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Incubation success and habitat selection of shore-spawning kokanee *Oncorhynchus nerka*: effects of water-level regulation and habitat characteristics

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Abstract – Changes to water-level regimes have been known to restructure fish assemblages and interfere with the population dynamics of both littoral and pelagic species. The effect of altered water-level regimes on shore-spawning kokanee *Oncorhynchus nerka* incubation success was evaluated using a comprehensive *in situ* study in Lake Pend Oreille, ID, USA. Survival was not related to substrate size composition or depth, indicating that shore-spawning kokanee do not currently receive a substrate-mediated survival benefit from higher winter water levels. Substrate composition also did not differ among isobaths in the nearshore area. On average, the odds of an egg surviving to the preemergent stage were more than three times greater for sites in downwelling areas than those lacking downwelling. This study revealed that shoreline spawning habitat is not as limited as previously thought. Downwelling areas appear to contribute substantially to shore-spawning kokanee recruitment. This research illustrates the value of rigorous *in situ* studies both for testing potential mechanisms underlying population trends and providing insight into spawning habitat selection.

Key words: Water-level regulation; incubation; shoreline spawning; kokanee; groundwater

Introduction

Water resource development has greatly benefited human populations by providing irrigation, municipal water sources, flood control and hydropower. Unfortunately, these benefits often come at the expense of freshwater fish populations of substantial economic, cultural, and ecological value (Dynesius & Nilsso 1994; Coleman 1996; Rosenberg et al. 1997). Some of the negative consequences of dam construction are immediate and obvious (e.g., blockage of diadromous species), while others are indirect and only apparent at larger temporal and spatial scales (Friedl 2002; Milbrink et al. 2011). An important lesson synthesised from numerous case studies is that anthropogenic alterations to seasonal and annual hydrologic regimes often underlie undesired shifts in biological diversity, nutrient dynamics and habitat conditions (Richter et al. 1997; Wyatt et al. 2010; Milbrink et al. 2011). Thus, it is important to consider the potential influences of artificial hydrologic regimes in dam-influenced systems, regardless of how subtle deviations might be.

Natural lakes that have been modified by placement of dams on their outlets appear to be only slightly influenced by changes to their hydrologic regimes, but small changes in water-level regimes can have profound ecological consequences (Wantzen et al. 2008; Zohary & Ostrovsky 2011). Water-level regime changes affect the availability and diversity of aquatic and terrestrial vegetation and can restructure nearshore invertebrate and fish communities (Aroviita

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& Hämäläinen 2008; White et al. 2011). Shoreline erosion, brought on by water-level alterations, has been shown to increase lake-wide turbidity and disrupt the feeding behaviour of pelagic fishes and macroinvertebrates (Bodaly et al. 1984; Patalas & Salki 1984). Water-level regimes also directly affect the reproductive success of shore-spawning species, typically by dewatering littoral areas where eggs have been deposited or reducing nursery habitat used by newly hatched fry (Gaboury & Patalas 1984; Anras et al. 1999). Changes in littoral habitat that interfere with recruitment can threaten fisheries of considerable socio-economic value (Bodaly et al. 1984; Gafny et al. 1992; Cohen & Radomski 1993). A dramatic example of water-level manipulation being linked with changes in a fishery is in Lake Pend Oreille (LPO; 48°07′N, 116°22′W), Idaho, where hydropower-related water-level fluctuations have been implicated for nearly 40 years of depressed kokanee *Oncorhynchus nerka* reproduction.

Kokanee in LPO were once the centrepiece of a highly productive commercial and recreational fishery that lasted from the 1940s to the 1970s, although more recently, kokanee have been in a depressed state. Within 10 years of entering the lake in the 1930s, kokanee supported the largest commercial and recreational fishery in Idaho, while also providing a prey resource for world-class rainbow trout *O. mykiss* and bull trout *Salvelinus confluentus* sport fisheries (Simpson & Wallace 1982). Hydrologic modification of LPO began in the early 1950s, when dams were constructed upstream and downstream of the lake. Albeni Falls Dam was built downstream on the Pend Oreille River in 1955, which increased the summer water level by approximately 3.5 m and inundated the north-west arm of the lake. Cabinet Gorge Dam was constructed 15-km upstream on the lake's largest tributary, the Clark Fork River in 1952. Surprisingly, neither dam appeared to have a substantial effect on the kokanee fishery in the years immediately following construction. In fact, commercial harvest of kokanee exceeded one million fish in the mid-1950s, and recreational catch rates remained high (Paragamian & Bowles 1995). The decline of kokanee began in the mid-1960s, prompting closure of the commercial fishery in 1973. Since then, kokanee abundance has remained at a relatively low level. A number of hypotheses have been posited to explain the decline of the kokanee population, including overharvest and competition with non-native mysid shrimp *Mysis diluviana* (Rieman & Falter 1981; Chipps & Bennett 2000). However, no factor appeared to coincide more closely with the kokanee decline than a hydropower-related shift in the water-level regime to a consistently low winter water level (Maiolie & Elam 1993).

