KOKANEE SPAWNING ECOLOGY AND RECRUITMENT RESPONSE TO WATER LEVEL MANAGEMENT IN LAKE PEND OREILLE, IDAHO

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ABSTRACT

Kokanee were the centerpiece of a productive commercial and recreational fishery in Lake Pend Oreille, Idaho for decades, before declining substantially in the late 1960s. The decline has been attributed to poor recruitment caused by a reduction in quality shoreline spawning habitat, which was linked to a hydropower-related shift to a lower minimum water level. This thesis evaluated the effects of habitat characteristics and water level on shore-spawning kokanee incubation success using a laboratory experiment, two *in situ* incubation studies, and a stock assessment model. All three incubation studies found that substrate size composition was a poor predictor of survival. The *in situ* studies found that kokanee eggs deposited at depths >10 m were viable and intragravel survival appeared to be enhanced by downwelling in habitat that was ostensibly poor. The egg box investigations and stock assessment model together suggested that water-level management is not an effective strategy for increasing the recruitment of shore-spawning kokanee.

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DEDICATION

This thesis is dedicated to my exceedingly loving and supportive family.

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CHAPTER 1: GENERAL INTRODUCTION

Lake Pend Oreille (LPO) is the largest and deepest lake in Idaho and the fifth deepest lake in North America. Located in the Idaho panhandle, the lake contains one of the most valued fisheries in the state, generating approximately US$18 million annually for the local economy (Idaho 2003). The predominant fish species in the system is kokanee *Oncorhynchus nerka*, which functions as both a sport fish and a prey species (Wydoski and Bennett 1981; Simpson and Wallace 1982). The kokanee population in LPO provided the state of Idaho with its largest recreational fishery in the 1960s and 1970s, and a sustainable commercial fishery for three decades (1945-1973). Kokanee also serve as prey for large rainbow trout *O. mykiss* and bull trout *Salvelinus confluentus*; in fact, LPO produced the previous world record rainbow trout and current world record bull trout (Wydoski and Bennett 1981; Simpson and Wallace 1982; Paragamian and Bowles 1995).

The system changed dramatically in the late 1960s when kokanee abundance declined by more than 90% from a peak harvest just twelve years prior (Maiolie and Elam 1993). Kokanee have remained in a depressed state (i.e., 30% of their historic abundance) since the early 1980s despite intensive stocking, closure of the fishery, and numerous management actions by the Idaho Department of Fish and Game (IDFG; Maiolie and Elam 1993; Paragamian and Ellis 1994; Paragamian and Bowles 1995). In the last twenty years, kokanee recovery has become increasingly important due to the species' role as the principle prey for threatened bull trout (Vidergar 2000; Neraas and Spruell 2001). Since the late 1990s, IDFG has used water-level management in an attempt to bolster recruitment of shoreline spawning kokanee. Although IDFG has been working under the assumption that water levels are related to kokanee recruitment (Maiolie and Elam 1993), the mechanisms associated with the hypothesis are untested and the relationship between water levels and kokanee recruitment remains uncertain. Thus, there is a need to better understand kokanee shoreline spawning ecology and examine the hypothesized linkage between water level and kokanee abundance.

Kokanee exhibit highly plastic life history patterns and are an important sport and prey species in many lake and reservoir systems (Nelson 1968; Wydoski and Bennett 1981; Burgner 1991). The species *O. nerka* is composed of two forms: sockeye salmon are the anadromous form and kokanee are the non-anadromous form. Kokanee occupy pelagic habitats in lakes and feed strictly on zooplankton their entire lives, while sockeye salmon spend their early life history in lakes and rivers and then migrate to the ocean (Foerster 1968; Burgner 1991). Kokanee are significantly smaller, earlier maturing, and less fecund than sockeye salmon (Ricker 1972). Both sockeye salmon and kokanee are semelparous and bury their eggs in gravel in streams, rivers, and lakeshores (Woodey 1965; Foerster 1968; Scott and Crossman 1973; Hassemer 1984). *O. nerka* deposit their eggs in impressions made in gravel for the purpose of protecting eggs during incubation (Burgner 1991), but are also known to broadcast eggs over coarse substrates (Kerns and Donaldson 1968; Hassemer and Rieman 1981). After hatching, kokanee alevins remain in the gravel and absorb their yolk before emergence (Bams 1969).

Spawning sockeye salmon and kokanee populations extend from California to Alaska and west to the Kamchatka Peninsula and Japan, while introduced populations of kokanee occur throughout the United States, South America, Australia, and Scandinavia (Nelson 1968; Burgner 1991; Crawford and Muir 2008). Natural kokanee populations diverged from sockeye salmon in parallel across numerous basins in their distribution, and both forms often exist sympatrically (Foote et al. 1989; Wood and Foote 1990; Beauchamp et al. 1995; Taylor et al. 1996). Kokanee spend their life as lake residents using inflowing rivers, small tributaries, and shorelines for spawning (Vernon 1957; Averett and Espinosa 1968; Foerster 1968; Ricker 1972; Smith et al. 1987). Due to their popularity among anglers and dual role as a sport and prey species, kokanee are commonly stocked in western lakes and reservoirs where they often become the dominant pelagic planktivore (Wydoski and Bennett 1981; McGurk 1999).

Kokanee are not native to LPO, but have become naturalized in the system. The native fish assemblage in LPO consists of bull trout, westslope cutthroat trout *O. clarki lewisi*, northern pikeminnow *Ptychocheilus oregonensis*, mountain whitefish *Prosopium williamsoni*, pygmy whitefish *P. coultreii*, slimy sculpin *Cottus cognatus*, peamouth *Mylocheilus caurinus*, longnose sucker *Catostomus catostomus,* and largescale sucker *C. macrocheilus* (Hoelscher 1993). Kokanee emigrated from Flathead Lake, MT in the 1930s and quickly established a spawning population in LPO. The majority of kokanee in LPO are considered "late-run", spawning between mid-November and late-December in tributaries and on the shoreline of the lake, especially in Scenic and Idlewilde bays (Hassemer 1984). A minor stock of "early-run" kokanee spawn in tributaries of LPO during September. Other nonnative salmonids have also become important fixtures in LPO. Gerrard-strain rainbow trout were intentionally introduced in 1942 from Kootenay Lake, BC, to provide a trophy fishery (Stross 1954; Hansen et al. 2010). Lake trout *Salvelinus namaycush* were introduced in 1925, but remained at low density and had little influence on kokanee in LPO until recently. Between 1950-1970, the kokanee and trout fishery in LPO experienced a "heyday" with annual kokanee harvests regularly exceeding one million fish (Chipps and Bennett 2000) at the same time that LPO was undergoing profound system-wide alterations.

Major alterations to LPO included the construction of multiple dams, the introduction of the macrozooplankton species *Mysis diluviana* (hereafter mysid shrimp), and the initiation of an altered water-level regime for hydropower production. In 1952, Cabinet Gorge Dam and Albeni Falls Dam were constructed on the Clark Fork and Pend Oreille rivers, respectively (Irving 1986; Maiolie and Elam 1993; Paragamian and Bowles 1995). Cabinet Gorge Dam eliminated access of kokanee and other fishes to a large portion of the upstream spawning habitat; however, no evident reductions in the abundance of adfluvial species were observed following construction of the dam (Paragamian and Bowles 1995). The second major alteration occurred from 1966 to 1970 when mysids were introduced in LPO to bolster kokanee production (Rieman and Falter 1981). In many North American lakes, mysids compete with kokanee for zooplankton (Morgan et al. 1978; Lasenby et al. 1986; Nesler and Bergersen 1991). Mysid introduction did not have an apparent effect on kokanee in LPO, although it did trigger changes in species composition and seasonal distribution of the lake's zooplankton community (Rieman and Falter 1981). Changes to the zooplankton community have likely influenced the food availability and potential biomass for kokanee in the system (Rieman 1976; Bowles et al. 1991; Chipps and Bennett 2000). A number of large-scale perturbations pre-dated the decline of kokanee in LPO, but no factor coincided more closely with the decline than the changes in the operation of Albeni Falls Dam (Maiolie and Elam 1993). Albeni Falls Dam is situated on the Pend Oreille River, the lake's only outlet, thereby allowing the water level to be manipulated (Figure 1). In 1966, Albeni Falls Dam began holding the minimum winter lake elevation at a stable and relatively low elevation. In a review of the kokanee decline, Maiolie and Elam (1993) proposed a relationship between the winter water level and recruitment of lakeshore-spawning kokanee. In 1996, IDFG adopted the water-level hypothesis and initiated a water-level management strategy for restoring kokanee to historic abundances.

The water-level management strategy is based on the premise that there is a scarcity of quality spawning gravels available to kokanee that significantly limits recruitment by impairing shoreline intragravel egg and alevin survival (Maiolie and Elam 1993). Prior to dam construction, water level in LPO peaked during spring runoff in May or June, and rapidly fell during the summer to an annual minimum elevation of near 624 m by December. After construction of Albeni Falls Dam, the water in LPO was maintained at a high level throughout the summer and rapidly dropped in the late fall to 625.1 m (Hoelscher 1993). The water-level hypothesis proposed by Maiolie and Elam (1993) stated that when the water level drops in the fall, quality spawning habitat existing above 625.1 m becomes dewatered, thereby relegating lakeshore-spawning kokanee to lower quality habitats. Gravels beneath the 625.1 m water line are not purged of fine sediment by wave action throughout summer and are thought to significantly reduce egg-to-fry (EF) survival and recruitment. The hypothesis suggests that increasing the winter lake elevation will increase the recruitment and abundance of kokanee (Fredericks et al. 1995; Maiolie et al. 2002). Major assumptions of the water-level hypothesis are that the kokanee population in LPO is limited by fry production, intragravel survival is the most significant recruitment bottleneck, and shoreline spawning habitat is limited.

In 1996, IDFG adopted an experimental water-level management strategy to restore kokanee abundance (Maiolie et al. 1999). An agreement was made between IDFG and operators of the Albeni Falls Dam (U.S. Army Corp of Engineers) to test the water-level hypothesis over several years using an experimental framework. The method chosen to evaluate the hypothesis was to alternate between winters with the preexisting 625.1 m minimum elevation and those with an experimentally raised minimum water elevation of 626.4 m, and then evaluate the recruitment response using a back-calculated EF survival estimate. The EF survival estimate is an annual survival percentage calculated by dividing the estimated number of shoreline-origin fry by the estimated potential number of eggs deposited the previous fall (Maiolie et al. 2002).

Although the water-level strategy has continued for sixteen years, the effect of water-level management on kokanee recovery remains equivocal. No definitive recruitment or population increase has been observed, casting uncertainty as to the magnitude of the effect of additional spawning habitat. Some have postulated that the effect has been obscured by major interferences that occurred during the evaluation period, including flood events, total dissolved gas supersaturation, small sample sizes, and unprecedented predation by lake trout (Maiolie et al. 1999, 2002; Wahl et al. 2011). For instance, the lake trout population expanded exponentially in the late 1990s and threatened kokanee extirpation (Hansen 2007). This prompted the closure of the kokanee recreational fishery and the implementation of an intensive and highly successful lake trout removal effort from 2006-present (Maiolie et al. 2002; Hansen et al. 2008, 2010).

Biological and environmental interferences aside, there are additional concerns that the EF survival estimator may be unreliable and that several of the premises of the water-level hypothesis are not supported by spawner observations. The EF survival estimator is composed of sub-estimates that represent a combination of sampling methods including midwater trawling, hydroacoustics, and a weir on one of the lake's tributaries. Each sub-estimate carries additional variability and biases that have not been described previously and could lead to instability in the overall estimate that is produced. Spawner observations, before and since the water-level management strategy began, have been inconsistent with the water-level hypothesis. By far, the highest spawning densities of kokanee occur in Scenic Bay where substrate appears to be unsuitable. In the last five years, sizeable kokanee aggregations have also been observed spawning at depths in excess of 10 m, where they are likely unaffected by water-level fluctuations.

To address these concerns, several investigations were undertaken to inform management of kokanee in LPO. The goal of this research was to improve kokanee recovery efforts in LPO by thoroughly describing kokanee spawning ecology and testing the water-level management hypothesis. The objectives set for accomplishing this goal were to (1) use a laboratory experiment and a fine scale *in situ* incubation study to directly measure the relationship between kokanee EF survival and spawning habitat characteristics, (2) test whether survival is enhanced in the habitat provided by a high water year, and (3) use existing data to evaluate the EF survival estimator and develop alternative methods for measuring the effect of the water-level management strategy on recruitment.

THESIS ORGANIZATION

This thesis is divided into five chapters. Chapter two describes laboratory and *in situ* incubation studies that were conducted during the winter of 2011-2012 and which evaluated the fine-scale habitat requirements of shore-spawning kokanee in LPO. This chapter has been submitted to the *Canadian Journal of Fisheries and Aquatic Sciences* for publication. Chapter three describes a comprehensive *in situ* study designed to directly test for higher survival in the additional habitat provided by a higher water level, and will be submitted to the journal *Ecology of Freshwater Fish*. Chapter four explores issues with the current egg-to-fry survival estimator and presents a model-based assessment method that uses existing data to test the water-level hypothesis. Chapter four also evaluates the effect of stocking on kokanee recruitment. This chapter will be submitted to the journal *Fisheries Management and Ecology*. Chapter five provides general conclusions and recommendations from this work.

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CHAPTER 2: INFLUENCE OF HABITAT CHARACTERISTICS ON SHORE-SPAWNING KOKANEE

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ABSTRACT

Sockeye salmon and kokanee *Oncorhynchus nerka* commonly spawn in both lotic and lentic environments; however, the habitat requirements of shore-spawners are virtually unknown relative to those of stream-spawners. A laboratory experiment and an in situ incubation study were conducted to better understand the influence of habitat characteristics on the shoreline incubation success of kokanee. Substrate size composition was a poor predictor of survival in both the laboratory experiment and in situ study. In the laboratory, fry condition and counts of emerged fry were lowest for the substrate treatment with the highest proportion of fine sediment. In some cases, eggs deposited at depths greater than 10 m had higher survival than those deposited in shallow water. Results of the in situ study suggest that groundwater flow plays an important role in enhancing intragravel survival in habitats generally considered unsuitable for spawning.

INTRODUCTION

The spawning habitat requirements of Pacific salmon *Oncorhynchus* spp. have been studied extensively in lotic systems (Bjornn and Reiser 1991, Kondolf et al. 2008, Sear and DeVries 2008). Decades of laboratory and field investigations have focused on describing the relationship between substrate composition and intragravel survival (Chapman 1988, Kondolf 2000, Jensen et al. 2009); recent investigations have been concerned with interactions between hyporheic flows and redd morphology (Montgomery et al. 1996, Tonina and Buffington 2007, Malcolm et al. 2008). Although many advancements have been made towards understanding intragravel survival of salmonids in lotic systems, knowledge of habitat requirements for shore-spawning ecotypes is considerably less developed (Leonetti 1996). This is likely due to the fact that sockeye salmon *Oncorhynchus* *nerka* and its landlocked form, kokanee, is the only member of the genus that commonly spawns on shorelines as well as in streams (Foerster 1968, Burgner 1991). To date, most of the published work on shore-spawning *O. nerka* has been observational (Foerster 1968, Kerns and Donaldson 1968, Hassemer and Rieman 1981, Burgner 1991) with no attempts to simulate shore-spawning conditions in the laboratory and only a small number of in situ incubation studies (Hassemer 1984, Gipson and Hubert 1993, Fincel et al. 2009). A better understanding of shoreline intragravel survival is important for managing *O. nerka* populations because shore-spawning ecotypes contribute greatly to recruitment in many systems (Hassemer 1984, Blair et al. 1993, Jeric 1996). Furthermore, experimental knowledge about what constitutes favorable shoreline spawning habitat is essential for gauging the impacts of anthropogenic alterations to littoral habitats through shoreline development and water-level regulation (Smokorowski and Pratt 2007).

Intragravel survival is controlled by a suite of abiotic factors that are manifest differently in streams and on shorelines (Leonetti 1996, Greig et al. 2007). Interrelated factors that influence survival are dissolved oxygen (DO), temperature, water flow, and substrate composition. Egg-to-fry survival and fry condition are dependent on the delivery of dissolved oxygen to the intragravel environment (Silver et al. 1963, Einum et al. 2002). Temperature determines the oxygen capacity of water and the developmental rate of eggs and sac-fry (Cooper 1965, Greig et al. 2007). Substrate composition influences the amount of water exchanged between surface water and the egg pocket (Greig et al. 2007, Malcolm et al. 2011). The proportion of particles less than 1 mm in diameter is considered to be a particularly important determinant of incubation success for salmonids (Chapman 1988, Jensen et al. 2009). Water flow provided by groundwater can sometimes negate the deleterious effect of fine sediments on survival (Sowden and Power 1985, Garrett et al. 1998). In streams, surface, hyporheic, and groundwater flows supply oxygenated water to egg pockets (Malcolm et al. 2003, Gibbins et al. 2008, Malcolm et al. 2008). The absence of horizontal flow on shorelines changes the relationship between substrate composition and survival, and influences where spawning takes place. Shore-spawners often select habitats with alternative sources of water flow provided by wave action or groundwater (Woodey 1965, Foerster 1968, Lorenz and Eiler 1989, Burger et al. 1995). However, spawning also occurs in areas apparently lacking in supplemental water flow, such as deepwater habitats (Hassemer 1984, Jeric 1996).

