmon in the upper reaches of the Kamchatka River. Oxygen isopleths associated with groundwater ranged from 6.5-10.5 mg l⁻¹ whereas those influenced by subsurface river flow ranged from 4.8-6.5 mg l⁻¹ DO. It is likely that some of the variability between our study reaches and egg pockets was also related to different water sources. Stream bed topography can affect the interchange of surface and subsurface waters (Vaux, 1962), which is an important factor in intragravel DO (Woods, 1980). We expected that egg pockets in the lateral bars and some of those in glides would be exposed to relatively little surface water interchange because local flow patterns and elevation breaks in bed form might not create the flow vectors needed to inject surface waters into the gravel at these locations. To the extent that temperature differences between surface and subsurface water indicated separation of water sources, this expectation was not supported. The differences between surface and subsurface temperatures were similar among habitat units, and generally of the magnitude expected for winter conditions in this region (Shepherd et al., 1986).

The levels of DO we observed were generally within the range expected to produce good STE for chum salmon. Koski (1975) identified 2 mg l⁻¹ as the threshold below which survival decreased rapidly. Wickett (1954) determined that 1.67 mg l⁻¹ was the lethal level for chum salmon and more recent work has established that chum salmon have slightly lower oxygen requirements than do coho *O. kisutch* (Walbaum) or chinook salmon *O. tshawytscha* (Walbaum) (Fast, 1987). Interpretation of the DO levels would have been aided by estimates of intragravel water flow rates but these were not obtained. Sublethal effects on size and fitness of fry after prolonged exposure to low DO have been reported for several salmonids including chum salmon (Brannon, 1965; Mason, 1969; Koski, 1975; Bams & Lam, 1983). However, Koski (1975) found no differences in the size of chum salmon fry emerging from redds with prolonged minimum DO concentrations less than 6.0 mg l⁻¹. DO requirements increase from fertilization to hatching (Davis, 1975) but we observed high DO levels through hatching in most pockets. DO concentrations tended to be lowest near the time of emergence and were low enough to affect
emergence or fry size in as many as 10–15% of our egg pockets. However, alevins move to avoid low DO levels (Fast, 1987) so they may not have experienced the low levels that we measured in some of the pockets.

Several factors might explain our failure to reject the fourth null hypothesis, that DO levels would not vary with gravel composition. First, the relationship between fine sediment and DO levels is often weak (e.g. Shapley & Bishop, 1965; Scrivener & Brownlee, 1989). Second, the levels of fine sediments in our stream bed may have been too low to restrict intragravel flow and delivery of oxygenated water. Koski (1975), for example, described a relationship between fine sediment and DO in gravel consisting of 30–70% sand. Even though we used dry gravimetric methods and Koski (1975) used wet volumetric methods to analyse sediment samples, our samples were much ‘cleaner’ (fewer fines) with only four to six of our 33 samples as fine as Koski’s (1975) ‘cleanest’ samples. Finally, low DO groundwater distribution may be largely independent of gravel size (Sowden & Power, 1985). In any case, our results indicated that the relationship between fine sediment and DO should not be accepted uncritically. We hope that other investigations of natural egg pocket conditions can be conducted to test this assumption, as it underlies many assessments of the consequences of land use practices on salmonid fishes.

Finally, we hypothesized that egg pockets that were deeper below the stream bed might be lower in DO than those constructed shallower. If this were true, it might imply a tradeoff between the relative security of deep egg pockets from scour and the problems associated with incubating embryos in water with low DO levels. In 1991–1992 season, many parts of Kennedy Creek experienced scour to the depths of egg pockets (Montgomery et al., 1996) and eight of our 41 egg pockets were lost to scour or dig-up by other females. We conclude that scour can be a significant source of mortality. Contrary to our prediction, we detected no relationship between DO and depth, hence large chum salmon in Kennedy Creek might protect their eggs from scour and redd superimposition by digging deep, as van den Berghe & Gross (1984) and Crisp & Carling (1989) have shown in other salmonids, without sacrificing high levels of DO. While the patterns of sediment and water sources in other streams might result in the expected correlation between egg pocket depth and DO, this relationship cannot be assumed.

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References