The hypothesis associated with how water level affects incubation success in LPO differs from that given in other systems where water levels are known to affect shore-spawning kokanee. Under most circumstances, drawdowns during incubation negatively affect reproduction by dewatering shoreline redds and desiccating eggs (Stober et al. 1979; Matthews 1981; Decker-Hess & Clancey 1990; Modde et al. 1997). Although some shore-spawned eggs in LPO suffered this fate in the years immediately following construction of Albeni Falls Dam, agreements between managers and dam operators in 1968 and 1975 stabilised water levels during incubation (Hoelscher 1993; Maiolie & Elam 1993). Instead, the hypothesis describing how kokanee are affected by water level in LPO is tied to a reduction in suitable shoreline spawning habitat (Maiolie 1994). Prior to dam construction, the water level in LPO peaked at 628.1 m during spring run-off in May or June and fell to an annual minimum elevation of near 624 m beginning in July (Maiolie & Elam 1993). Between 1955 and 1964, the water level was held high (628.3 m) throughout the summer and dropped more rapidly in the fall, to between 624 and 628 m. Beginning in 1965, the winter water level of LPO was consistently held at 625.1 m. Under this regime, shore-spawning kokanee are thought to be relegated to lower quality spawning substrate that has not been 'cleaned' by wave action throughout summer. Poor spawning substrate quality is thought to have reduced intragravel survival such that recruitment was affected, thereby leading to an overall decrease in kokanee abundance.

The Idaho Department of Fish and Game (IDFG) responded in 1996 and began an experimental water-level management strategy designed to evaluate whether reducing winter drawdown would enhance shore-spawning kokanee recruitment. The strategy involved alternating between years of the pre-existing lake elevation (625.1 m) and an experimentally raised elevation (626.4 m). A population-level egg-to-fry survival estimate was then used to test whether a higher water level enhanced kokanee incubation success (Maiolie et al. 2002). The egg-to-fry survival estimate was calculated by dividing the estimated number of shoreline-spawned fry in a given year by the estimated number of eggs deposited on the shoreline in the previous year.

Assessment of the water-level management strategy has been stymied by sampling limitations, as well as biological and environmental perturbations. The most significant problem with using the population-level estimate to assess the strategy is that too few mature fish were sampled in annual midwater trawls to reliably estimate shoreline egg deposition. Low abundances of mature kokanee come largely as a result of unprecedented lake trout *Salvelinus* *namaycush* predation in the past decade (Hansen et al. 2008, 2010). Another issue caused by the recent low densities is that the water-level strategy will not enhance shoreline recruitment if there are not enough spawners to take advantage of the added habitat. This argument has justified extending the water-level strategy until the survival estimates can be obtained from years with both a high number of spawners and a high water level. If low densities were not enough, unpredictable flooding during the study also caused unknown entrainment losses of fry and adult kokanee, leading to additional uncertainty in one of the annual survival estimates (Maiolie et al. 2002). Given the limitations of the current assessment method, it is clear that the water-level strategy needs to be tested more directly and with a method that does not rely on spawner density or environmental stability.

A direct evaluation of the water-level hypothesis is critical for better understanding kokanee spawning ecology in LPO and has broad implications for many reservoirs and regulated lakes. For stakeholders, the evaluation is crucial for reconciling the demand for hydropower with the potential to help recover a long depressed kokanee population. For regulated lakes and reservoirs generally, the *in situ* study provides an opportunity to evaluate the potential for anthropogenic water-level regimes to reduce spawning habitat quality and alter fish population dynamics. Furthermore, system-wide assessments of survival–habitat relationships are uncommon for any species and thus can greatly inform the current understanding of kokanee spawning behaviour and habitat requirements (Smokorowski & Pratt 2007). The goal of this research was to directly test for the theorised survival benefit provided by a higher winter water level using a comprehensive *in situ* study. Additional objectives of the study were to inventory current and potential spawning habitats in the lake, describe the relationship between survival and habitat variables at multiple scales and evaluate the contention that shoreline spawning habitat is limited. The water-level hypothesis would predict higher survival above versus below 625.1 m according to differences in substrate composition. Also, if spawning habitat in LPO is as limited as the water-level hypothesis suggests, then intragravel survival should be higher in areas within the current spawning distribution than at random locations throughout the lake.

Methods

The *in situ* incubation study was carried out in two phases. In the first phase, a habitat survey was conducted to map shoreline reaches where incubation boxes could be buried. After samplable reaches were identified, they were further classified by kokanee spawning activity. During the second phase of the study, incubation sites were randomly assigned within the sampling frame and intragravel survival was evaluated in relation to habitat characteristics.

The sampling frame was defined by excluding reaches of shoreline where boxes could not be buried consistently or where kokanee spawning was implausible. Criteria were established to determine what portions of shoreline were to be excluded. Sites were excluded from the sampling frame if they contained predominantly (i) macrophytes, (ii) bedrock or (iii) homogenous cobbles greater larger than 127 mm in diameter (i.e., larger than what spawners of average length would be expected to move; Kondolf et al. 1993). Inclusion in the sampling frame was not based on an opinion about habitat quality, but instead was concerned with the ability to bury boxes as consistently as possible among sites. The Clark Fork and Pack river deltas were excluded from the survey because their shallow depth restricted boat access and because *O. nerka* are not known to spawn in mudflat habitat (Burgner 1991).