Shoreline habitat selection and egg deposition behaviors also differ from those found in streams. Shoreline redds lack the flow-oriented structure of redds in streams (e.g., pit, tailspill; Jeric 1995). Shore-spawners also select a wider array of substrates sizes than *O. nerka* in streams (Hassemer 1984, Kondolf and Wolman 1993). The inability to displace larger particles in some areas has resulted in alternative egg deposition behaviors (Hassemer and Rieman 1981, Kondolf et al. 1993). In some cases, shore-spawned eggs are “broadcast” over large (50-300 mm) immovable substrate rather than buried (Foerster 1968, Kerns and Donaldson 1968, Hassemer and Rieman 1981, Burgner 1991). Lentic environments present additional habitat characteristics for *O. nerka* to select from in terms of depth and shoreline slope, and habitat selection is anything but uniform among lakes and reservoirs. Shore-spawning *O. nerka* select shallow, fine sediment beaches (Woodey 1965, Olsen 1968, Leonetti 1996), rocky island shores (Kerns and Donaldson 1968, Blair and Quinn 1991), and talus slopes with up to 60° angles (Stober et al. 1979, Hassemer 1984). In Lake Coeur d’ Alene, ID, and Flaming Gorge Reservoir, WY-UT, shore-spawning has been observed at depths down to 20 m (Foerster 1968, Hassemer and Rieman 1981, Hassemer 1984, Gipson and Hubert 1993). The diversity of egg deposition behaviors and spawning environments used by *O. nerka* across systems makes habitat assessment challenging and necessitates the evaluation of shore-spawning under a variety of conditions.

Understanding the influence of habitat characteristics on kokanee intragravel survival is of particular importance in Lake Pend Oreille (LPO), ID, because shore-spawners are the most abundant kokanee ecotype and because their recruitment is thought to be limited by habitat availability (Maiolie and Elam 1993, Maiolie 1994). Kokanee in LPO are a popular sport fish that also serve as a prey resource for trophy rainbow trout *O. mykiss* and threatened bull trout *Salvelinus confluentus* (Wydoski and Bennett 1981, Clarke et al. 2005). Kokanee sustained a commercial fishery from 1945-1973 and were the largest recreational fishery in Idaho for more than a decade before declining in the 1970s and remaining in a depressed state. One cause of low kokanee abundance is thought to be winter water-level regime alterations associated with hydropower production at Albeni Falls Dam, located on the lake's outlet (Maiolie and Elam 1993; Figure 1). The hypothesis has been that the minimum winter water level affects kokanee recruitment by influencing shoreline spawning habitat availability. Beginning in the 1960s, operators of the Albeni Falls Dam lowered the water level of LPO to an annual minimum that dewatered shoreline substrate typically used for spawning in the winter months. The lower water level is thought to have relegated spawners to poor-quality habitat (i.e., finer substrate), thereby reducing intragravel survival and ultimately recruitment (Maiolie and Elam 1993).

Managers acted on the water-level hypothesis by altering the water-level regime to provide a higher quality and quantity of habitat for shoreline spawners. Since 1996, water levels have alternated between years of the preexisting lake elevation (625.1 m) and an experimentally raised elevation (626.4 m; Maiolie et al. 2002). The higher water level is intended to restore the band of wave-washed spawning substrate around the lake that kokanee are thought to have spawned in prior to the population decline. The strategy assumes that substrate made available by water-level management produces higher intragravel survival. However, past observations of shore-spawners are not congruent with the water-level management hypothesis. Hassemer (1984) reported that 90% of redds observed in Scenic Bay were constructed in gravels containing high amounts of sand and fine particles. Furthermore, shoreline redd counts from 1972 to 2012 suggest that the majority of shore-spawning occurred in Scenic Bay (Wahl et al. 2011), which is highly developed and dominated by sand substrate (Fincel et al. 2009). Recent underwater videography has also discovered substantial deep-spawning aggregations in Scenic Bay and areas on the southwestern shore of the lake. Deep-spawners are likely unaffected by water-level fluctuations and wave action. The occurrence of spawning in apparently suboptimal habitats and deep areas of LPO calls into question key aspects of the water-level management strategy. Kokanee spawning behavior in LPO also raises broader questions about the role that habitat characteristics, particularly substrate composition and depth, play in regulating intragravel survival of *O. nerka* on shorelines.

The purpose of this research was to further our understanding of shoreline incubation requirements, and in so doing, evaluate several components of the water-level management hypothesis. Specific objectives for this research were to (1) develop a relationship between substrate composition and intragravel survival in a simulated shoreline environment and (2) elucidate habitat characteristics influencing shore-spawning kokanee incubation success in major spawning areas of LPO. The first objective was addressed by completing the first known kokanee incubation experiment designed to simulate shoreline intragravel conditions. The laboratory experiment was intended to describe how the relationship between substrate composition and intragravel survival is manifest under shoreline water flow conditions. For the second objective, an in situ incubation study was conducted to evaluate how habitat conditions at multiple scales influence intragravel survival. The in situ study evaluated aspects of the water-level management strategy by measuring the influence of substrate composition on kokanee survival and by examining the viability of kokanee eggs deposited at depths greater than 5 m.

METHODS

Study area

Lake Pend Oreille is meso-oligotrophic with a surface area of 38,000 ha, a mean depth of 164 m, and 310 km of shoreline (Figure 1). The northern half of the lake is relatively shallow, while much of the southern half is over 300 m deep and contains steep rocky shorelines. The Clark Fork River is the largest tributary of LPO, draining approximately 96% of the lake's watershed (Hoelscher 1993). The lake is affected by two dams constructed in 1952: Cabinet Gorge Dam located on the Clark Fork River and Albeni Falls Dam located on the lake's outlet. Other major tributaries in the system include the Pack River, Trestle Creek, South Gold Creek, and Granite Creek. The timing of stratification in LPO varies temporally and spatially, but the thermocline is typically established by July at a maximum depth of 20 m. In winter, the water column remains aerobic and the water temperature drops below 4°C, but does not freeze (Stross 1954).

Kokanee immigrated to LPO from Flathead Lake, MT, in the 1930s and rapidly became the dominant prey species for large-bodied piscivores (Simpson and Wallace 1982, Waples 1995). Spawning occurs at two time periods during the year, late September (early-run) and November-December (late-run). Early-run kokanee consist of only the stream ecotype and primarily spawn in Granite Creek, South Gold Creek, Trestle Creek, and the Clark Fork River. A portion of the late-run spawners use the same streams as the early-run fish, but most of the late-run fish are thought to spawn in Scenic Bay, Idlewilde Bay, and shelf-like beaches on the southern half of the lake (Maiolie 1994). The Idaho Department of Fish and Game operates a weir on Sullivan Springs, a tributary of Granite Creek, to supply eggs for annual stocking efforts in the lake.

Egg boxes

Whitlock-Vibert egg boxes were used in both the laboratory experiment and in situ study to simulate kokanee redds (Whitlock 1979, Garrett and Bennett 1996). The boxes are artificial salmonid egg pockets composed of an upper incubation chamber and a lower nursery chamber (Whitlock 1979). Whitlock-Vibert boxes have been used in numerous laboratory and in situ kokanee incubation studies (Hassemer 1984, Garrett et al. 1998, Fincel et al. 2009), although methods of deployment vary considerably (i.e., number of eggs per box, inclusion of gravel, open or closed; Reiser and White 1983, Tappel and Bjornn 1983, Reiser and White 1988, Garrett et al. 1998). For this study, 50 fertilized kokanee eggs were loaded in the upper chamber along with 9.5 mm gravel (Irving and Bjornn 1984, Fincel et al. 2009). Egg boxes were retrieved at two points during incubation to evaluate survival to the eyed and preemergent stages of development. The eyed stage begins when an embryo’s eyes are visible through the chorion of the egg and lasts until hatching. The preemergent stage is the period after hatching when sac-fry remain in gravel absorbing their yolk sac. Egg boxes used to assess preemergent survival were wrapped in 1 mm nitex mesh to prevent sac-fry from escaping (Fincel et al. 2009, Garrett and Bennett 1996).

Laboratory

The laboratory experiment was conducted in experimental incubation troughs located at the University of Idaho to simulate winter incubation conditions in LPO. Water movement in troughs provided surface-to-surface flow, rather than horizontal movement through gravel common in many stream-based experiments (Tappel and Bjornn 1983; Reiser and White 1988). The intention of the trough design was to produce a gradient of surface and intragravel water exchange rates, produced by differing substrate permeabilities across treatments (Greig et al. 2007). Water was supplied to each of 24 experimental troughs via a 1.5 horsepower pump and drained to a reservoir containing a chiller and air stones, which recirculated water. Chilled, dechlorinated make-up water was added to the reservoir through an aeration column at a rate of 5 $L \cdot min^{-1}$ to maintain DO levels and reduce fungal growth (Waterstrat 1997). Water inflow to each trough was supplied by three vinyl tubing “dribblers” (4.76 mm inner diameter) centered over the trough and distributed evenly across its length. Dribblers were suspended approximately 3 cm above the water’s surface in each trough. Valves in the tubing network were adjusted so that 1.1 $L \cdot min^{-1}$ of water was evenly distributed across dribblers. A standpipe in each trough maintained the water depth at 25 cm, providing a distance of approximately 8 cm between the water and substrate surface. Water temperature in the system was maintained at 4-8°C and surface-water DO was at saturation (~9-12 $mg \cdot L^{-1}$) to match the overwinter conditions in LPO (Stross 1954, Hassemer 1984). A thermograph (Onset, Cape Cod, MA, USA) was placed in the trough located the farthest from the pump (i.e., warmest trough) to monitor temperature throughout the experiment.

Substrate treatments were based on those used in the only known stream-based kokanee laboratory incubation experiment (Irving and Bjornn 1984). The authors related kokanee intragravel survival to the proportion of particles less than two size classes of spawning gravel (i.e., 9.5 mm and 0.85 mm), based on methods described in Tappel and Bjornn (1983). Eight of the sixteen gravel treatments used by Tappel and Bjornn (1983) and Irving and Bjornn (1984) were selected for this experiment in the interest of producing a variety of survival responses under sample size constraints. The exact treatments described by Irving and Bjornn (1984) were created by sifting commercially supplied rock using the following sieve sizes: 50.8 mm, 25.4 mm, 12.7 mm, 9.5 mm, 6.35 mm, 4.76 mm, 1.7 mm, 0.85 mm, and 0.42 mm. Rocks less than 9.5 mm were composed of commercially supplied angular particles, whereas particles greater than 9.5 mm were composed of rounded rocks, typical of the LPO shoreline. Substrate treatments were described in terms of the percentage of particles by weight less than 9.5 mm and less than 0.85 mm in diameter. For instance, 50:20 is equal to a homogenous substrate mixture where 50% of particles were less than 9.5 mm and 20% were less than 0.85 mm by weight (Tappel and Bjornn 1983, Bennett et al. 2003). The remaining particles in each treament varied in diameter, but were primarily between 12.7 mm and 25.4 mm (see Table 1 in Tappel and Bjornn (1983)). The eight substrate treatments randomly assigned to the 24 troughs in the laboratory experiment included 50:20, 40:16, 35:8, 30:12, 25:6, 20:8, 20:1, and 0:0.

Green kokanee eggs were obtained from the Sullivan Springs spawning weir and transported to the University of Idaho where they were disinfected with iodophore (100

$mg{\cdot}L^{-1}$ for ten minutes; Piper et al. 1982). Fertilized eggs from multiple donors were mixed together. All handling was conducted within 48 hours of fertilization to avoid handling during the period when salmonid eggs are most sensitive to physical shock (Piper et al. 1982, Crim and Glebe 1990). Gravel and green kokanee eggs were loosely placed in the incubation chamber of each egg box. Eggs were discarded if they appeared whitened, bloody, or not water hardened. Six egg boxes were assigned to each experimental trough. Boxes were buried in substrate to a depth of 5-10 cm, similar to stream-spawning kokanee egg burial depths (Scott and Crossman 1973, Steen and Quinn 1999). Of the six boxes placed in each trough, two were covered in 1 mm mesh and randomly positioned for measurement of preemergent survival. Both the laboratory and in situ investigations assumed that intragravel survival was unaffected by mesh coverings.

A monitoring stake was placed in each experimental trough, enabling intragravel water samples to be drawn via a syringe. Monitoring stakes were modified from the design used by Leonetti (1996). Stakes were 254 mm galvanized nails. Vinyl tubing was attached to the stake with cable ties. The tubing was plugged at the end and contained 1 mm perforations in the bottom 5 cm. The perforated portion of the tubing was positioned at the depth of the egg box nursery chamber, approximately 5 cm beneath the substrate surface. One monitoring stake was placed in each trough between the pair of egg boxes in the center and the pair of boxes nearest the standpipe. Intragravel and surface DO was measured four times during incubation. Samples were drawn from monitoring stakes using a 70 ml syringe and DO concentration was measured to the nearest 0.1 $mg{\cdot}L^{-1}$ by placing the probe of a calibrated electrode-based DO meter (YSI Inc., Yellow Springs, Ohio; model Pro 2030) inside each syringe and gently agitating. Surface water DO was measured along with intragravel DO over the course of the experiment.

Kokanee eggs were treated with formalin once during the experiment in an attempt to prevent fungal (*Saprolegnia* spp.) growth in egg boxes (Argent and Flebbe 1999, Bennett et al. 2003). Fungal growth was a concern for this experiment because of the low flow rate in troughs relative to stream-based experiments and hatchery incubation systems (McCuddin 1977, Reiser and White 1983, Reiser and White 1988, Rach et al. 1995). As such, formalin was administered on January 27, 2012 in the form of a bath treatment of Parasite S (Western Chemical, Ferndale, WA, USA) brought to a concentration of 1667 $mg \cdot L^{-1}$ for 15 minutes. Formalin treatment was discontinued after one use because of logistic challenges and concerns that draining troughs regularly would disturb the stratigraphy of substrate.

Survival of kokanee to eyed and preemergent stages of development was measured by retrieving egg boxes at different times. On February 21, 2012, two uncovered egg boxes per trough were retrieved at random to determine survival to the eyed stage. Afterwards, experimental troughs were darkened with opaque polyethylene sheeting. Troughs were darkened because *O. nerka* are negatively phototactic before emergence and can expend additional energy avoiding light (Heard 1964, Bams 1969). Sheeting was removed and the two mesh-covered boxes were retrieved on April 1, 2012 to measure survival of embryos to the preemergent stage. Fry were allowed to emerge from residual boxes.

Troughs were surveyed for emergent fry nightly from April 20, 2012 until termination of the experiment on May 4, 2012. The number of fry visible on the surface water of each trough was enumerated with the aid of a flashlight. Troughs were surveyed in random order each night to reduce the effect of fry disturbance in adjacent troughs. Nightly counts after peak emergence were used as an index of abundance of emergent fry among treatment groups. Detectability of fry during counting was assumed to be constant across all substrate treatments. Emergent fry condition was assessed among troughs by collecting fry from the surface water of each trough with a vacuum pump at the end of the experiment. Fry fork length was measured to the nearest 0.1 mm using a stereoscope coupled with a camera and image analysis software (MediaCybernetics, Bethesda, MD, USA, Image-Pro Plus 5.1). Dry weight was measured to the nearest milligram after desiccating for 24 hours at 60°C (Steinhart 2003).

Eyed egg survival, preemergent survival, emergent fry count, and emergent fry condition were analyzed using a mixed model approach (Pinheiro and Bates 2000). Substrate treatments were modeled as categorical fixed effects nested within a trough random variable:

$$y_{\mathrm{ij}} = \beta_0 + \beta_1 \mathrm{x}_{\mathrm{i1}} + \cdots + \beta_{\mathrm{j}} \mathrm{x}_{\mathrm{ij}} + a_{\mathrm{i}} + \mathrm{e}_{\mathrm{ijk}}, \qquad \mathrm{a}_{\mathrm{i}} \sim \mathrm{N}\left(0,\ \sigma^2\right),$$

where y_{ij} is the response variable for the *j*th substrate treatment and the *i*th experimental trough, and a_i is the random effect for trough. Intragravel survival proportion and fry counts were modeled using generalized linear mixed models (GLMMs), estimated using the Laplace approximation (Warton and Hui 2011). Logistic regression was used to model survival proportions because it is preferred for modeling dichotomous outcomes (Warton and Hui 2011, Hosmer et al. 2013). Logistic regression assumes a binomial error structure and models the log odds of the observed proportion via a logit link function (McCullagh and Nelder 1989). Minimum DO measured in each trough up until box retrieval was included as a variable in the survival models and its effect was described using the exponential function of the parameter value (i.e., odds ratio) interpreted as the estimated increase in the odds of survival associated with a one-unit change in the value of the predictor (McCullagh and Nelder 1989). Minimum DO was used assuming that total survival to a particular stage would be affected if hypoxic conditions were encountered at any point during the experiment (Sear et al. 2012). Accidental aeration of intragravel water samples would only bias DO samples upwards. Poisson regression was used to model emergent fry counts because responses consisted of positive integers with heterogeneous variance. The method assumes a Poisson error distribution and relates the linear combination of parameters to count data using a log link function. Counting events were considered independent replicates, under the assumption that all fry remained in surface water after emergence, unless disturbed. The relative condition of emergent fry was summarized using a dry weight version of Fulton's fry condition factor (K_{DW}; Reiser and White 1988):

$$K_{DW} = \frac{\text{dry weight (mg)}\times 10^3}{[\text{wet fork length(mm)}]^3}\,.$$

Fry condition factor was modeled using a linear mixed model estimated with restricted maximum likelihood.

Goodness of fit for all models was assessed using deviance residual plots. Overdispersion of GLMMs was evaluated using a dispersion parameter ($\hat{c}$) calculated from deviance residuals (McCullagh and Nelder 1989). Logistic model discrimination was also assessed using the area under the receiver operating characteristic curve (ROC curve; Hosmer et al. 2013). Likelihood ratio tests were used to test for fixed effects in logistic and Poisson regression models (Warton and Hui 2011). The effect of substrate on fry condition factor was assessed using an F-test with the between-within degrees of freedom adjustment (Pinheiro and Bates 2000). When treatment effects were detected, Tukey pair-wise comparisons were used to test for differences among treatments (Zar 2009).

In situ

An in situ incubation study was conducted at three major shoreline spawning sites in LPO to identify relationships between habitat characteristics and survival. Egg boxes were buried in substrate and laid out using a double matrix design modified from the one used by Hassemer (1984) in Lake Coeur d’Alene, ID. Matrices were placed in three current shoreline spawning sites where kokanee spawn at relatively high densities. Spawning sites included in the current study were Eagle Marina, located on the northern shore of Idlewilde Bay east of the Farragut State Park boat ramp; Bernard Mine, located southeast of Idlewilde Bay on the lake’s main body; and a site on the southern shore of Scenic Bay. The three shoreline sites were selected because they characterized dissimilar habitat types. The Scenic Bay site consisted primarily of sand substrate with larger particles at depth, the Eagle Marina site consisted of a mixture of cobble, gravel, and sand; Bernard Mine was located on an active talus slope and was the steepest and most exposed of the three sites.

Egg boxes were laid out within each site in two 4 × 4 matrices at shallow (1-4 m) and deep (10-14 m) isobaths. Both matrices were arranged with 1 m spacing in the direction parallel to shore and 1.5 m spacing perpendicular (Hassemer 1984). The matrix of egg boxes was laid out by running a weighted line, marked at 0.5 m intervals, perpendicular to the shoreline with the aid of an underwater compass. Shallow matrices were laid out from the point on the weighted line where a depth of 1 m was reached and the deep matrix was laid out when a depth of 10 m was reached. The metered slope line and a 1 m × 1.5 m polyvinyl chloride rectangle served as a guide for spacing egg boxes. As a consequence of the layout method, the depth range encompassed by a given egg box matrix and the spacing between deep and shallow matrices was governed by the slope of the shoreline. The slope of matrices was estimated after boxes were placed by measuring depths of each egg box to the nearest 0.3 m with a dive computer (Gipson and Hubert 1993).

Eggs boxes were deployed using the same methods as those in the laboratory experiment; gravel and 50 green eggs were loaded into each box, a portion of egg boxes were wrapped in 1-mm mesh, and egg boxes were retrieved at two points in time to measure survival of embryos to eyed and preemergent developmental stages. Eggs were fertilized using gametes obtained from kokanee captured at the Sullivan Springs weir. After water-hardening, viable embryos were loaded into egg boxes and buried in substrate within 48 h of fertilization. A total of 96 egg boxes was planted in the lake between 8 and 12 December, 2012, among the three shoreline sites. Of the sixteen egg boxes placed in each matrix, six were randomly assigned to measure eyed survival and ten for preemergent survival. Four additional "handling mortality" boxes were buried adjacent to each matrix to estimate mortality resulting from the transport, loading, and burial of boxes (Hassemer 1984, Fincel et al. 2009). Handling boxes were retrieved within three days of placement. Egg boxes without mesh (i.e., eyed stage) were retrieved between February 28 and March 1, 2012, and egg boxes with mesh (i.e., preemergent stage) were retrieved between April 24 and April 26, 2012.

Temperature and intragravel DO were monitored during the in situ incubation study using methods similar to the laboratory experiment. Ambient water temperature was monitored by four thermographs placed in the vicinity of egg box matrices. Thermographs were placed at depths of 1 m and 10 m in Scenic and Idlewilde bays. The Scenic Bay thermographs were used to monitor Scenic Bay matrices. The Idlewilde Bay thermograph was used to monitor both the Eagle Marina and Bernard Mine sites. Thermograph data were used to calculate accumulated temperature units (ATUs) at sites. Accumulated temperature units were defined as the cumulative daily temperature. Intragravel DO concentration was measured at half of the egg box locations at four points during incubation. Monitoring stakes, described for the laboratory experiment, were randomly placed at two egg boxes per row (parallel to shore). Intragravel DO was measured by extracting water samples from monitoring stakes at depth using 70 ml syringes. Filled syringes were capped immediately after sample collection and carried to a DO meter at the surface. Intragravel DO was first measured at each monitoring stake 2-3 days after egg boxes and stakes were installed and monthly thereafter.

Substrate was sampled at every egg box location following completion of the study using an underwater bulk sampling device. Bulk core sampling is considered the most accurate method for characterizing spawning substrate (Young et al. 1991, Kondolf 2000). The sampler used in this study was modified from the "cookie-cutter" design described by Klingeman and Emmett (1982) and consisted of a cylinder (50 cm diameter × 40 cm height), with handles at the top and "teeth" at the bottom. Divers pressed the sampler into the substrate and excavated encircled material to a depth of 8 cm using a cylinder (140 mm diameter × 165 mm height). Each sample was composed of three to four full cylinders of material from the same location that were placed in a 68 L plastic bag. The cylinder was capped during transfer from the sampler to the bag to minimize loss of fine sediment. Plastic bags were sealed at depth with cable ties and hoisted to the surface in sealed buckets (Marsden and Krueger 1991). Substrate samples were likely biased due to unavoidable losses of particles less than 2 mm (Young et al. 1991). Fine sediment losses were assumed to be consistent across all sites and depths. Substrate samples were dried in an oven and sorted using the suite of sieves described in the laboratory portion of the experiment.

An information theoretic approach was used to select parsimonious logistic regression models for the effect of box- and matrix-level habitat characteristics on kokanee intragravel survival (Burnham and Anderson 2002). Four model selection procedures were performed in total, using Akaike's Information Criterion adjusted for small sample sizes (AIC_c). Separate model selection procedures evaluated the effect of habitat variables on survival to eyed and preemergent stages. Two procedures were performed for each developmental stage: one using all egg boxes and another using only egg boxes where intragravel DO was measured through time (DO subset). The goal of model selection procedures that included all boxes was to evaluate the influence of habitat characteristics on survival. The DO subset model selection procedures contained fewer observations, thus the number of candidate models and their complexity was reduced (Table 1). The purpose of model selection for the DO subset was to assess whether inclusion of intragravel DO would improve fit or produce a different conclusion compared to procedures that included all available boxes.

Habitat variables included in this analysis were site, depth, slope, and substrate composition. Minimum DO was also included in DO subset candidate models. Depth was treated as a categorical variable indicating whether an egg box was placed in the shallow or deep isobath. Slope was included as a continuous matrix-level variable that described the plane angle of shoreline. Slope was calculated as the difference in the average depth at the top and bottom rows of boxes in a given matrix, divided by 5 m. There is no unifying statistic for describing substrate conditions; therefore, median particle diameter (D_{50}) and percentage of particles less than 0.85 mm by weight (hereafter "fines") were included in model selection procedures (Kondolf 2000). Median particle diameter is an indicator of the overall composition of the substrate and was informative for this study considering the wide range of particle sizes selected by shoreline spawners. "Fines" reflects the proportion of what is considered the most harmful size category. Median particle diameter and fines were examined separately, due to their lack of independence. Minimum DO observed at each egg box through time was included as a variable in the in situ analysis for the same reason as in the laboratory experiment.

Candidate models consisted of additive models for all variables as well as several biologically plausible two-way interactions. Interactions were only included in candidate models when both main effect terms were also present (Table 1). "Substrate" here refers to both fines and D_{50}. Two-way interactions were site × substrate, depth × substrate, and site × depth. Models containing site × substrate and depth × substrate interactions hypothesized that the effects of substrate composition on survival varied by depth or site because wave action or water flow in an area might counteract the effect of substrate composition. Models containing the site × depth interaction hypothesized that intragravel survival was related to the particular matrix containing an egg box. Candidate models for DO subset boxes were assembled differently because they possessed fewer observations and would have exceeded the recommended number of events per variable for model selection (Vittinghoff and McCulloch 2007). Site and depth variable main effects and their interaction were collapsed into a categorical variable with six levels named "matrix" (Table 1). This reduced both the number of candidate models and events per variable at the cost of obscuring site and depth main effects, but was reasonable considering the purpose of the DO subset model selection procedure.

When initial fitting of candidate models indicated overdispersion ($\hat{c} > 1$) quasi-AIC adjusted for small samples ($QAIC_c$) was used to rank models and an additional parameter was added to each model to account for the estimation of dispersion (Burnham and Anderson 2002). The variance inflation factor for $QAIC_c$ was fixed using the lowest $\hat{c}$ value among candidate models because there was no global model among candidates (Burnham and Anderson 2002). Top models were judged as those with AIC_c or $QAIC_c$ scores within 2.0 of the model with the lowest score ($\Delta < 2$). Goodness of fit for top models was assessed using methods described in the laboratory section and parameters for continuous variables were interpreted using odds ratios.

Habitat variables were also analyzed independent of the model selection procedures. Substrate composition and intragravel DO were described both among and within egg box matrices. Substrate size distributions were described using cumulative particle size distribution curves and box and whisker plots (Platts et al. 1979, Kondolf et al. 2008). Changes in intragravel DO over the incubation period and across matrices were modeled using a linear mixed model fit with restricted maximum likelihood (Pinheiro and Bates 2000). An appropriate covariance structure for repeated measures was determined based on AIC ($\Delta < 2$) and an assessment of standardized residuals. Potential covariance structures included compound symmetric, autoregressive (lag 1), autoregressive heterogeneous, and general (Pinhero and Bates 2003). This method was advantageous because it enabled egg box locations with incomplete DO records to be included in the analysis. When observations were missing, it was usually because tubing on the monitoring stake was clogged or kinked.

RESULTS

Laboratory

The experimental trough system remained within the range of temperature and DO for simulating winter conditions in LPO. Water temperature varied from 6.8 to 7.6°C and surface DO was at greater than 90% saturation over the course of the experiment. Surface water DO concentration was between 9.2 and 11.5 $mg \cdot L^{-1}$ and intragravel DO was between 8.4 and 11.3 $mg \cdot L^{-1}$. Intragravel DO differed significantly from surface water based on an asymptotic paired-comparison permutation test ($P < 0.001$), indicating that a DO gradient was established between the intragravel area and surface water.

Fry emergence occurred over a five day period, beginning on April 22, 2012. No fry were observed in one of the three troughs containing the 50:20 substrate treatment. Emerged fry remained below gravel during the day and moved into surface water at night. All fry emerged with fully absorbed yolk sacs. Fry counts peaked on April 26, 2012 and were relatively consistent until termination of the experiment on May 4, 2012. Between 8 and 28 fry were sampled from all experimental troughs that contained fry.

Substrate treatments and intragravel DO had only a small effect on intragravel survival. All model assumptions were met based on visual inspection of residual plots, GLMMs did not show evidence of overdisperion ($\hat{c} > 1$), and logistic regression models showed adequate discrimination (ROC > 0.7). Likelihood ratio tests indicated that survival of kokanee to the eyed stage was influenced by the minimum intragravel DO concentration, but not by substrate treatment (Table 2). Minimum intragravel DO had a significant positive effect on survival to the eyed stage but not to the preemergent stage. The odds ratio estimate for the eyed stage was 1.22 (1.03, 1.44 [LCL, UCL]) and 1.13 (0.96, 1.33) for the preemergent stage. Fry counts and condition were negatively affected by substrate treatments (Table 2). Tukey pairwise comparisons indicated that the substrate treatment with the largest proportion of fine sediment (50:20) had a significantly lower fry count than all other treatments, and significantly lower condition factor (K_{DW}) than all others besides the 25:6 treatment (Figure 2).

In situ

Intragravel DO was measured at 2, 29, 76, and 113 d after placement of the last egg box matrix, eyed egg boxes were retrieved at days 82 and 83, preemergent egg boxes were retrieved between days 140 and 142, and substrate was sampled between days 149 and 155. The estimated shoreline slope of deep matrices was 22.9° for Eagle Marina, 24.0° for Scenic Bay, and 32.8° for Bernard Mine. The slope of shallow matrices more variable with 3.8° for Eagle Marina, 12.7° for Scenic Bay, and 28.3° for Bernard Mine. Although not quantified, periphyton cover increased throughout incubation at all matrices and was pronounced in shallow sites. The Scenic Bay site was dominated by filamentous green algae (e.g., *Cladophora* spp.); whereas, the Bernard Mine and Eagle Marina sites were dominated by stalked diatoms (e.g., *Cymbella* spp.). Handling box survival averaged 97% among matrices indicating that the effect of handling mortality could be ignored. Several egg boxes were not recovered during the study including two eyed egg boxes from the Bernard Mine—deep matrix, one preemergent egg box from the Eagle Marina—deep matrix, and one preemergent egg box at the shallow matrix in Scenic Bay. One monitoring stake failed at the Scenic Bay—deep matrix and another at the Bernard Mine—deep matrix.

Temperature trends were relatively consistent across sites and depths, while trends in DO varied across matrices. Temperature remained between 3.1°C and 8.9°C during incubation and varied by less than 1°C across all locations until approximately March 20, 2012, when the shallow area of Scenic Bay began to warm. This pattern is reflected in ATUs among locations during incubation. At the time when eyed eggs were retrieved, the range of ATUs among the four thermograph locations was less than six ATUs. When preemergent boxes were retrieved, the shallow location in Scenic Bay was 12 ATU ahead of deep location in Scenic Bay, 17 ATU ahead of the shallow location in Idlewilde Bay, and 32 ATU ahead of deep location in Idlewilde Bay. The top ranking, and also best fitting, repeated-measures DO model contained a general covariance structure where the maximum number of correlation parameters was estimated. Intragravel DO measurements of three egg box locations in the Bernard Mine—shallow matrix deviated from others by remaining at low levels. These egg boxes were dropped from the repeated-measures analysis in an attempt to conservatively describe patterns in declining DO (Figure 3). Intragravel DO declined through time at all matrices except Scenic Bay—shallow and Eagle Marina—deep, with the most rapid decline occurring at the Bernard Mine—shallow (Table 3).

Substrate size distributions differed greatly among and within sites. Deep matrices in Bernard Mine and Scenic Bay were characterized by higher proportions of large cobbles at depth, while substrate composition at Eagle Marina was similar for both isobaths (Figure 4). Variability in substrate size distributions among egg boxes differed across matrices. Relatively homogenous substrate composition was observed at the shallow matrix in Scenic Bay and deep matrices of Bernard Mine and Eagle Marina. Substrate composition was heterogeneous at shallow matrices of Bernard Mine and Eagle Marina, and the deep matrix of Scenic Bay (Figure 5).

Model selection procedures supported the hypothesis that intragravel survival was influenced by matrix and intragravel DO. Candidate models were overdispersed ($\hat{c} > 1$) in all model selection procedures except the preemergent DO subset (Table 4). Top models showed adequate fit and discrimination (ROC > 0.7; Hosmer et al. 2013). Top models had either the lowest dispersion parameter estimate or were within 0.1 of the lowest. All top models demonstrated support for matrix-level effects on survival based on the presence of the “site × depth” interaction or “matrix” variable. Akaike weights of the top three models exceed 0.95 for all procedures. Model selection procedures that included the DO variable received support for matrix and DO variables. Substrate variables (D_{50}; <0.85mm) were included among top models for all eyed egg boxes. However, similar likelihood among the top three models and the error surrounding substrate odds ratio estimates demonstrated little to no effect of substrate size on survival.

Findings from model selection procedures support the interpretation of intragravel survival data on a matrix-by-matrix basis. Therefore, the results presented here are based on interpretations of parameter estimates from the top-ranking models, none of which contained substrate variables. Survival to the eyed stage was generally higher than to the preemergent stage (Figure 6). Survival to both stages of development was higher at shallow than deep matrices in Scenic Bay and Eagle Marina; the opposite was true at Bernard Mine. Survival to the eyed stage was highest at the shallow matrices of Eagle Marina (55 ± 3.8% [mean ± SE]) and Scenic Bay (48 ± 3.8%), followed by the deep matrices of Scenic Bay (38 ± 3.7%), Bernard Mine (37 ± 0.4.5%), Eagle Marina (19 ± 3.0%), and the shallow matrix at Bernard

Mine (3 ± 1.1%). The Eagle Marina—shallow matrix had the highest survival to the preemergent stage (39 ± 2.9%), followed closely by the shallow matrix of Scenic Bay (33 ± 3.0%). Preemergent survival at all deep matrices was comparable. The Bernard Mine—shallow matrix had the lowest survival among matrices at the eyed stage (3 ± 1.2%). No fry survived to the preemergent stage at the Bernard Mine—shallow matrix. Complete mortality of eggs at the Bernard Mine—shallow matrix created issues in estimating parameters using regular maximum likelihood estimation. All candidate models for preemergent survival containing a "site × depth" interaction experienced quasi-complete separation of points where one of the parameter estimates diverged to infinity. Therefore, penalized maximum likelihood estimation was used to obtain parameter estimates and profile likelihood confidence intervals (Figure 6). Top models for the DO subset provided evidence of an effect of intragravel DO in addition to a matrix-specific effect. The estimated odds ratio for the effect of minimum dissolved oxygen on survival to the eyed stage was 1.24 (1.08, 1.45 [LCL, UCL]) for the eyed stage and 1.34 (1.15, 1.57) for the preemergent stage. These estimates indicate that DO had a more pronounced effect on survival to the preemergent than to the eyed stage.

DISCUSSION

Survival responses were homogenous among treatments in the laboratory incubation experiment. It is uncommon for incubation studies to fail to detect substrate treatment effect on survival; a meta-analysis by Jensen et al. (2009) found that substrate treatment did not significantly affect survival in 8% of previous lab and field incubation experiments involving Pacific salmon. Water flow rates are the most likely cause of similar intragravel survival among treatments. Although flow rates in the experiment were lower than in the stream-based literature, guidance on water flow rates in shoreline environments is limited. It would appear that although the system succeeded in producing different dissolved oxygen concentrations between surface and intragravel water, it was evidently not enough to produce a lethal response among substrate treatments.

Subtle differences in surface and intragravel DO are unlikely to have influenced survival in the laboratory experiment. Minimum DO affected survival to the eyed but not the preemergent stage. However, considering the nearly uniform survival for eyed and preemergent embryos across all treatments, this finding does not appear to be biologically meaningful. Critical DO levels for eggs have been described as between 2 and 8 $mg \cdot L^{-1}$ (Coble 1961, Silver et al. 1963, Davis 1975); intragravel DO was above these concentrations during the experiment. In addition, embryonic oxygen demand is initially low and increases as the embryo develops (Geist et al. 2006, Rombough 2007), so preemergent kokanee were more likely than eyed eggs to have been influenced by DO concentration.