Following exclusion of unsampleable areas, the remaining shoreline was divided into one of three nonoverlapping strata: current, historic or unused. Current spawning reaches were defined as areas where spawners had been observed at least twice in the last 15 years during lake-wide spawning surveys conducted by IDFG (Wahl et al. 2011). The definition of current spawning sites was liberal because recent low densities have likely reduced the spatial distribution of spawners detected in shoreline surveys. Historic spawning reaches were defined as areas where kokanee spawners have been sighted, but not in the previous 15 years. Descriptions of spawning and distribution maps from the 1950s were used to delineate historic spawning areas (Jeppson 1953, 1955). The remainder of the samplable shoreline was considered unused.

Incubation sites were selected using a stratified random design, which allowed for lake-wide generalisation about substrate and survival conditions (Thompson 2012). Potential incubation sites consisted of 20-m reaches within the sampling frame. Sixty incubation sites were randomly selected for the study; boxes within sites were regarded as clusters. Half of the sites were allocated to unused shoreline reaches, and remaining sites were proportionally allocated between current and historic spawning reaches. Allocation proportions were defined in the interest of adequately testing the water-level hypothesis. Simple random sampling of all shoreline areas would not necessarily represent the effect of water level on the current spawning distribution, because so little of the total shoreline is currently used for spawning.

Alternatively, if sites were only placed in current spawning reaches, then the study would have ignored potential for a higher water level to enhance previously unused habitats. Each site contained three pairs of egg boxes that were spaced 10 m apart. Divers used stadia rods to identify the 625.1 m elevation line and buried egg boxes 0.5 m above and 0.5 m below that depth contour, measured along the substrate surface.

Whitlock–Vibert egg boxes were buried in a manner that would simulate natural kokanee redds. Egg boxes are commonly used to simulate egg pockets created by salmon and trout species (Reiser & White 1988; Argent & Flebbe 1999; Fincel et al. 2009). In this study, egg boxes were used to measure survival from fertilisation to the preemergent stage (i.e., after hatching but before fry emergence). Fertilised kokanee eggs were obtained by combining gametes from multiple donors that were captured at a weir on Granite Creek, LPO. All egg handling was conducted within 48 h postfertilisation to avoid shock during the sensitive period of egg development (Piper et al. 1982). Fifty live kokanee eggs were loosely placed into the upper chamber of Whitlock–Vibert egg boxes along with clean 9.5-mm-diameter gravel (Fincel et al. 2009). Gravel was added to the egg chamber to reduce contact between individual eggs and prevent the spread of fungus (Whitlock 1979). Egg boxes were then placed in 1-mm mesh bags and sealed with cable ties. The mesh bag prevented hatched embryos from leaving the area surrounding the box so that they could be counted (Garrett & Bennett 1996; Fincel et al. 2009). Egg boxes were buried to a depth of approximately 5 cm to simulate natural kokanee redds (Scott & Crossman 1973; Steen & Quinn 1999). Mortality associated with egg box loading and burial was assessed by burying additional ‘handling mortality’ egg boxes adjacent to sites that were retrieved in 2–3 days. A total of 16 handling mortality boxes were buried, representing different batches of eggs, burial days and areas of the lake.

Habitat variables were measured at the box and site levels. Box-level variables included dissolved oxygen (DO) and substrate composition. Dissolved oxygen was measured using monitoring stakes placed at each egg box location. Monitoring stakes consisted of 254-mm galvanised nails with vinyl tubing (4.76 mm inner diameter) attached. The tubing was plugged at the lower end and contained 1-mm perforations in the bottom 5 cm. Stakes were driven into the substrate beside boxes and perforations positioned at the depth of egg box. Intragravel water samples were then drawn from monitoring stakes by divers using 70-ml syringes. Dissolved oxygen was measured by placing the probe of an electrode-based DO meter (YSI Instruments, Yellow Springs, OH, USA, Pro 2030) inside the syringe and gently agitating. Dissolved oxygen was sampled twice during the study, once halfway through incubation and again immediately prior to retrieval of egg boxes. The minimum DO measured at a given box location was later used as a predictor in the survival model. Substrate was sampled at every box location by scooping material to a depth of 8 cm using an aluminium cylinder (140 mm diameter × 165 mm height). The cylinder was capped immediately after substrate was sampled underwater to avoid loss of fine sediments. Substrate samples were dried in an oven and sorted among 10 size categories using the following sieve sizes: 50.8, 25.4, 12.7, 9.5, 6.35, 4.76, 1.7, 0.85 and 0.42 mm (Tappel & Bjornn 1983). Substrate size distributions were summarised using median particle diameter (D_{50}), which was used as predictor in the intragravel survival model (Kondolf et al. 2008).