Postemergent fry counts and condition reflect a survival bottleneck prior to emergence and sublethal effects of substrate composition. Although emergence timing was similar among treatments, postemergent counts and condition were lower for the substrate treatment containing the highest proportion of fine sediment. The nearly spontaneous emergence of fry in this experiment is contrary to previous experiments involving *O. nerka* which have reported sac-fry emerging prematurely from troughs containing large proportions of fine sediment (Bams 1969, Irving and Bjornn 1984). Emergent fry counts suggest that kokanee in the treatment with the highest proportion of fine sediment had the lowest survival to emergence, despite comparable survival to eyed and preemergent stages. Emergent fry counts may have underestimated the relative abundance of fry in the poorest treatments because finer substrate offered better concealment. Fry in treatments with the largest proportions of fine sediment were often observed plunging into substrate when disturbed by observers. Differences in emergent fry condition indicate a sublethal effect of substrate composition. Fry condition is an important component in determining recruitment because smaller fry are less competitive for food resources and can experience growth depensation (Mason 1969, Einum and Fleming 2000). Fry condition in this experiment was not related to intragravel DO measured during the experiment, similar to several other studies (Maccrimmon and Gots 1986). Diminished condition of fry could be the result of added energy expenditure of escaping from substrate with a large proportion of fine particles (Koski 1966). If the act of escaping from fine sediment decreases fitness or causes additional mortality, then fry emerging from areas with fine sediment are potentially less viable regardless of their survival to previous stages. Postemergent fry were not included in the in situ study due to logistic constraints, so the effect of escaping from the gravel could not be assessed.

Models provided evidence of intragravel DO and matrix-level effects on survival in the in situ study but little effect of substrate composition. Substrate composition varied greatly within several sites, yet variability in survival and intragravel DO was low. The discovery of matrix-specific effects is informative for understanding the scale necessary for assessing shoreline habitat. It appears that patches of habitat, large enough to contain multiple redds, may be more useful for predicting shoreline incubation success than substrate composition at individual redd locations. These findings were similar to other incubation studies in LPO. Fincel and Chipps (2009) found similar site-specific effects on survival of kokanee among three areas in Scenic Bay, which were attributed to differences in substrate composition between sites. Hassemer (1984) reported 43% survival of kokanee to the preemergent stage in Scenic Bay, which was similar to the 33% survival observed in the in situ study. In addition, egg boxes removed from some areas of Scenic Bay were filled with silt, yet had between 24% and 60% survival (Hassemer 1984). The pattern of high survival despite high proportions of fine sediment was also observed at the shallow matrix of the Scenic Bay site in this study.

The contrast between shallow matrices at Scenic Bay and Bernard Mine stands out in the analysis of matrix-specific substrate, DO, and survival. The substrate distribution in the Scenic Bay—shallow matrix contained the highest proportion of fine sediment of any matrix. For example, on average, 50% of the particle size distribution was less than 5.5 mm in diameter and 20% was less than 2 mm. Despite having the finest substrate, the Scenic Bay—shallow matrix also had high intragravel DO throughout the study and the second highest survival to the preemergent stage. On the other hand, the Bernard mine—shallow matrix had a higher proportion of larger particles than both matrices in Scenic Bay. However, the Bernard Mine—shallow matrix had the lowest intragravel DO readings and no fish survived to the preemergent stage. Either the Bernard Mine—shallow matrix had exceptionally low survival or Scenic Bay—shallow matrix had exceptionally high survival. Bernard Mine was the most exposed of the three sites and wave disturbance might explain the low survival in shallow water. However, the fact that egg boxes at the Bernard Mine—shallow site were not dislodged or unburied seems to contradict this contention. Furthermore, low intragravel DO was routinely measured at the shallow matrix, although wave action is generally associated with higher intragravel flow and DO (Leonetti 1996, Leonetti 1997).

High survival of eggs and fry at the Scenic Bay—shallow matrix may have been due to a supplemental source of water flow provided by groundwater interactions. Groundwater influence was a reasonable explanation because Scenic Bay and Eagle Marina are situated on a recharge area of the Spokane Valley Rathdrum Prairie Aquifer (Drost and Seitz 1978, Hsieh et al. 2007). Groundwater has been shown to enhance survival (Sowden and Power 1985, Garrett et al. 1998) and influence spawning site selection for a variety of species, including kokanee (Foerster 1968, Lorenz and Eiler 1989, Burgner 1991, Geist 2000). Garrett et al. (1998) found that stream-spawning kokanee redds in areas of upwelling had higher hatching success, despite having a higher proportion of fine sediment than redds in non-upwelling areas. In a study of sockeye salmon redd site selection in off-channel habitats, Hall and Wissmar (2004) demonstrated that not only did spawners select redd sites in upwelling areas, but they were also less selective of substrate quality in areas of upwelling. The hypothesis that groundwater enhances kokanee survival in Scenic Bay led to a post hoc investigation of groundwater dynamics at egg box matrixes.

The presence or absence of groundwater influence at egg box matrices was assessed by measuring the vertical hydraulic gradient of the intragravel zone beneath egg box locations using a PushPoint sampler (M.H.E Products, East Tawas, MI, USA) equipped with 6.35 mm inner diameter vinyl tubing (Rosenberry and LaBaugh 2008). The probe was inserted approximately 20 cm into substrate at previous egg box locations. Clear vinyl tubing was attached to the opening at the top of the probe and extended above the water's surface. Upwelling or downwelling was determined by whether the water level in the tubing was situated above or below the surface water, respectively (Sowden and Power 1985, Geist and Dauble 1998, Mull and Wilzbach 2007). Groundwater was assessed at deep matrices by divers and an observer floating on the surface. Water level displacement was then measured to the nearest centimeter. To ensure accuracy of groundwater detection, air bubbles were removed tubing before sampling each site and the tubing was encircled by a life ring to dampen wave action around the tubing. Groundwater was not considered detected unless the tubing water level showed a stable deviation from the surface water level of at least 3 cm. The groundwater assessment described here was not fully integrated with the situ study (e.g., inclusion of groundwater covariates) because the bottom two rows of egg boxes at the Eagle Marina—deep site could not be identified and thus precluded complete groundwater assessment at every matrix.

The groundwater assessment detected downwelling at two of the six egg box matrices and helped to address unanswered questions from the in situ study. Downwelling was detected at nine of the sixteen egg box locations at the Scenic Bay—shallow matrix and at one of the egg boxes in the Eagle Marina—deep matrix. Downwelling may have existed at additional egg boxes at that site had the bottom two rows of the matrix been located. These findings are unique in that downwelling is seldom reported in the spawning habitat literature compared to upwelling (Geist and Dauble 1998, Lapointe 2012). Because downwelling carries surface water into intragravel habitats, it has several advantages over upwelling. Downwelling does not expose eggs to harmful groundwater that may be outside optimal incubation temperatures, contaminated, or anoxic due to long residence times (Youngson et al. 2004, Lapointe 2012). Results of the groundwater assessment suggest that downwelling plays a key role in enhancing the survival of embryos in LPO and might explain why so many kokanee spawn in what appears to be sub-optimal habitat in Scenic Bay.

Although downwelling may explain the higher and more consistent intragravel DO at the Scenic Bay—shallow matrix, the reason for the decline in intragravel DO at the Bernard Mine—shallow matrix remains unclear. Temperature does not appear to be a significant driver of DO concentration during incubation. The shallow matrix in Scenic Bay warmed the most rapidly during incubation, yet the intragravel DO remained relatively constant. Another explanation is that diminished intragravel DO at Bernard Mine was associated with accumulation of organic matter or periphyton. Periphytonic biomass increased at all three sites during the study, but the Bernard Mine—shallow matrix had the largest accumulation of stalked diatoms. Accumulated organic matter has been shown to increase biological oxygen demand in the intragravel area and reduce egg-to-fry survival (Greig et al. 2007, Pattison et al. 2012). If periphyton biomass or composition is the source of mortality, then periphyton cover is another site-level variable that helps explain why intragravel survival is better explained by habitat patches than by substrate immediately surrounding the egg pocket.

The laboratory experiment presented here was the first attempt to simulate the shoreline incubation environment of Pacific salmon. The in situ study was one of few studies to examine the effects of habitat characteristics on intragravel survival at multiple depths and in multiple habitat types. Surprisingly, neither the laboratory experiment nor in situ study investigation found evidence that substrate composition greatly affects intragravel survival in shoreline environments, although, survival was related to DO. Future in situ studies in LPO will likely have greater success elucidating the relationship between substrate quality and shoreline intragravel survival if more sites lacking groundwater flow are included. This was the first shoreline incubation study involving *O. nerka* to link enhanced survival with shoreline groundwater flow. Another important finding was that intragravel survival was better explained by habitat patches than by redd-scale substrate composition, regardless of depth. A lake-wide assessment of shoreline survival conditions is needed to fully test the water-level hypothesis in LPO; however, the viability of deep-spawning and the presence of supplemental groundwater flow in Scenic Bay challenges the hypothesis's definition of suitable shoreline spawning habitat. Downwelling appears to enhance survival of embryos in LPO and is a compelling explanation for why the majority of kokanee spawn in apparently sub-optimal habitat in Scenic Bay.

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Table 2.1. Candidate models for kokanee intragravel survival to eyed and preemergent stages of development for an in situ incubation study conducted at three shoreline spawning sites on Lake Pend Oreille, ID, 2011-2012. The left column indicates candidate models in which all egg boxes were used to assess survival. The right column shows candidate models that were evaluated using a subset of boxes for which minimum intragravel dissolved oxygen (DO) through time was measured. The variable "substrate" represents two substrate variables that were modeled separately: median particle diameter and the proportion of particles less than 0.85 mm.

All boxes	Dissolved oxygen subset
[null]	[null]
site	matrix
depth	slope
substrate	substrate
slope	DO
site, depth	matrix, substrate
site, substrate	slope, substrate
depth, substrate	matrix, DO
depth, slope	substrate, DO
substrate, slope	slope, DO
site, depth, slope	matrix, substrate, DO
site, depth, substrate	slope, substrate, DO
site, slope, substrate	
site, depth, slope, substrate	
site, depth, site × depth	
site, substrate, site × substrate	
depth, substrate, depth × substrate	
site, depth, site × depth, substrate	

Table 2.2. Likelihood ratio (LR)- and *F*-tests of kokanee egg and fry survival in a laboratory incubation experiment conducted at the University of Idaho, 2011-2012. Likelihood ratio tests were used in global tests for the effect of eight substrate treatments and minimum intragravel dissolved oxygen on the proportion survival of embryos to the eyed and preemergent stages of development. Post-emergence tests included a LR-test to evaluate the effect of substrate treatments fry counts. An *F*- test was used to examine the effect of substrate treatments on Fulton's dry weight condition factor of fry.

Measurement	Statistical test	df	LR or *F*	*P*-value
Intragravel survival				
Eyed stage				
Dissolved oxygen	*LR*-test	1	6.67	0.010
Treatment	*LR*-test	7	10.64	0.155
Preemergent stage				
Dissolved oxygen	*LR*-test	1	2.64	0.104
Treatment	*LR*-test	7	8.50	0.291
Post-emergence				
Fry count	*LR*-test	7	25.57	<0.001
Fry condition	*F*-test	7, 15	3.69	0.016

Table 2.3. Slope parameters for intragravel dissolved oxygen versus days of incubation at kokanee egg boxes located in shallow (1-4 m) and deep (10-14 m) isobaths at three shoreline spawning sites in Lake Pend Oreille, ID, 2011-2012.

Egg box matrix	Slope parameter	SE	*t*	df	*P*-value
Bernard Mine					
Shallow	-0.039	0.005	-7.2	148	< 0.001
Deep	-0.011	0.003	-0.5	148	0.002
Eagle Marina					
Shallow	-0.012	0.006	-2.2	148	0.032
Deep	-0.003	0.005	-0.6	148	0.579
Scenic Bay					
Shallow	-0.004	0.005	-0.8	148	0.414
Deep	-0.015	0.006	-2.6	148	0.009

Table. 2.4. Top three ranked models for the effect of habitat variables on kokanee egg survival to eyed and preemergent stages of development during an in situ incubation study conducted at three shoreline spawning sites in Lake Pend Oreille, ID, 2011-2012. Akaike's information criterion adjusted for small sample sizes (AIC_c) was used to rank candidate that were not overdispersed (i.e., $\hat{c} < 1$), and quasi-AIC_c ($QAIC_c$) was used to rank models when overdispersion was present among candidate models ($\hat{c} > 1$). "All boxes" are models that included all egg boxes. "Dissolved oxygen subset" are models that only used a subset for which intragravel dissolved oxygen was measured. The number of egg boxes included in the model selection procedure (n), number of parameters in the model (K), Akaike model weights (w_i), Log likelihood and quasi-log likelihood of each model (Log_e (L)), and variance inflation factor ($\hat{c}$) incorporated into model selection with $QAIC_c$ are all shown. The minimum intragravel dissolved oxygen measured at a given egg box over the course of incubation, median particle diameter (D50) and the proportion of substrate particles less than 0.85 mm (fines) collected at egg box locations were important covariates in the models.

Data set	n	K	ΔAIC_c / $QAIC_c$	w_i	Log_e (L)	$\hat{c}$
Eyed survival						
All boxes						
$S_{\text{(site , depth, site×depth)}}$	34	7	0	0.48	-53.75	1.62
$S_{\text{(site, depth, site×depth, D50)}}$	34	8	1.03	0.29	-52.54	1.62
$S_{\text{(site, depth, site×depth, fines)}}$	34	8	1.61	0.22	-52.82	1.62
Dissolved oxygen subset						
$S_{\text{(matrix, DO)}}$	21	8	0	0.86	-35.82	1.30
$S_{\text{(matrix, DO, D50)}}$	21	9	5.61	0.05	-35.44	1.30
$S_{\text{(matrix, DO, fines)}}$	21	9	6.10	0.04	-35.69	1.30
Preemergent survival						
All boxes						
$S_{\text{(site , depth, site×depth)}}$	58	7	0	0.62	-75.14	1.77
$S_{\text{(site, depth, site×depth, D50)}}$	58	8	2.46	0.18	-75.02	1.77
$S_{\text{(site, depth, site×depth, fines)}}$	58	8	2.69	0.16	-75.13	1.77
Dissolved oxygen subset						
$S_{\text{(matrix, DO)}}$	25	7	0	0.79	-49.43	< 1
$S_{\text{(matrix, DO, fines)}}$	25	8	4.13	0.10	-49.29	< 1
$S_{\text{(matrix, DO, D50)}}$	25	8	4.21	0.10	-49.33	< 1

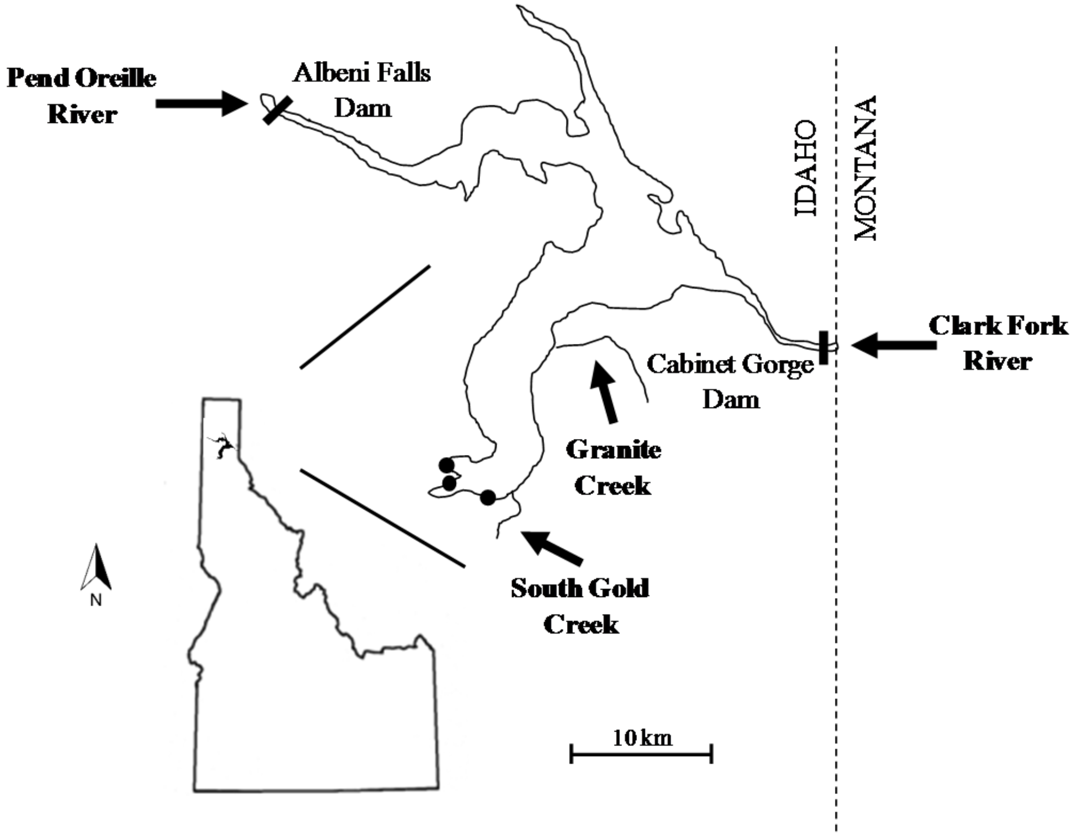

Figure 2.1. Map of Lake Pend Oreille, ID, with study sites represented by closed circles (●).

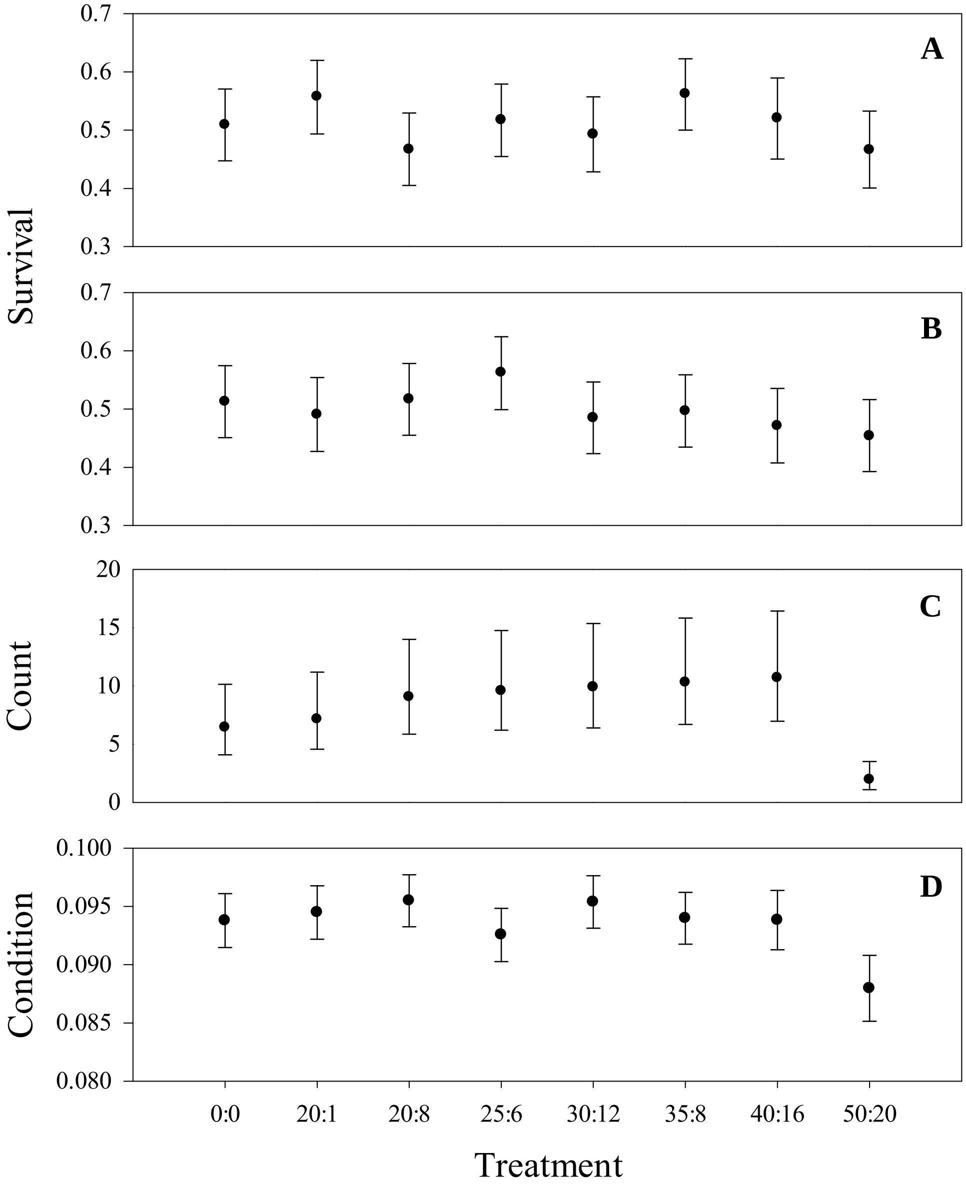

Figure 2.2. Mean survival of kokanee eggs to the eyed **(A)** and preemergent **(B)** developmental stages, counts of emergent fry **(C)**, and condition of emergent fry **(D)** from a laboratory incubation experiment conducted at the University of Idaho, 2011-2012. Error bars denote 95% profile likelihood confidence intervals for proportions and counts and pivotal confidence intervals for condition estimates. Mean fry counts are based on the average number of fry counted per experimental trough during nightly fry counts. Fry condition is based on fry collected from experimental troughs at termination of the experiment and calculated using the dry weight modification of Fulton’s condition factor.

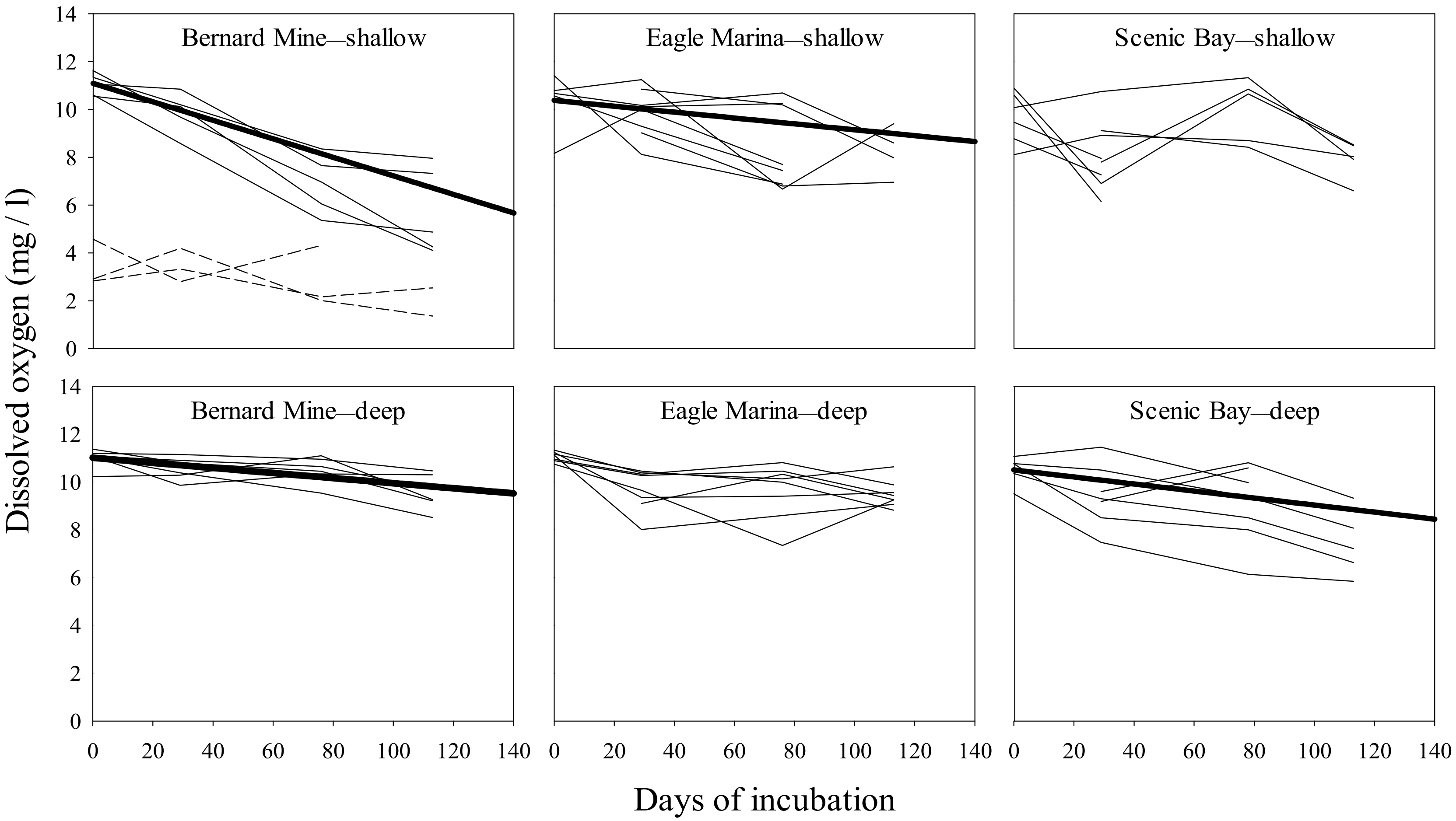

Figure 2.3. Intragravel dissolved oxygen measurements taken at four points from six egg box matrices during an in situ kokanee incubation study on Lake Pend Oreille, ID, 2011-2012. Thin lines represent measurements at individual egg box locations, thick lines represent the expected value for dissolved oxygen over the incubation period for matrices with nonzero slopes (< 0.05), and dashed lines in the Bernard Mine—shallow matrix denote egg boxes that were excluded from model (see text).

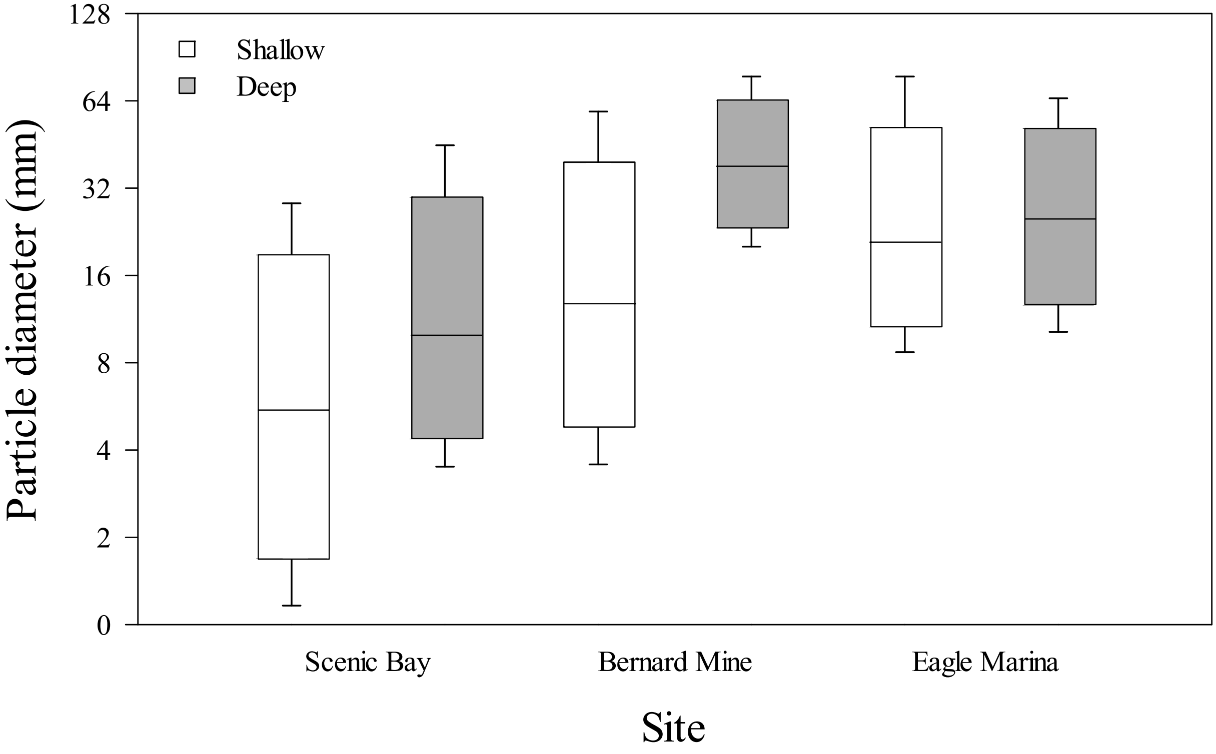

Figure 2.4. Particle size distributions for substrate sampled across six egg box matrices following an in situ kokanee incubation experiment on the shoreline of Lake Pend Oreille, ID, 2011-2012. Box plots were created by averaging the particle size distributions of 16 egg box locations per matrix. Particle diameter is shown on a Log_2 scale.

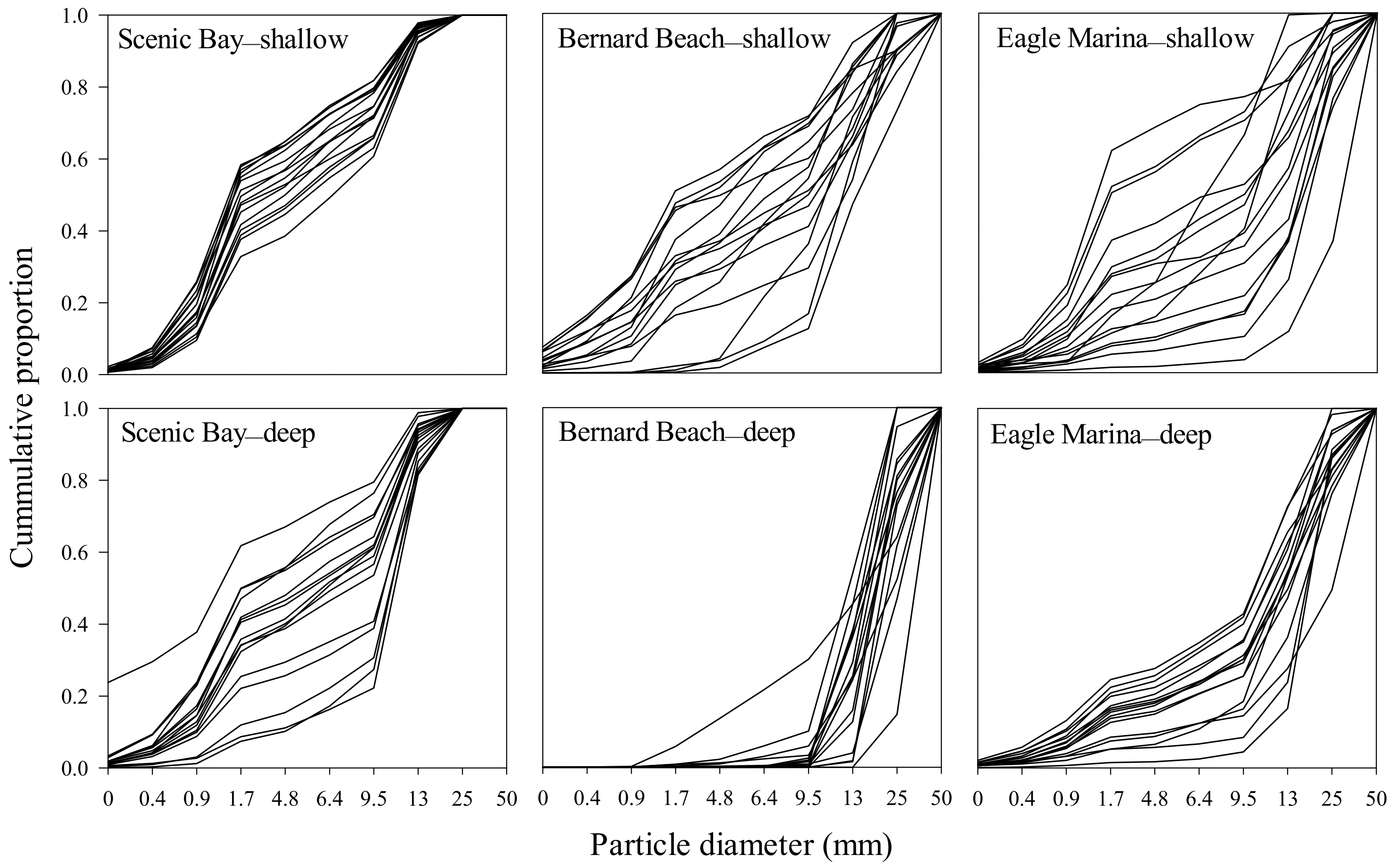

Figure 2.5. Cumulative particle size distributions for samples collected at 96 Whitlock-Vibert egg box locations in an in situ kokanee incubation study on Lake Pend Oreille, ID, 2011-2012.

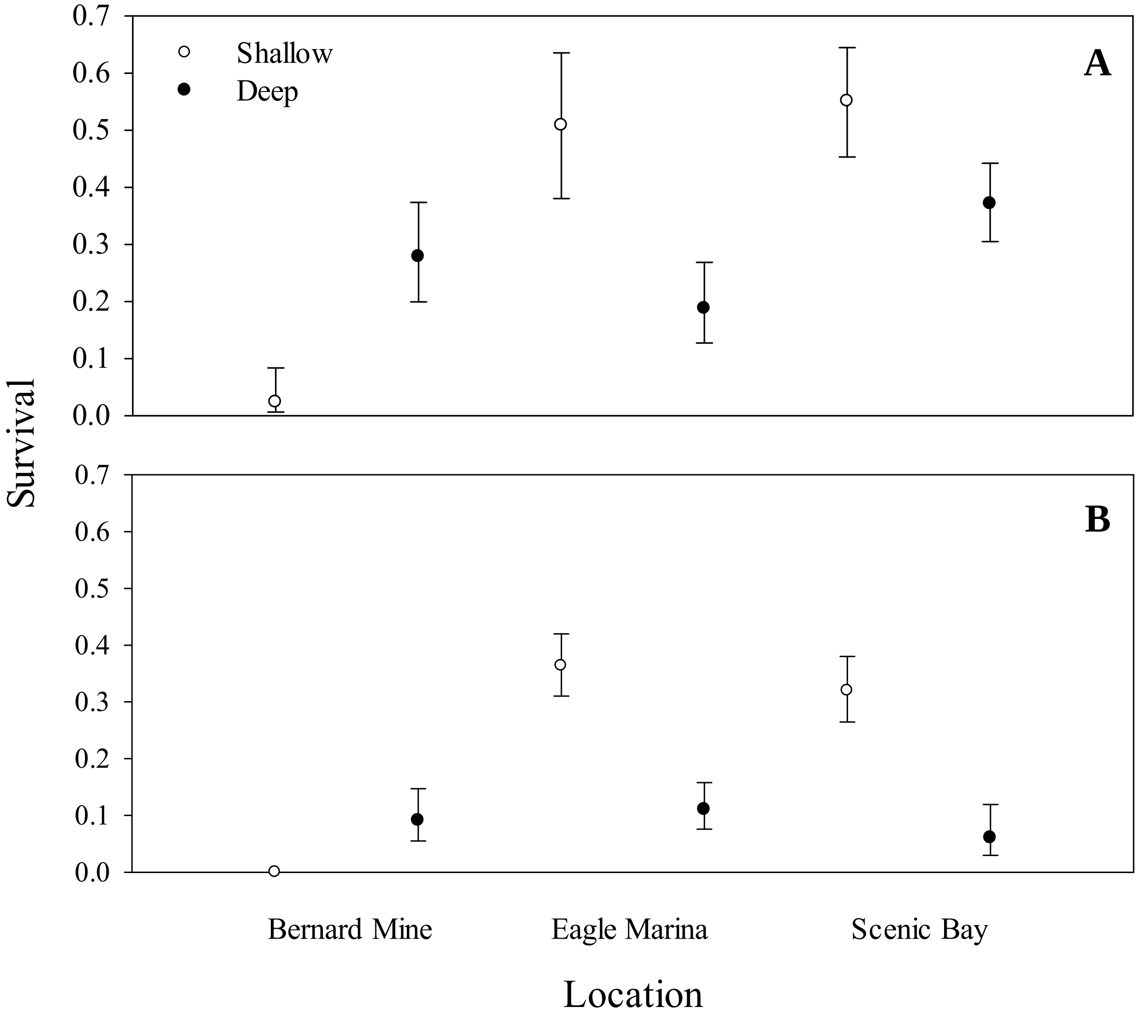

Figure 2.6. Mean survival of kokanee embryos to eyed (**A)** and preemergent **(B)** developmental stages in Lake Pend Oreille, ID, 2011-2012. Estimated survival for egg boxes located at shallow isobaths (1-4 m) are symbolized with open circles (○) and deep isobaths (10-15 m) with closed circles (●); error bars denote 95% profile likelihood confidence intervals.