Site-level variables included water temperature, wave disturbance and presence or absence of groundwater flow. Water temperature was evaluated with 14 thermographs that were strategically spaced at sites throughout the lake. Thermograph data were used to calculate maximum and minimum water temperature, and cumulative daily temperature (°C). Temperature information was not included as a predictor in the survival model because not every site received a thermograph, but was used to identify any anomalies that might interfere with the study. Wave disturbance was measured indirectly at incubation sites by placing a line of crushed limestone perpendicular to the shoreline between two of the pairs of boxes. The ‘white line’ was put in place at the time when boxes were buried and extended across the depth contour from 0.1 to 3.0 m of depth. At the end of the study, the depth to which the line had been erased was recorded and used as an index of wave disturbance. A common white line was used to assess wave disturbance at adjacent sites. Groundwater was measured in the summer immediately following the study after the water level had risen by approximately 3 m. The presence or absence of groundwater influence was assessed by measuring the difference in head pressure between intragravel and surface water using a probe and clear vinyl tubing (Baxter et al. 2003). At each site, the probe was inserted within 5 m of each egg box location. Water displacement above or below the surface water level indicated upwelling or downwelling, respectively (Geist & Dauble 1998; Mull & Wilzbach 2007). Groundwater probes and seepage metres can fail to detect flow at a location due to a high degree of spatial heterogeneity in hydraulic conductivity (Shaw & Prepas 1990); thus, groundwater influence was considered to be detected at a site if at least one of the box locations had >2.5 cm of displacement in the tubing (Hall & Wissmar 2004).

Design-based generalised linear models were used to compare substrate size distributions above and below the 625.1 m elevation line and to evaluate the effect of habitat variables on intragravel survival (Lumley 2010). Design-based regression methods incorporate the sampling design (e.g., strata, clusters) and information about the population of interest (e.g., sampling fraction) into the estimation of parameters, standard errors and test statistics (Hosmer et al. 2013). The effect of variables are tested and interpreted within this framework using adjusted Wald *F*-tests and confidence intervals. A multinomial logit model was used to test the effect of box position (i.e., above or below 625.1 m) on the proportion of particle weights in 10 substrate size categories (Agresti 2013). A logistic regression model was used to evaluate the effect of habitat variables and box position on intragravel survival. Main effects that were tested included box position, D_{50}, DO, wave disturbance and groundwater influence. Two-way interactions included $D_{50} \times$ groundwater, position $\times D_{50}$, position × disturbance and position × groundwater. The effect of habitat variables was described using odds ratios, which are a measure of effect size. Odds ratios are the exponential function of parameter estimates, interpreted as the multiplicative effect of a categorical variable or a one unit change in a continuous variable on the odds of the response. Goodness of fit was assessed using adjusted global *F*-tests, plots of standardised residuals and leave-one-out cross-validation (Roberts et al. 1987; Archer et al. 2007).

Higher survival among upper boxes alone would not provide evidence supporting the water-level hypothesis, because survival could be linked to depth and not substrate conditions. Rather, the water-level management hypothesis was considered to be supported by the model if there were significant and positive main effects for box position above and below 625.1 m elevation line, and D_{50}. Significantly, similar survival between current and unused shoreline sites, based on a design-adjusted *t*-test, would provide evidence that suitable shoreline spawning habitat is not physically limited in LPO.

Results

A relatively small proportion of the total shoreline of LPO was included in the sampling frame, because most of the shoreline was classified as unsampleable. Approximately 36 km of the 160 km shoreline was included in the sampling frame. Within the frame, approximately 6 km of shoreline was classified as current and 2 km as historic spawning reaches; the remaining 28 km was classified as unused (Table 1). Thirty sites were randomly allocated to unused shoreline reaches; 22 sites were randomly allocated to current spawning reaches and eight to historic spawning reaches. Shoreline reaches of all strata were fragmented in the main body of the lake because boxes could only be buried on small (<100 m long) shelf-like beaches (Fig. 1). Unused sites were evenly distributed throughout much of the lake, whereas the majority of current spawning sites were located in the southern portion of LPO. Historic spawning sites were almost evenly divided among the extreme north and south of the lake.

Table 1. Summary of current, historic and unused shoreline reaches in Lake Pend Oreille, ID, USA.

Strata	Total length (m)	Number of sampling units	Incubation sites
Current	6115	277	22 (21)
Historic	2128	109	8 (8)
Unused	28,099	1281	30 (29)

Shoreline reaches were divided into 20-m shoreline segments, from which incubation sites were selected at random. Reaches were delineated using historical spawning records and a lake-wide habitat survey that was conducted in the fall of 2012. The number in parenthesis indicates the number of sites that were included in the final analysis, after accounting for unrecoverable boxes.

Egg boxes were recovered from nearly every site, and handling mortality was minor. Egg boxes were planted between 26 November and 7 December 2012 and were retrieved between 22 April and 2 May 2013. Dissolved oxygen was measured midway through incubation between 25 February and 1 March 2013. One of the random sites and one of the current spawning sites were excluded from the analysis, because egg boxes were not recovered. Three egg boxes among the remaining 58 sites were also excluded from the analysis because DO samples were not obtained from monitoring stakes during either of the attempts. Survival of handling mortality boxes averaged 92 ± 5% (±SE) and was ignored in the intragravel survival analysis.

Habitat characteristics varied considerably within strata and among shoreline areas. Lake-wide water temperature during incubation remained between 1 and 8 °C. Cumulative degree days varied from 525 to 635, with the lowest number at the most northwesterly thermograph and the highest number at the most easterly site. The depth of wave disturbance, adjusted for water-level change, varied from 0.1 to 1.5 m. Unsurprisingly, sites located in bays had substantially less wave disturbance than areas on the main body of the lake. Downwelling was the only type of groundwater influence detected and was found at nine sites: two of the unused sites (7%), two of the historic spawning sites (25%) and five of the current spawning sites (24%).

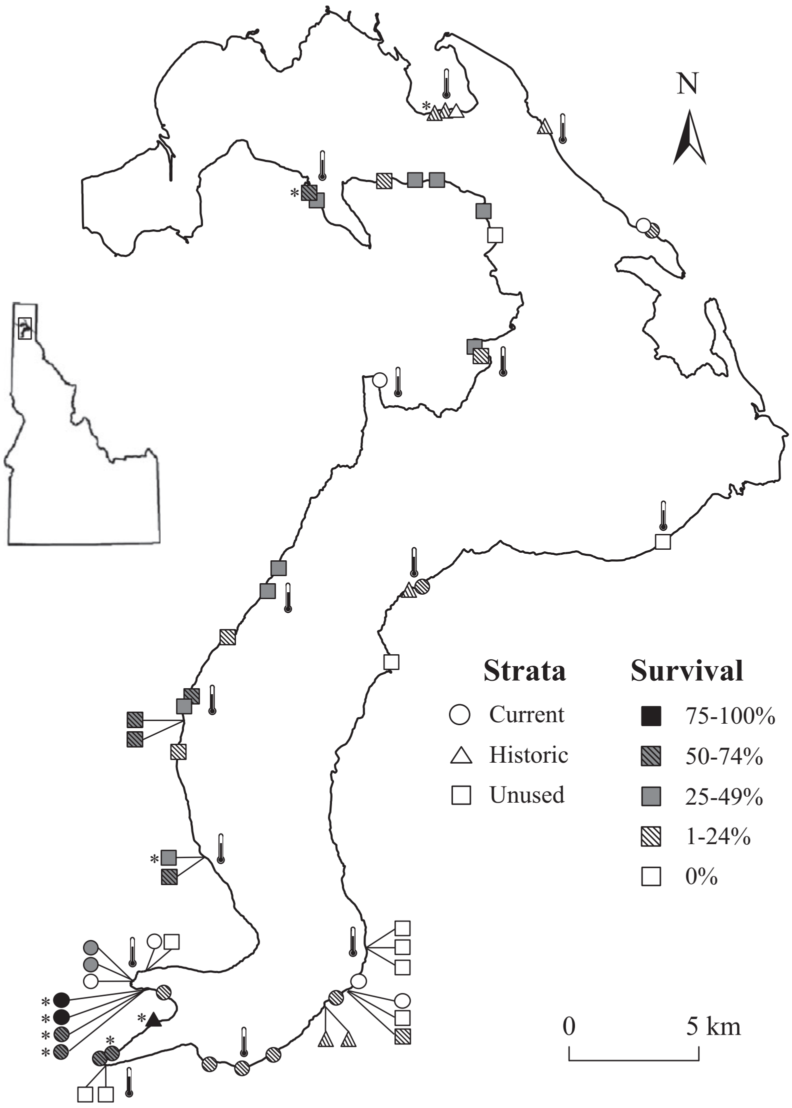

Fig. 1. Map of Lake Pend Oreille, ID, USA. Asterisks denote sites where downwelling was detected, and thermometers denote thermograph locations.

Substrate size distributions varied considerably among sites but not between box positions within sites. The multinomial logit substrate model revealed that the relative frequency of particle sizes did not vary between box positions ($F = 1.08$, d.f. = 9, 46, P-value = 0.40). Substrate size distributions also showed considerable overlap in the middle size categories (2–25 mm diameter; Fig. 2). Unused shoreline areas contained more sites with higher proportions of particles <2 mm than the other two strata. Substrate composition also did not appear related to DO at box locations, with the exception of those largely composed of particles <2 mm (Fig. 2).

Kokanee intragravel survival varied considerably among strata and areas of the lake but not within sites. Survival among egg boxes varied from 0% to 94%, and site-level mean survival varied from 0% to 81%. Intragravel survival observed at some sites in the study was considerably higher than typical population-level estimates for sockeye salmon (Bradford 1995). Survival appeared to be higher at sites on the western shore of the lake compared to that on the eastern shore (Fig. 1). All three of the sites that had survival >75% were influenced by downwelling and located in LPO's two southern bays. Sites located in the south-eastern corner of the lake experienced relatively poor survival, regardless of strata. There were a number of sites on the western shore of the lake with relatively poor survival amid areas with considerably higher survival.

Although the intragravel survival model did not support the hypothesis behind the water-level strategy, it provided other insights. The lack of any significant interaction indicated that survival responses to box position were unaffected by D_{50} and site-level variables (Table 2). As for main effects, box position, D_{50}, and the depth of wave disturbance were not significant predictors of egg survival (Table 2; Fig. 3).