CHAPTER 3: EFFECTS OF WATER LEVEL REGULATION AND HABITAT CHARACTERISTICS ON SHORE-SPAWNING KOKANEE *ONCORHYNCHUS NERKA* INCUBATION SUCCESS AND HABITAT SELECTION

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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, Idaho. 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 a 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 was 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 and that downwelling contributes 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.

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 and 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 synthesized 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 and 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 and 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 behavior of pelagic fishes and macroinvertebrates (Bodaly et al. 1984; Patalas and 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 and 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 and Radomski 1993). A dramatic example of water-level manipulation being implicated for 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 centerpiece of a highly productive commercial and recreational fishery that lasted from the 1940s to the 1970s, though more recently, has 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* fisheries (Simpson and 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 northwest 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 and 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 hypothesis have been posited to explain the decline of the kokanee population, including overharvest and competition with nonnative mysid shrimp *Mysis diluviana* (Rieman and Falter 1981; Chipps and 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 and Elam 1993).

The hypothesis for 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 and 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 stabilized water levels during incubation (Hoelscher 1993; Maiolie and 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 during spring runoff in May or June, and fell to an annual minimum elevation of near 626 m by the end of July (Maiolie and Elam 1993). Between 1955 and 1964, the water level was held high throughout the summer and dropped more rapidly in the fall, to approximately the same minimum. 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 preexisting 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 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; Hansen et al. 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 been made to justify 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.

The goal of this research was to directly test for the theorized 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. 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 and can greatly inform the current understanding of kokanee spawning behavior and habitat requirements (Smokorowski and Pratt 2007).

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 sampleable 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 (1) macrophytes, (2) bedrock, or (3) 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 lakewide 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; Jeppson 1955). The remainder of the sampleable shoreline was considered unused.

Incubations sites were selected using a stratified random design, which allowed for lake-wide generalization 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; and 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 625.1m elevation line and buried egg boxes 0.5 m above and 0.5 m below that depth contour, measured along the substrate surface.

Egg boxes were buried in a manner that would simulate natural kokanee redds. Egg boxes were used to measure survival from fertilization to the preemergent stage (i.e., after hatching but before fry emergence). Fertilized 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 post fertilization 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). 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 and Bennett 1996; Fincel et al. 2009). Egg boxes were buried to a depth of approximately 5 cm to simulate natural kokanee redds (Scott and Crossman 1973; Steen and 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 level. 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 galvanized 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, Ohio, 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 aluminum 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 mm, 25.4 mm, 12.7 mm, 9.5 mm, 6.35 mm, 4.76 mm, 1.7 mm, 0.85 mm, and 0.42 mm (Tappel and Bjornn 1983). Substrate size distributions were summarized using median particle diameter (D_{50}), which was used as predictor in the intragravel survival model (Kondolf 2000).

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 m 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). Sites were relocated and the probe was inserted within 5 meters of each egg box location. Water displacement above or below the surface water level indicated upwelling or downwelling, respectively (Geist and Dauble 1998; Mull and Wilzbach 2007). Downwelling was considered to be detected at a site if at least one of the box locations had greater than 2 cm of displacement in the tubing.

Design-based generalized 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 ten substrate size categories. 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, D50, DO, wave disturbance, and groundwater influence. Two-way interactions included D50 × groundwater, position × D50, position × disturbance, and position × groundwater. The magnitude and direction of the effect of habitat variables were described using odds ratios. Odds ratios are the exponential function of parameter estimates, interpreted as the multiplicative effect of a categorical variable or as 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 standardized residuals, and leave-one-out crossvalidation (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 D50. 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 were included in the sampling frame. Within the frame, approximately 6 km of shoreline were classified as current and 2 km as historic spawning reaches; the remaining 28 km were classified as unused (Table 1). Thirty sites were randomly allocated to unused shoreline reaches; 22 sites were randomly allocated to current spawning reaches and 8 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 (Figure 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.

Egg boxes were recovered from nearly every site and handling mortality was minor. Egg boxes were planted between November 26 and December 7, 2012 and were retrieved between April 22 and May 2, 2013. Dissolved oxygen was measured midway through incubation between February 25th and March 1st, 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°C 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 m 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%).

Substrate size distributions varied considerably among sites but not between box positions within sites. The multinomial logit substrate model revealed that box position did not significantly affect the relative frequency of particles found in any of the size categories ($F = 1.08$, df = 9, 46, P-value = 0.40). Substrate size distributions also showed considerable overlap in the middle size categories (2-25 mm diameter; Figure 3). Unused shoreline areas contained more sites with higher proportions of particles less than 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 less than 2 mm (Figure 3).

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%. Survival appeared to be higher at sites on the western shore of the lake compared to that on the eastern shore (Figure 1). All three of the sites that had survival greater than 75% were influenced by downwelling and located in LPO's two southern bays. Sites located in the southeastern corner of the lake experienced relatively poor survival, regardless of strata. There were a number of sites relatively poor survival sites amid areas with considerably higher survival, which appeared to suggest microhabitat differences.

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 D50 and site-level variables (Table 2). As for main effects, box position, D50, and the depth of wave disturbance were not significant predictors of egg survival (Table 2; Figure 2). 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 less than 4.0 $mg \cdot L^{-1}$, suggesting a 4.0 $mg \cdot L^{-1}$ 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 $mg \cdot L^{-1}$ and 0% survival (Figure 3). The presence of downwelling had a significant effect on lake-wide 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 (Figure 2). 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, df = 47, P-value = 0.41).

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 not even change the quality of available habitat. The second major challenge to the theory 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 (Figure 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, elaborate mechanisms relating water-level and reproduction have been confirmed using similar *in situ* methods (Fudge and 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 additional 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 behavioral 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 and Donaldson 1968; Hassemer and 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 suggests that kokanee have substantially more habitat available for spawning than just the shallowest few meters 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 D50. 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 behaviors 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 behavior 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 and 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, though 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). Groundwater flow has been shown to be preferentially selected by *O. nerka* and to enhance survival (Garrett et al. 1998). Hall and 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 and 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 southeastern 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 southeastern 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 was missing from the analysis. Many of the sites on the southeastern shore of LPO were hypoxic (<4.0 mg·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. Spawners in the southeastern 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 behavioral 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 southeastern 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 emphasized the importance of placing spawner-habitat relationships into a spatial and behavioral 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 behavioral 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 hypothesis 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 and 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 hypothesis, *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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Table 3.1. Summary of current, historic, and unused shoreline reaches in Lake Pend Oreille, Idaho, USA. 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.

Strata	Total length (km)	Number of sampling units	Incubation sites
Current	6,115	277	22 (21)
Historic	2,128	109	8 (8)
Unused	28,099	1,281	30 (29)

Table 3.2. Parameter estimates for 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. 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 ($mg \cdot L^{-1}$) recorded at the egg box during incubation; disturbance, an index of depth of wave action at each site (decimeter); and downwelling, whether downwelling was detected at a site.

Variable	Coefficient	SE	*F*	df	*P*-value
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

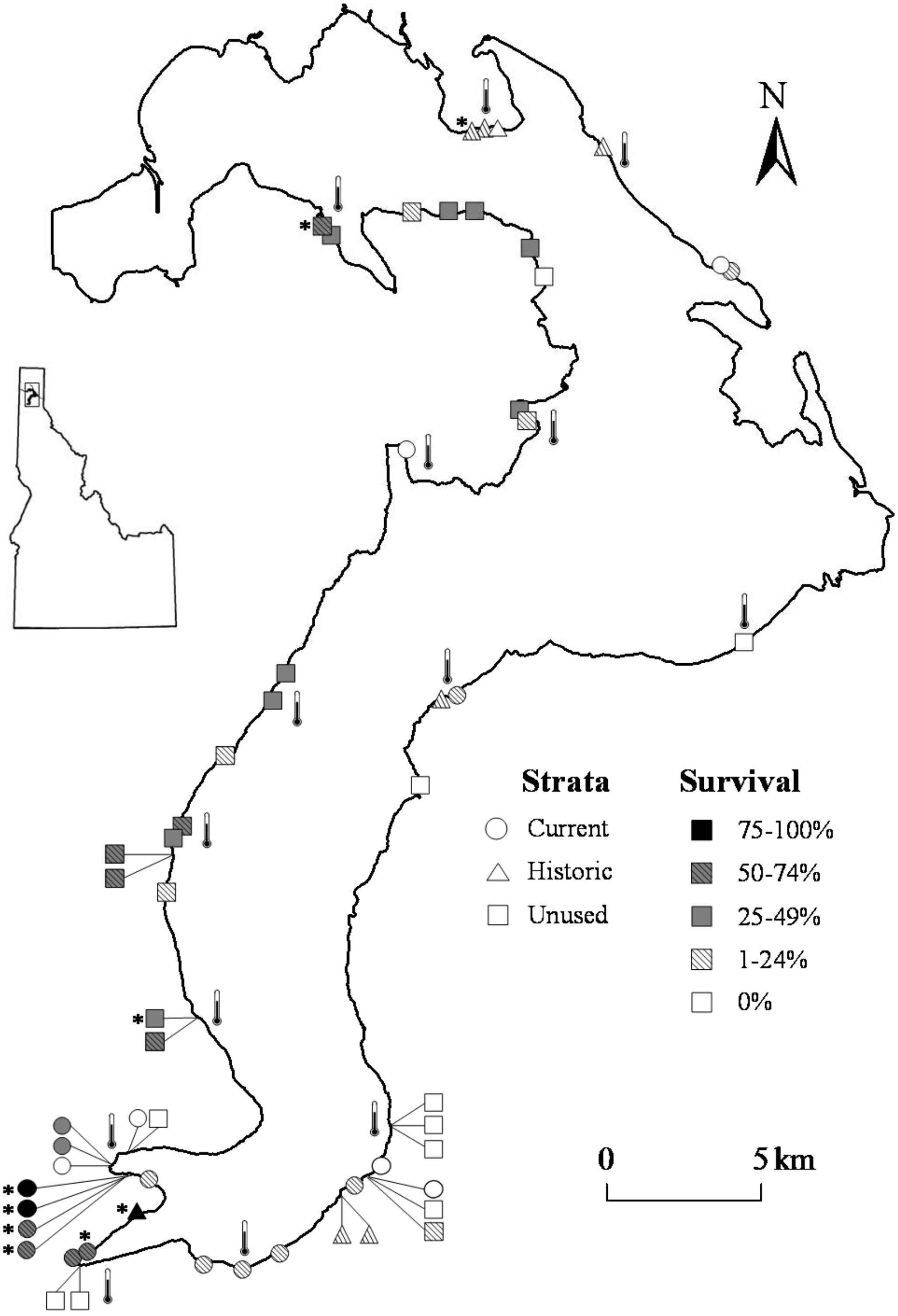

Figure 3.1. Map of Lake Pend Oreille, Idaho, USA. Asterisks denote sites where downwelling was detected and thermometers denote thermograph locations.

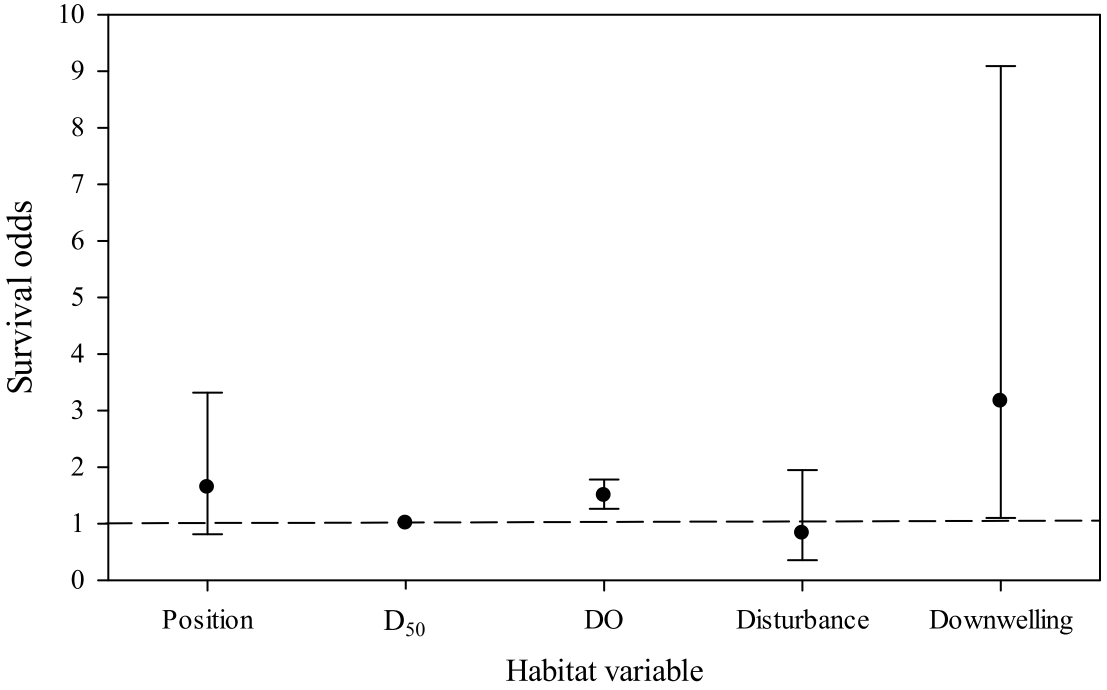

Figure 3.2. Odds ratio estimates for habitat variables measured in an *in situ* kokanee incubation study conducted during winter 2012-2013 at randomly selected shoreline locations in Lake Pend Oreille, Idaho, USA. Survival odds describe the multiplicative effect of a categorical variable or a one unit 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 (decimeters); and downwelling, whether downwelling was detected at a site. To aid in visualization 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.

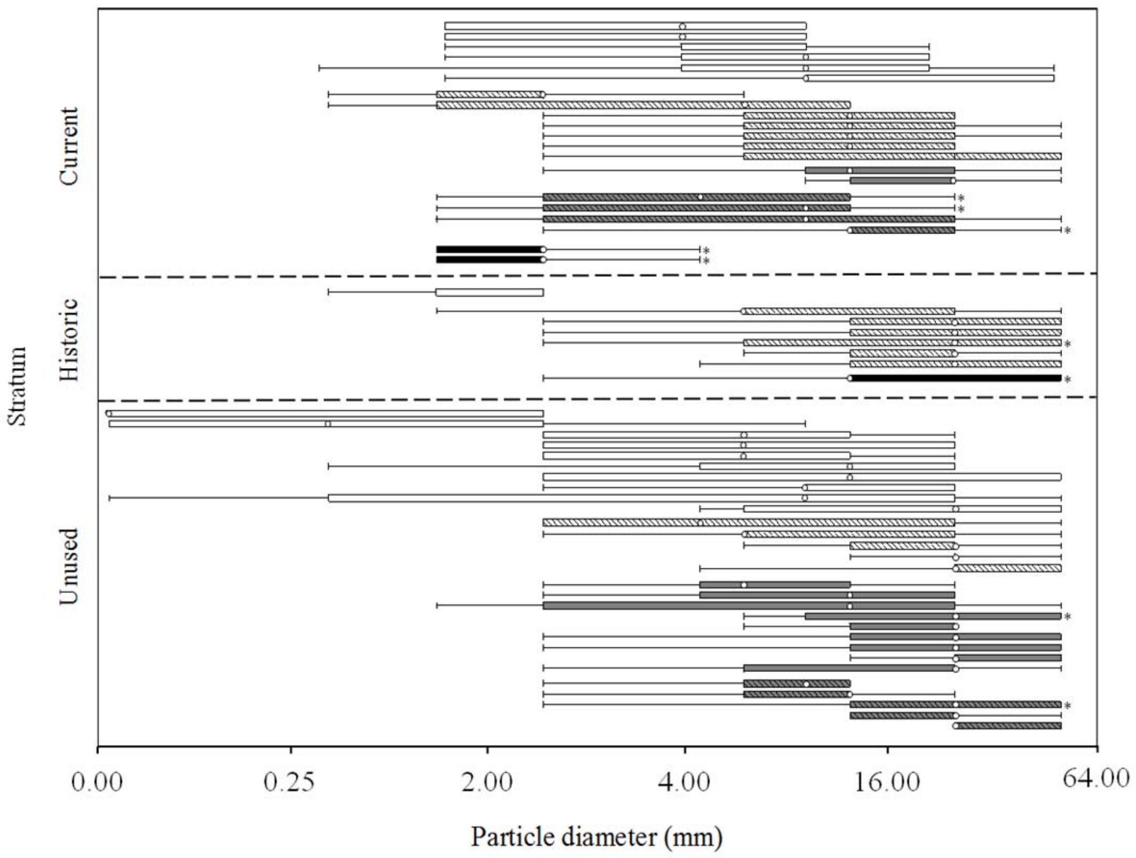

Figure 3.3 Box plots of particle size distributions for 58 substrate samples among current, historic, and unused shoreline locations in Lake Pend Oreille, Idaho, USA. Given the lack of box position effect, substrate size distributions were best summarized by pooling particle weights within size categories 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 boxplots symbolize size categories containing the median particle diameter. Asterisks denote incubation sites were downwelling was detected.