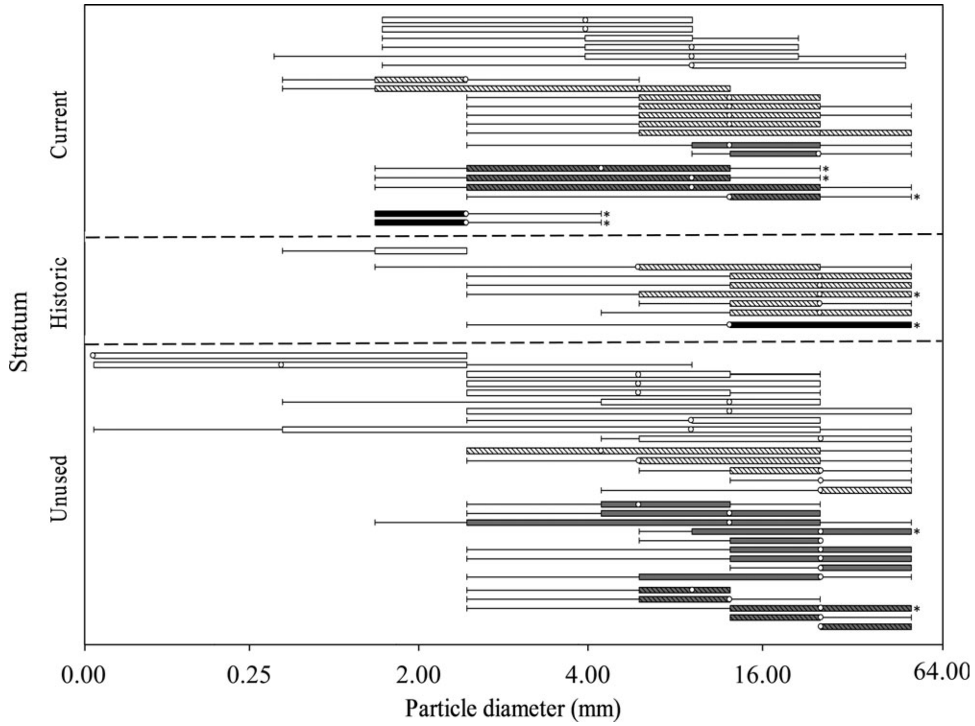

Fig. 2. Box plots of particle size distributions for 58 substrate samples among current, historic and unused shoreline locations in Lake Pend Oreille, ID, USA. Given the lack of box position effect, substrate size distributions were best summarised by pooling particle weights within size categories at each site. Shading and patterns indicate five different intragravel survival levels: 0% (□), between 1% and 25% (▧), between 26% and 50% (▩), between 51% and 75% (▨), between 76% and 100% (■). White circles within box plots symbolise size categories containing the median particle diameter. Asterisks denote incubation sites where downwelling was detected.

Survival was positively related to minimum DO and the presence of downwelling at a given site. All but two of the egg boxes with 0% survival also had minimum DO that was <4.0 mg·l^{-1}, suggesting a 4.0 mg·l^{-1} minimum survival threshold. Substrate composition was generally a poor predictor of survival in incubation at all sites, except for those with the largest proportions of fine sediment. All egg boxes with substrate distributions entirely below 4.0 mm also had minimum DO below 4.0 mg·l^{-1} and 0% survival (Fig. 2). The presence of downwelling had a significant effect on preemergent survival. On average, the odds of an egg surviving to the preemergent stage were more than three times greater for sites in downwelling areas than in sites without downwelling (Fig. 3). The positive effect was most pronounced at current spawning reaches. Not only was the water-level strategy not supported, but spawning habitat in LPO also did not appear to be physically limited, as mean survival at unused (0.21 ± 0.04) sites did not differ significantly from that of current sites (0.27 ± 0.06; $t = -0.82$, d.f. = 47, P-value = 0.41).

Table 2. Parameter estimates for explanatory variables in a design-based logistic regression model used to assess kokanee shoreline incubation success at 58 randomly selected shoreline spawning sites during winter 2012–2013 in Lake Pend Oreille, ID, USA.

Variable	Coefficient	SE	F	d.f.	P
Main effects					
Position	0.497	0.359	1.93	1, 46	0.172
D_{50}	0.002	0.009	0.06	1, 46	0.804
Dissolved oxygen	0.202	0.044	21.32	1, 46	<0.001
Disturbance	−0.184	0.434	0.18	1, 46	0.673
Downwelling	1.152	0.538	4.58	1, 46	0.038
Two-way interactions					
D_{50} × downwelling	−0.014	0.010	2.14	1, 46	0.150
Position × D_{50}	0.001	0.007	1.01	1, 46	0.928
Position × downwelling	−0.312	0.325	0.92	1, 46	0.342
Position × disturbance	−0.235	0.294	1.64	1, 46	0.430

Variables include: position, whether incubation boxes were buried above or below the 625.1-m contour; D_{50}, the median particle diameter (mm) of substrate collected at each box location; DO, the minimum dissolved oxygen (mg·l^{-1}) recorded at the egg box during incubation; disturbance, an index of depth of wave action at each site (decimetre); and whether downwelling was detected at a site.