CHAPTER 4: EFFECTS OF WATER-LEVEL MANAGEMENT AND HATCHERY SUPPLEMENTATION ON KOKANEE RECRUITMENT IN LAKE PEND OREILLE, IDAHO

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ABSTRACT

Managers have been attempting to recover the kokanee *Oncorhynchus nerka* (Walbaum) population in Lake Pend Oreille, Idaho for more than three decades using an annual stocking program and an experimental water-level management strategy. This study evaluated the effect of both management actions on kokanee recruitment using a long-term dataset. The existing method for assessing the water-level strategy was evaluated using sensitivity analysis and shown to be unreliable. An alternative assessment method was developed and applied using a bootstrap-based generalized Ricker model. No recruitment response to water-level management was detected. Wild kokanee exhibited a depensatory stock-recruitment relationship, whereas hatchery recruitment was positively related to stocking. Density dependence and variable stocking appeared to explain the synchronized and cyclic recruitment of wild and hatchery fry.

INTRODUCTION

Kokanee *Oncorhynchus nerka* (Walbaum) were introduced to Lake Pend Oreille (LPO) in the 1930s and rapidly became the dominant prey species. Kokanee are a popular sport fish that provide prey for trophy rainbow trout *O. mykiss* (Walbaum) and threatened bull trout *Salvelinus confluentus* (Suckley) in the system (Wydoski & Bennett 1981; Simpson & Wallace 1982; Clarke *et al.* 2005). Kokanee in LPO were Idaho's largest recreational fishery during the1960s and 1970s and supported a commercial fishery from 1945 to 1973 (Paragamian *et al.* 1992). The kokanee population fell into decline beginning in the late 1960s and has since remained at a depressed level (Bowles *et al.* 1991; Wahl *et al.* 2011). A number of perturbations occurred in LPO prior to the decline, including the construction of two dams and the introduction of *Mysis diluviana* (Audzijonyte & Väinölä;

Bowles *et al.* 1991, Chipps & Bennett 2000); however, no alteration appeared to coincide more closely with the decline of kokanee than a change to the lake's water-level regime (Maiolie & Elam 1993).

The Idaho Department of Fish and Game has taken several management actions aimed at improving kokanee year-class strength over the last 30 years. Agreements with hydropower operators prevented significant drawdowns after shoreline spawning began each year and prevented egg desiccation (Hoelscher 1993). Kokanee fry were stocked beginning in 1973 and the Cabinet Gorge Hatchery was completed in 1985, dramatically increasing stocking levels. In the mid-1990s, changes to the stocking program increased hatchery contributions (Paragamian & Bowles 1995); however, managers perceived improvements to stocking practices as a small victory compared to a much larger limiting factor, quality of shoreline spawning habitat (Maiolie 1994; Paragamian & Bowles 1995). Prior to the kokanee decline, the winter water level of LPO remained at or above 626.4 m. In the late 1960s, the water level was regularly dropped an additional 1.3 m immediately prior to when the majority of kokanee spawn on the shoreline. Researchers hypothesized that the lower water-level regime relegated spawners to poor-quality habitat, thereby reducing intragravel survival and recruitment (Maiolie & Elam 1993). Like all salmonids, kokanee incubation success is negatively related to the amount of fine sediment in spawning substrates (Chapman 1988; Kondolf 2000). Drawdowns prior to spawning were thought to have dewatered high-quality substrate that had been purged of fine sediment by wave action during the summer (Fredericks *et al.* 1995). According to this hypothesis, even a slight increase in the winter water level would be expected to result in a sizeable increase in shoreline incubation success. An experimental water-level management strategy was implemented in 1996 to evaluate whether raising the winter water level would improve kokanee recruitment. The plan for evaluating the strategy was that the lake would alternate between years of the preexisting water level (625.1 m) and an experimentally raised water level (626.4 m), then managers would test for an improvement in egg-to-fry survival (EF survival) between the two water levels.

Since the water-level management strategy began, several problems with the EF survival estimator have been identified. The most obvious concern is that recent estimates (2007-present) have described unrealistically high and impossibly low kokanee egg survival (Figure 1). For instance, the 2007 estimate of survival was -85% and the 2010 estimate exceeded 65%, which is well above typical levels for *Oncorhynchus* spp. (Bradford 1995). The second issue is that the estimator provides only point-estimates of survival with no measure of variability. Measures of variability are important for evaluating the strategy because the EF survival estimator is composed of numerous sub-estimates that are all measured with error. Even if intra-annual sampling variability were not an issue, the estimator would still be problematic because it does not account for spawner abundance. Spawner abundance is relevant to assessing the effects of water level because it is possible that additional habitat may only enhance recruitment when spawning densities are high enough for quality habitat to become limiting (Maiolie *et al.* 2002).

The goal of this study was to describe the effect of the water-level strategy and hatchery supplementation on the recruitment of kokanee. The EF survival estimator was evaluated using sensitivity analysis. Theoretical limitations of the estimator and insights from the sensitivity analysis were then used to develop an alternative assessment method. The alternative method incorporated an additional 15 years of data and used principles of resampling and stock-recruitment modeling to test for an effect of the water-level management strategy, while accounting for measurement error and spawner abundance. The influence of hatchery supplementation on kokanee recruitment was also evaluated by examining the effect of annual stocking on the estimated number of hatchery fry. Supplementation was further evaluated by examining the relationship between hatchery and wild fry abundance and exploring factors that influence stocking decisions each year.

METHODS

Kokanee abundance, age structure, and wild-hatchery composition has been monitored in LPO since the 1970s. The LPO kokanee research program can be thought of as having two phases. During the early phase of monitoring (1977-1994), kokanee abundance was estimated annually using only midwater trawling surveys. The lake contained between six and seven management sections, which were treated as strata when kokanee abundance was estimated. Age-length keys were calculated from the trawl catch and used to estimate age-specific abundances (Quinn and Deriso 1999). Another important component of the early monitoring program was estimating the contribution of hatchery kokanee to overall recruitment. Hatchery fry were identified by examining otoliths for diet-induced oxytetracycline or thermal marks (Paragamian et al. 1992; Paragamian & Bowles 1995; Volk et al. 1999). Between 1995 and 2001, the research program grew more complex as new sampling techniques were added to the annual assessments. The number of lake management sections was also reduced to three by combining previously adjacent lake sections. Additional sampling techniques included hydroacoustic surveys, which began in 1995, and fry netting surveys, which began in 1999. Hydroacoustic estimates of kokanee abundance used the same stratified design as the midwater trawling survey. Although both methods are still used to estimate abundance annually, hydroacoustic estimates are considered to be more reliable. Midwater trawling is currently used to provide demographic information (e.g., age, maturity), although trawling abundance estimates remain valuable for comparison with historical data (Wahl *et al.* 2011). Fry netting was added to the annual sampling program because of concerns that smaller fry were not being retained by the relatively large mesh in the midwater trawl net. This was an important issue for estimating the proportion of wild versus hatchery fry, because hatchery fry tended to be larger at the time when trawling occurred, and thus more easily sampled (Maiolie *et al.* 2002).

Midwater trawl surveys in LPO have been conducted in the same manner since the program began, although two different types of trawl nets have been used. Midwater trawling occurred annually over a span of three to five nights between 8 August and 22 September during the dark phase of the moon. Trawling stations and headings were randomly selected within each of the lake's management sections. The vertical distribution of kokanee was identified using a depth sounder. Stepwise oblique tows were then performed to sample the entire vertical distribution of kokanee. The otter trawl, which was used between 1983 and 2002, had a 3 × 3 m mouth, was 13.7 m in length, and contained graduated mesh (i.e., 32 mm, 25 mm, 19 mm, and 13 mm in the body to 6 mm at the cod end). The fixed frame trawl, used from 2003 to present, had a 3 × 2.2 m mouth, was 10.5 m in length and contained the same mesh sizes as the otter trawl. The speed of the trawl was approximately 1.5 $m \cdot s^{-1}$ and the time spent at each step was approximately 3.0 minutes. Midwater trawling surveys were used to estimate abundance of kokanee by expanding density estimates in each section, based on the volume of water kokanee were estimated to occupy. Information about the sex and maturity of adult kokanee was gathered by dissecting all kokanee greater than 170 or 180 mm that were captured in the trawl.

Hydroacoustic surveys replaced midwater trawling as the primary method for estimating kokanee density in LPO. Surveys were performed at a speed of approximately 1.5 $m \cdot s^{-1}$ using a portable Simrad EY500 or EK60 echo sounder, which was set to ping at either 0.6 or 1.0 s intervals (Maiolie *et al.* 2002; Wahl *et al.* 2011). The number of fish present along a transect was estimated with echo integration techniques. The density of fish was then estimated using the mean target strength (dB), nautical area scattering coefficient, and volume of pelagic habitat that kokanee are assumed to occupy (Parker-Stetter *et al.* 2009). The abundances of two size groups of kokanee were estimated separately by partitioning traces according to target strength. Targets between -45.9 dB and –33 dB were classified as age-1 to age-5 kokanee, while targets between –33 dB and -60.0 dB were classified as age-0 kokanee. Two hydroacoustic sampling designs have been used in LPO. Surveys in 1995 and 1996 consisted of 12 randomly selected transects per lake section that were approximately 1.3 km in length. The number of transects was increased to 20 between 1997 and 1999 and the length of individual transects was reduced to approximately 0.8 km. Since 2000, IDFG has used a systematic sampling design with six to eight uniformly spaced zig-zag transects per lake section, with transects between 3.4 to 9.5 km in length. The most recent (i.e., 1995-present) method for estimating age-specific abundances of kokanee involves combining abundance estimates from hydroacoustic estimates with age information from midwater trawling (Wahl *et al.* 2011).

Fry netting surveys were conducted in much the same way as the midwater trawling survey. Between five and eight trawl transects were randomly selected within each lake section. Fry were sampled during the new moon phase, typically in early September. The vertical distribution of fry was identified using an echosounder and between three and five stepwise oblique tows were performed. The net was towed at a speed of approximately1.5 $m \cdot s^{-1}$ for 3 minutes per step. The fry net was 1.27 m × 1.57 m wide and 5.5 m in length. The net was composed of 0.8-mm × 1.6-mm bar mesh size and contained a 1 mm sampling bucket on the cod end. Fry netting surveys have been used to estimate lake-wide fry abundance, but their primary purpose was to provide unbiased estimates of the proportion of hatchery and wild age-0 kokanee.

Another important source of information about kokanee in LPO was from annual egg-take operations at a weir located on Sullivan Springs Creek. The weir operates from mid-November to mid-December. Gametes are collected from spawners trapped by the weir and used for hatchery rearing. The majority of kokanee fry are stocked the following June or July. The weir provides information about spawners by recording the number and sex of kokanee trapped each year. In addition to spawner counts, fecundity is also estimated.

Egg-to-fry survival estimator

The kokanee EF survival estimator used data from many of the same sampling techniques used in the monitoring and recovery effort. Abundance and demographic information is combined in an equation that divides the estimated number of shoreline-origin fry by the estimated number of eggs that were deposited on the shoreline in the previous year. The resultant estimator is:

$$\text{EF survival} = 100\% \times \left[\frac{\sum_{i=1}^{3}(f_i \times w_i)}{\left[\left(\left[\sum_{i=1}^{3}(a_i \times m_i)\right] \times 0.5\right) - h\right] \times e}\right]$$

where f_i is a lake section-specific hydroacoustic fry abundance estimate, w_i is an estimate of the lake section-specific proportion of wild fry estimated from fry netting, a_i is a lake section-specific hydroacoustic adult abundance estimate (age 1-5) from the previous year, m_i is a lake section-specific estimate of the proportion of sexually-mature adults (age 1-5) from the previous year, 0.5 is the assumed proportion of females, h is the number of mature females captured in the weir at Sullivan Springs Creek during the previous year, and e is an estimate of mean fecundity for those female kokanee captured in the weir (Maiolie *et al.* 2005). Females captured at the weir are subtracted to eliminate tributary spawning kokanee from consideration.

Sensitivity analysis is a technique used to explore the relative influence of fixed and random components within an estimator or model (Starfield & Bleloch 1986; Hilborn & Peterman 1996; Nicolson *et al.* 2002). This technique is helpful for evaluating *ad hoc* estimators because it can be used to reveal the component(s) with the greatest influence on the estimate. The simplest method is known as piece-wise sensitivity analysis, which involves two steps: first a baseline output is established for the estimator or model being evaluated, then individual components are altered one at a time while all other components are held constant. Each component's deviations from the baseline are then compared and used to identify the component(s) with the greatest influence on the estimate. The kokanee EF survival estimator was evaluated by calculating the mean of each of the sub-estimates from 1996-2011 and inserting them into the equation to produce a baseline EF survival estimate (5.8%). Altered sub-estimates were then inserted into the estimator piecewise and the difference in EF survival percentage from the baseline was calculated. Alterations to sub-estimates were based on the distribution of observed sub-estimates during the study period and included ±10% and ±20% of the mean, ±10% and ±20% of the range, and the maximum and minimum (Table 1). The lake section-specific nature of abundance, maturity, and fry origin estimates was ignored in order to measure the general influence of each sub-estimate and reduce the number of permutations in the analysis.

Bootstrap stock-recruitment model

A model-based method for evaluating the water-level hypothesis was developed using data from annual midwater trawl surveys. The water-level hypothesis was tested by combining bootstrap regression methods with a generalized Ricker stock-recruitment model. The purpose of using a stock-recruitment model was to account for density-dependent dynamics, while bootstrapping was used to incorporate intra-annual sampling variability into the parameter estimates (Efron & Tibshirani 1993). The analysis used midwater trawling surveys conducted from 1983-2012.

Midwater trawl data were ideal for testing the water-level hypothesis because they provided both abundance and demographic information, and the sampling protocol has changed little over time. Several measures were taken to ensure that abundance estimates were comparable over the time series. Changes to the trawling program over time included a reduction in the number of strata from seven to three, a small change in the way the volume of water sampled by the trawl was calculated for each transect, and a switch from an otter trawl to a fixed-frame trawl in 2003. Changes in the number of strata across years were accounted for by retrospectively calculating abundance estimates using only the three current lake sections (Cochran 1977). In 1992, the time between trawl steps was included in the calculation of the volume of water filtered by the net (m^3), which led to an overall decrease in the estimated abundance of kokanee from that point forward. Available data revealed that the time between steps was relatively consistent during much of the time series. Accordingly, abundance estimates were standardized for this study by ignoring the time between steps in the later years of the time series. This analysis also assumed that gear selectivity was not affected by changes in the type of net, because mesh sizes did not change.

Age and origin information from midwater trawling were used to calculate annual estimates of wild fry and mature wild kokanee. Only wild kokanee were included in the stock-recruitment analysis because kokanee of hatchery origin primarily spawn in the lake's tributaries (Maiolie 1994; Wahl *et al.* 2011). The abundance of wild fry was measured annually, whereas the abundance of wild spawners was estimated by carrying the proportion of wild fry forward in time and applying it to age-specific estimates of mature kokanee. The analysis made several assumptions about the ontogeny and behavior of hatchery and wild kokanee: (1) all hatchery-origin kokanee spawned in tributaries and all wild kokanee spawned on the shorelines; and (2) the ratio of hatchery to wild fry at age 0 remained constant within each cohort; and (3) the relative proportion of hatchery and wild kokanee was comparable between the midwater trawl and the fry net. The first of these assumptions is no different from the one made by the EF survival estimator, which assumed that all hatchery-origin and tributary spawners could be removed by subtracting the number of female spawners captured the Sullivan Springs Creek weir. The second assumption could only be assessed for the most recent years (2007-2012), where both age and origin of the entire trawl catch was estimated using thermal marks (Wahl *et al.* 2011). Abundance estimates based on thermal marks suggested that the ratio of hatchery to wild kokanee remained largely unchanged through time for a given cohort.

Stock-recruitment modeling has a long history and a number of modifications have been made to the original models. Ricker (1954) introduced the first model, which describes a negative density-dependent relationship between the parental stock size (S_t) in one year and the number of recruits that are produced in the following year (R_{t+1}):

$$R_{t+1} = \alpha S_t e^{-\beta S_t}.$$

The α parameter is the number of recruits-per-spawner when the stock level is zero and the β parameter is the rate at which the number of recruits decreases in relation to increasing stock size (depensation). Density dependence occurs for a variety of reasons including predation, competitive interactions, and habitat limitations (Rose *et al.* 2001; Greene & Guilbault 2008). The degree of depensation can also be affected by variables that change from year to year (Olsen *et al.* 2011). Intra-annual variation can be modeled using a generalized Ricker model which allows the exponentiated portion of the model to be expressed as a linear combination of spawning stock size and one or more auxiliary variables (Adkison *et al.* 1996). Although other stock-recruitment models (e.g., Beverton-Holt, Cushing) can be similarly generalized (Quinn & Deriso 1999), the Ricker model was selected for this analysis for several reasons. First, recruitment of *O. nerka* is often described using the Ricker model (Martell *et al.* 2008; Askey & Johnston 2013); in fact sockeye salmon stock-recruitment relationships are often used as examples in texts on stock assessment (Hilborn & Walters 1992; Haddon 2011). Another reason for choosing the Ricker model was that it has been used previously to describe kokanee recruitment in LPO (Fredericks *et al.* 1995; Maiolie *et al.* 2006). A technical reason for selecting the generalized Ricker model is that it can be easily linearized by dividing the number of recruits by the number of spawners and taking the natural logarithm of both sides; this avoids subjectivity in specifying starting values for nonlinear model fitting algorithms (Ritz & Streibig 2008). For the purposes of this analysis, a single parameter (γ) and indicator variable (X_t) were added to the exponentiated portion of the equation to allow changes in the degree of depensation between years with high and low water levels:

$$R_{t+1} = \alpha S_t e^{-\beta S_t + \gamma X_t}.$$

High water years were defined as those when the minimum water level was above 626 m. If the water-level hypothesis was supported, then the curve for years with the higher water level would be expected to have a greater apex and would not decrease as rapidly with increasing stock size as the curve for the lower water level.