Discussion

The proposition that kokanee in LPO benefit from a higher water level was not supported by the *in situ* study because many of the premises of the water-level hypothesis were not substantiated. Not only was substrate composition unrelated to kokanee survival, but substrate composition was not different between box positions, suggesting that higher water levels do

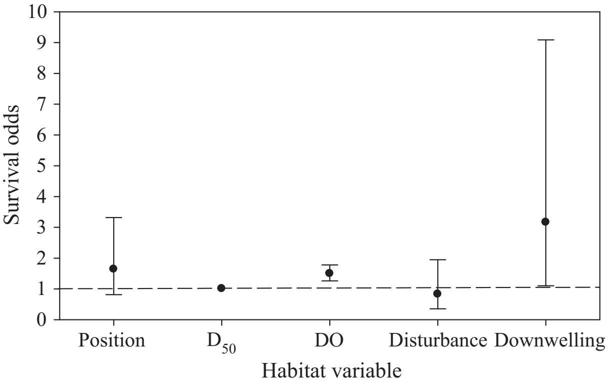

Fig. 3. Odds ratio estimates for habitat variables measured in an *in situ* kokanee incubation study conducted during winter 2012–2013 at randomly selected shoreline locations in Lake Pend Oreille, ID, USA. Survival odds describe the multiplicative effect of a categorical variable or a one unit increase in the value of a continuous predictor on the odds that a kokanee embryo will survive incubation. Variables include position, whether incubation boxes were buried above or below the 30 year low water-level contour (625.1 m); D_{50}, the median particle diameter (mm) of substrate collected at each box location, DO, the minimum dissolved oxygen recorded at the egg box during incubation; disturbance, an index of depth of wave action at each site (decimetres); and whether downwelling was detected at a site. To aid in visualisation, the DO odds ratio estimate represents a two unit increase rather than a one unit increase in $mg{\cdot}l^{-1}$. Error bars depict Wald 95% confidence intervals; overlap with the horizontal line at 1.0 describes nonsignificant effects on intragravel survival.

not even change the quality of available habitat. The second major challenge to the hypothesis was that it implicitly assumes that if suitable spawning habitat is made available, kokanee will use it for spawning. However, the *in situ* study showed that intragravel survival was variable across sites in current spawning areas and that there was ample habitat outside the current distribution (Fig. 1).

The findings of this study by no means diminish the general importance of water levels for shaping physical habitat characteristics and affecting fish and invertebrate communities. Indeed, complex mechanisms relating water-level and reproduction have been confirmed using similar *in situ* methods (Fudge & Bodaly 1984; Gafny et al. 1992). Furthermore, the limited temporal scope of the *in situ* study should be acknowledged. The work presented here only confirms that water-level increases do not enhance kokanee survival by providing better habitat, not that artificial water-level regimes in LPO have never affected shoreline habitat quality. Habitat alterations due to water-level regime changes often occur over long temporal scales (Hofmann et al. 2008), and water-level regime changes can have lasting effects on shoreline habitat quality (Hecky et al. 1984; Lorang et al. 1993). Reductions to the amplitude of water-level fluctuations and the lengthened duration of full pool in LPO may have gradually changed shoreline substrate conditions to the extent that minor increases in water level provide no additional benefit. Historical habitat and recruitment data would be helpful for evaluating the extent to which water level might have mattered in the past. Unfortunately, such data are unavailable, and even if they were, it would not change the fact that the water-level strategy does not appear to significantly benefit the intragravel survival of kokanee.

An additional objective of the *in situ* study was to evaluate the contention that spawning habitat is limited in LPO. Habitat did not appear to be physically limited based on the fact that kokanee survival was just as high in areas where kokanee currently spawn as in unused areas. However, limitations in how the study was designed and behavioural considerations make the contention difficult to judge. Study design limitations are related to how the sampling frame was defined and which habitat variables were measured. First, the ability to bury egg boxes was a requirement for inclusion in the sample frame of this study, but is not necessarily a requirement of shoreline spawners. Shore-spawning *O. nerka* are highly plastic and have been known to spawn at depths of at least 20 m and also to broadcast eggs over immovable substrate (Kerns & Donaldson 1968; Hassemer & Rieman 1981). Plasticity in relation to the type of substrate that may be used for spawning may have caused the sampling design to overlook productive spawning habitats composed of larger substrate, thus biasing survival estimates. On the other hand, spawning plasticity related to depth implies that kokanee have substantially more habitat available for spawning than just the shallowest few metres of the shoreline, as the water-level management strategy would suggest. A second limitation of this study was that embeddedness of substrates was not measured along with particle size distribution and D_{50}. Kokanee cannot bury eggs in habitats where substrate is tightly packed (Kondolf et al. 2008). Overlooking this fact may explain why areas deemed suitable by the *in situ* study may not have been selected by kokanee in the past. However, divers reported that unused sites generally required the same amount of digging effort to bury boxes as sites within the current spawning distribution. Even with these inherent limitations, the manner in which habitat limitation was assessed still corresponds to an oversimplification of how kokanee select spawning habitat. After all, it is unlikely that kokanee survey the entire shoreline and select redd locations that meet microhabitat requirements. Habitat selection is driven in part by natal homing behaviours and other social factors (Hendry et al. 2001a; Rich et al. 2006).

Kokanee did not appear to spawn in only the most productive habitats, but were clustered in the southern portion of the lake where they experienced variable incubation success. Clustering of kokanee in southern LPO is likely the result of strong natal homing tendencies that shore-spawning *O. nerka* are known to exhibit (Hendry et al. 1995; Stewart et al. 2003). Social factors such as conspecific cueing and competition may also contribute to the distribution of spawning (Parenskiy 1990; Hendry et al. 2001b). Redds in LPO are often difficult to distinguish individually because groups of spawners often deposit their eggs together in gravel patches, from which fine sediment has been swept. This behaviour may reflect a preference for spawning in areas that are occupied by other spawners, which has been documented among other shore-spawning salmonid species (Curry & Noakes 1995; Essington et al. 1998). Another factor that may explain why spawning is concentrated in the southern end of the lake is related to habitat fragmentation. Research on the habitat requirements for stream-spawning salmonids has revealed the importance of patch size and connectivity for predicting where redds are likely to be located (Isaak et al. 2007). Fragmented beach habitats in LPO, although suitable, may not be used because of their isolation and small patch size.

The presence of downwelling in Scenic and Idlewilde bays could be another explanation for why spawners are drawn to the southern end of the lake (Lapointe 2012). The higher prevalence of downwelling in the southern end of LPO is likely due to the fact that this is a recharge area for the Spokane Valley Rathdrum Prairie Aquifer (Hsieh et al. 2007). Groundwater flow has been shown to be preferentially selected by *O. nerka* and to enhance survival (Garrett et al. 1998). Hall & Wissmar (2004) found that sockeye salmon spawning in backwaters not only selected redd locations influenced by groundwater, but that when they spawned in upwelling areas, they were less selective about substrate composition and detritus. Shoreline spawner surveys conducted over the last 20 years in LPO have documented the highest density of spawners in Scenic and Idlewilde bays, near where downwelling was detected in the *in situ* study (Wahl et al. 2011). Although confirmatory evidence is needed, the mechanism driving spawning site selection in LPO could be similar to the case described by Curry & Noakes (1995) where the distribution of brook trout *Salvelinus fontinalis* shoreline redds was structured by competition for areas influenced by groundwater.

Associated with the fact that kokanee more commonly spawn in southern LPO is the question of why kokanee currently spawn in the south-eastern shore of LPO, which yields poor survival. It is conceivable that less fit spawners radiate from preferred downwelling habitat into nearby and lower quality habitat. Another, more plausible, explanation is that spawners in the south-eastern shore might be falling into an ecological trap. Apart from downwelling at some of the sites, none of the other habitat variables in the *in situ* study appeared to explain site-level differences in survival, suggesting that one or more critical explanatory variables were missing from the analysis. Many of the sites on the south-eastern shore of LPO were hypoxic ($<4.0\ \text{mg}\cdot\text{l}^{-1}$), but there was also a considerable decrease in DO between the measurements taken midway through incubation and those at the end of the study. Mean DO at sites in the south-eastern portion of the lake decreased approximately twice as much as sites in the remainder of the lake. Spawners in the south-eastern portion of LPO may construct redds in areas based on habitat cues (i.e., substrate sizes), only to have their eggs suffer relatively high mortality from hypoxia during incubation. A number of variables affect the temporal availability of DO in the incubation environments, namely temperature, fine sediment accumulation and biochemical oxygen demand (Greig et al. 2007; Sear et al. 2012). Relatively similar temperature among sites in southern LPO and the poor predictive ability of substrate composition suggest a biochemical explanation for low DO and survival in that area.

Although further research is required for describing the relative importance of behavioural and social factors on habitat selection in LPO and similar habitats, several lessons can be gleaned from this study that are relevant to other systems. Shoreline habitat surveys should not take substrate characteristics at face value because of unseen influences from groundwater or DO concentration. The majority of kokanee in LPO spawn in habitats in Scenic Bay where substrate appears unsuitable, but intragravel survival is relatively high. Alternatively, substrate conditions in the south-eastern portion of the lake appeared suitable, but had poor DO and survival conditions. Inferences from the *in situ* study in LPO echo some of the recent revelations in the stream-spawning literature, which have emphasised the importance of placing spawner–habitat relationships into a spatial and behavioural context, rather than relying on fine-scale habitat characteristics to describe redd distribution patterns (Fausch et al. 2002; Anderson et al. 2006; Torgersen et al. 2012). The habitat requirements of salmonids that spawn on shorelines and in atypical habitats have not been described in nearly as much detail as those that spawn in streams. Understanding the social and behavioural factors that contribute to site selection is integral for a useful understanding of shore-spawning habitat selection and incubation success.

The study presented here demonstrates the value of comprehensive *in situ* studies for testing hypotheses related to complex habitat issues and for supplying valuable ecological information. In the face of potentially harmful hydrologic modification, natural resource agencies often must rely on correlative fish–habitat relationships and indirect assessments (Smokorowski & Pratt 2007). Limited data under such circumstances warrant a precautionary approach in attempting mitigation efforts and responding to habitat alterations. In addition to testing locally significant hypotheses, *in situ* studies allow opportunities to refine broader ecological theory. The study in LPO tested an important hypothesis for management while adding to the current knowledge of kokanee spawning ecology and the consequences of altered hydrologic regimes.

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