Point-estimates of wild kokanee fry and wild mature kokanee abundance alone could be used estimate the stock-recruitment relationship; however, this approach would not account for the large amount of sampling variability tied to each estimate. Measurement errors are known to produce obscure relationships and misleading parameter estimates in stock-recruitment models (Ludwig & Walters 1981; Walters & Ludwig 1981). Given the potential for measurement errors to interfere with parameter estimation, a nonparametric bootstrap approach was used propagate the sampling-related uncertainty into parameter estimates (Efron & Tibshirani 1993). Nonparametric bootstrapping does not make distributional assumptions, except that the observed distribution approximates the true distribution. The method involves iteratively sampling independent observations with replacement to approximate the sampling distribution of a given statistic. Bootstrapping principles can be applied to regression models for the purpose of calculating robust parameter estimates. Bootstrap regression analysis is performed in one of two ways: either by resampling residuals or vectors of observations and predictors. Vectors of observations and predictors were resampled for this analysis because this approach makes fewer assumptions about model form and homoscedasticity (Chernick 2008). A rescaled form of the bootstrap was used for this study because naïve bootstrap methods underestimate variance for data from complex sample surveys (Rao & Wu 1988). Rescaling methods involve finite population adjustments and simulated sampling of fewer observations per strata than were originally used in the survey. Three fewer observations were resampled from each strata for this analysis based on the recommendations of Smith (1997).

The model fitting process required three steps: (1) a distribution of 10 000 bootstrap abundance estimates was generated for both wild age-0 and wild mature spawners for each brood year; (2) distributions of abundance estimates were sampled and used to fit separate stock-recruitment models, each containing a fixed vector of water levels; (3) distributions of parameter estimates across all models were then summarized and interpreted. The significance of water level as a predictor of wild recruitment was assessed based on the coverage of bias-corrected and accelerated 95% confidence intervals (Efron & Tibshirani 1993). Intervals containing zero indicate that a parameter does not differ significantly from zero at the $\alpha = 0.05$ level (Fox & Weisberg 2011). Minimum water levels remained fixed during the model fitting process because water levels are continually monitored by dam operators and the minimum for each year was measured with a high level of accuracy. Bootstrap distributions of all abundance and parameter estimates were visualized during the analysis using frequency histograms and normality plots. A total of 10 000 bootstrap iterations where performed based on recommendations by Smith (1997). The convergence behavior of estimates was also examined to ensure that enough iterations were performed.

Hatchery supplementation

Hatchery stocking and the abundance of wild and hatchery fry were examined over the time series. Linear regression was used to examine the relationship between the number of fry stocked and the number of hatchery fry sampled in the summer using the trawl. The relationship between hatchery and wild fry abundances was also evaluated using linear regression. The abundance of adult kokanee can be used to inform decisions about how many kokanee should be stocked the following year, so stocking levels were examined in relation to the abundance of age-3 to age-5 kokanee during the previous year.

RESULTS

Sensitivity analysis revealed that most of the sub-estimates had a relatively minor influence on the EF survival estimator, however, alterations to the mature proportion sub-estimate exposed profound instability in the estimator (Figure 2). Fry abundance, the abundance of female spawners captured in the weir, and fecundity appeared to have a relatively minor influence on EF survival estimates. Changes to adult abundance had little effect on the estimator, except for the 15-year minimum adult abundance estimate, which produced a difference in survival of nearly 60%. Changes to the mature proportion had the greatest effect on outcome of the estimator because this quantity has the largest effect on the lake-wide estimate of mature female kokanee. As the mature proportion was adjusted downward the EF survival estimator produced an estimate that was greater than 100% followed by an estimate less than 0%. When the mature proportion sub-estimate was decreased by 20% of its range, 7 000% was produced because such a large number of tributary spawners were subtracted that the number of eggs that were estimated to have been deposited in one year was less than the number of fry estimated in the following year. When the minimum mature proportion was input into the estimator, the survival estimate was -40.8% because more mature female spawners were subtracted from the lake than were estimated to exist. The mature proportion sub-estimate appeared to have an important bearing on the outcome of the estimator; however, the previous examples illustrate that subtraction of females spawners from the weir also contributed greatly to the production of unrealistic estimates.

The generalized Ricker model appeared to accurately represent the wild stock-recruitment relationship in LPO, but did not provide evidence to support the water-level management strategy. Estimates of intra-annual sampling variability illustrated that there was much greater uncertainty in estimates of wild mature kokanee abundance than in estimates of wild fry abundance (Figure 3). Bootstrap distributions of wild fry and wild mature kokanee estimates appeared normal based on histograms and normality plots. The distribution of wild mature kokanee estimates in some years were discretized due to the relatively low number of trawl transects where mature kokanee were detected. Estimates and confidence intervals for wild age-0 kokanee and mature kokanee exhibited the dome-shaped pattern, characteristic of the Ricker model. Confidence intervals for the water-level parameter spanned zero, indicating that years of higher water-level did not significantly influence the degree of depensation (Table 2). Furthermore, the point-estimate for the water-level parameter was negative, which is the opposite of what the water-level management strategy would predict (Figure 4).

Recruitment of wild and hatchery kokanee fry appeared to be synchronized over much of the time series, and also appeared to correspond with fluctuations in stocking levels (Figure 5A). Hatchery stocking and hatchery abundance were positively and linearly related to stocking rate ($R^2 = 0.66$; $P < 0.01$) and the abundance of wild fry ($R^2 = 0.15$; $P = 0.02$). Stocking was negatively related to the estimated abundance of age-3 to age-5 kokanee estimated from midwater trawling during the previous year (Figure 5B).

DISCUSSION

Sensitivity analysis was a valuable tool for understanding complications with the EF survival estimator in LPO. The analysis made a large assumption about the independence of sub-estimates but proved useful for identifying problematic components in the estimator. The EF survival estimator produced unreasonable estimates because of a combination of structural and sampling-related issues. The structural issue is that the equation contains a subtraction that allows for estimates of negative spawners or a low enough number of spawners that survival exceeds 100%. The possibility of arriving at unreasonable survival estimates does not necessarily make an estimator uninformative. What makes the estimate untenable are the issues resulting from the fact that the midwater trawling underestimates the abundance of mature fish. Underestimated mature abundances bring the estimator near a threshold in which small changes to the mature proportion sub-estimate cause unreasonable and nonlinear responses. Evidence of this profound sensitivity can even be seen when small changes are made to previous EF survival estimates. For instance, the EF survival estimate for 2007 was -85.3%, but if the estimated proportion of mature kokanee had been 1% higher in 2007, then the estimate would have been 30.2%.

Although the EF estimator used in LPO is highly intuitive, it illustrates many of the issues that can occur when complex *ad hoc* estimators are constructed. The following should be considered when constructing *ad hoc* estimators: (1) avoid combining numerous sampling techniques, (2) account for sampling variability in estimators, and (3) examine the properties of estimators using sensitivity analysis or simulation. Combining data from various sampling methods is problematic because all sampling methods are inherently biased (Bonar *et al.* 2009). In LPO, the proportion of mature kokanee was estimated using midwater trawling, which is known to underestimate the abundance of large kokanee (Parkinson *et al.* 1994; Beauchamp *et al.* 1997). Although trawling is biased, standardized surveys are still very useful. Problems with the EF survival estimator arose when the underestimate of abundance was combined with "census" information from the weir. Characterizing the uncertainty surrounding *ad hoc* estimates is crucial for insuring that intra-annual variability does not give false impressions or obscure important patterns (Peacock & Holt 2012). If the variability surrounding the EF survival estimates in LPO was calculated from the beginning of the water-level management strategy, problems with the EF survival estimator might have been identified earlier. Another reason for describing the uncertainty of estimates is that changes in variability are often just as valuable as the point-estimates for conveying useful ecological information (Benedetti-Cecchi 2003). When *ad hoc* estimators take on unusual structures, analytical variance calculations can become daunting. Resampling methods, such as the jackknife or bootstrap, are relatively simple methods for calculating variance under such circumstances (Dixon 1993). Sensitivity analysis and resampling methods are useful tools for testing the properties of complex estimators, whether data are available or not (Starfield *et al.* 1995). Resource managers should explore the properties of *ad hoc* estimators before and during their use by testing different combinations of inputs based on existing data, prior experience, or information from the literature (Starfield & Bleloch 1986; Nicolson *et al.* 2002).

The generalized Ricker model was a dramatic improvement over the *ad hoc* EF survival estimator for several reasons. The bootstrap-based generalized Ricker model overcame the theoretical limitations of the EF survival estimator by incorporating the abundance of spawners. A reduction in the number of sampling techniques used in the analysis prevented some of the issues in the original assessment method and enabled an additional 14 years of data to be incorporated. Although midwater trawling is known to be biased, the analysis was valuable because sampling was standardized and did not combine multiple data types. Bootstrap regression analysis also allowed parameter estimates to reflect intra-annual sampling variability. A problem common to all stock-recruitment investigations is that there are numerous stock-recruitment models to choose from and few observations to help inform the decision as to what model should be used (Haddon 2011). Fortunately, the sampling error surrounding observations in this study appeared to suggest that the Ricker stock-recruitment model was an appropriate choice.

Unfortunately, the model-based assessment method was affected by some of the same sampling-related issues as the original assessment method and also required additional assumptions. The model-based method was influenced by the low detection probability of mature fish, which indicates that minute increase in the number of mature kokanee detected might have had a large effect on the mature spawner estimates during some years. The low detection of mature kokanee is a recent problem that may be due to unprecedented lake trout *Salvelinus namaycush* (Walbaum) predation (Hansen *et al.* 2008, 2010). The effect of low detections was somewhat dampened by the fact that additional years were included in the analysis (1983-1995), many of which had higher densities of mature fish. Another disadvantage of using a model-based assessment method was that additional assumptions about the consistency of parameters through time were necessary (Haddon 2011; Askey & Johnston 2013). One factor that could have altered stock-recruitment parameters during the time series was the density of mysid shrimp. The introduction of mysid shrimp has had a profound effect on the community composition and seasonable distribution of zooplankton in LPO (Rieman & Falter 1981). Since the mid-1970s, the presence mysid shrimp have been considered to be a factor that restricts kokanee recruitment (Rieman & Falter 1981; Bowles *et al.* 1991; Chipps & Bennett 2000). Adult mysid density has remained relatively constant for the last four decades in LPO (Wahl *et al.* 2011). Although, in the final two years of the time series of this study, mysid density dropped by two orders of magnitude (unpublished data) and coincided with the highest kokanee recruitment in 30 years. This unusually high recruitment year might suggest that the decline in mysids has altered kokanee recruitment dynamics, however, additional monitoring is needed.

Findings from the model-based assessment of water-level are relevant to regulated lakes and reservoirs where there is potential for conflict between the needs of shore-spawning species and the water-level regimes desired by dam operators. Water-level alterations have been known to negatively affect the shoreline incubation success of kokanee in a number of systems (Stober *et al.* 1979; Matthews 1981; Decker-Hess & Clancey 1990; Modde *et al.* 1997). The water-level hypothesis in LPO is unique because it is the only known case in which spawning habitat quality is thought be primary the source of mortality (Maiolie and Elam 1993). In other systems and earlier in LPO's history, kokanee were negatively affected by drawdowns during incubation, which dewatered shoreline redds and desiccated eggs. Although this study was unable to establish a link between water-levels and spawning habitat quality, poor recruitment resulting from water-level management is not unprecedented. Water-level management has been shown to negatively affect the recruitment of several other shore-spawning species by altering littoral habitat conditions (Fudge & Bodaly 1984; Gafny *et al.* 1992). There are several reasons why an effect of water-level may not have been detected in LPO. One possibility is that there were too few spawners during high water years for a significant increase to be detected by the model. After all, the three highest spawner abundances occurred during years with a low water level (Figure 4). Another possibility is that water-level effects were obscured by latent variables such as changes in food availability or predation. On the other hand, if water levels were the cause of the initial decline in the kokanee population, it would seem that an effect would be obvious. A more definitive and more costly way to evaluate the water-level strategy would be to conduct a large-scale field study. Ideally, such a field study would both establish that spawning habitat in LPO is limited and directly compare kokanee intragravel survival above and below the low water mark.

Synchrony between the recruitment of wild and hatchery fry over much of the 30-year time series was an interesting discovery. Peaks in hatchery-origin fry appear to be explained by higher stocking. Peaks in wild fry during many of the same years are more difficult to explain, but the answer appears to be related to an unawareness of underlying density-dependent dynamics when stocking decisions were made. Managers consult abundance estimates from the previous year when they make stocking decisions and are more likely to stock more fish when they perceive that there will be a relatively low number of spawners. It appears that peaks in overall recruitment occurred when low spawner densities compelled managers to stock more fry, while the same low spawner density also produced relatively high wild recruitment according to an underlying depensatory stock-recruitment relationship. The depensatory relationship appears to affect wild fry but not hatchery fry, which are stocked 2-3 months later. In this way, peaks in recruitment appear to be produced because a large numbers of hatchery fry were added to what was already a relatively strong year class of wild fry.

The stock-recruitment relationship and stocking decisions explain coincidentally high recruitment of hatchery and wild fry, but not the apparent periodicity in recruitment. Peaks in the recruitment of kokanee appeared to occur every 4-5 years, which is consistent with the typical age-at-maturity of kokanee in LPO. Sockeye salmon populations are well known for similar quasi-periodic peaks in recruitment, which have been studied extensively (Levy & Wood 1992; Ricker 1997). Potential mechanisms that promote cycling are genetic differences and predator responses, or delayed density dependence where recruits compete with older age classes (Myers *et al.* 1997). Myers *et al.* (1998) described how dynamical processes can produce periodic recruitment without the need for outside mechanisms. The extent to which sockeye salmon fluctuations relate to kokanee is unclear, given differences in life history. What is clear, however, is that kokanee are profoundly affected by density-dependent growth, which often influences survival, age-at-maturity, and fecundity (Rieman & Myers 1992; Grover 2005; Patterson *et al.* 2008). One explanation for periodicity of kokanee recruitment in LPO might be that larger cohorts experience lower growth and delayed maturation, ultimately resulting in relatively few spawners five years later. Lower growth results in higher overwinter mortality early in life (Steinhart 2003) and delayed maturity would mean that a smaller portion of the cohort would spawn in five years. Low densities five years later would then be expected to result in a peak in stocking and high wild recruitment according to the mechanism that was previously discussed. This explanation is highly speculative, and overlooks several important ecological changes in the previous decade (e.g., lake trout predation). Nonetheless, the concept provides a hypothesis for future research that could easily make use of existing data.

Findings from both the stock-recruitment model and the examination of recruitment patterns suggest that the narrative concerning kokanee recovery efforts should be refined. This study failed to find evidence that the habitat provided by higher water levels enhances wild recruitment, thereby raising doubts as to the role water-level changes had in causing the decline of kokanee. Hatchery supplementation, which was viewed as only having a minor effect on recruitment, appears to be an important management tool for influencing the recruitment of kokanee in LPO. Coincident peaks in the recruitment of hatchery and wild kokanee appear to be explained by interplay between density-dependent stock-recruitment dynamics and the decision process involved with stocking. Apparent cycles in kokanee recruitment are difficult to explain, but may suggest that early life history is not the most important factor limiting kokanee recovery. Additional research should evaluate the role that density-dependence later in life might play in limiting the recovery of kokanee in LPO.

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Table 4.1. Summary of inputs used to evaluate kokanee shoreline egg-to-fry survival in response to water-level management in Lake Pend Oreille, Idaho. Minimum lake elevations below and above 626 m are described by low and high water-levels, respectively. Hydroacoustic surveys were used to estimate fry abundance and adult abundance. The proportion of mature age-1 to age-5 fish was estimated using midwater trawling. Tributary spawners describe the number of female kokanee captured using a weir located on Sullivan Springs Creek. Fecundity was estimated from a sample of kokanee collected at the same weir.

Brood year	Minimum water-level	Fry abundance (millions)	Adult abundance (millions)	Proportion mature	Tributary spawners	Fecundity	Egg-to-fry survival (%)
1996	Low	2.67	0.93	0.32	29,039	444	4.89
1997	High	2.58	7.33	0.11	12,735	353	1.82
1998	High	1.02	5.76	0.01	1,619	335	9.60
1999	High	6.02	5.03	0.06	26,908	333	13.95
2000	Low	5.03	2.82	0.14	65,297	379	9.85
2001	Low	3.63	3.65	0.09	33,623	417	6.49
2002	Low	1.15	4.81	0.02	17,796	481	7.79
2003	High	0.43	5.21	0.02	14,235	320	3.46
2004	Low	1.26	5.37	0.08	43,351	351	2.03
2005	High	5.67	2.62	0.15	50,023	406	9.41
2006	High	6.41	3.59	0.07	35,453	511	12.70
2007	Low	1.98	3.29	0.01	21,234	565	-85.32
2008	High	0.65	2.70	0.01	1,133	496	36.03
2009	Low	1.80	2.20	0.02	2,112	389	20.61
2010	Low	3.93	2.51	0.03	23,563	420	64.63
Mean		2.95	3.85	0.08	25,208	413	
Minimum		0.43	0.93	0.01	1,133	320	
Maximum		6.41	7.33	0.32	65,297	565	
Range		5.98	6.39	0.32	64,164	245	

Table 4.2. Summary of parameter estimates from a bootstrap-based generalized Ricker stock-recruitment model used to evaluate the effect of water-level management on shoreline kokanee recruitment in Lake Pend Oreille, Idaho. Lower (LCL) and upper (UCL) 95% confidence limits are based on bias-corrected and accelerated percentiles. Confidence interval overlap with zero indicates that parameters do not significantly differ from zero at $\alpha = 0.05$.

Parameter	Estimate	LCL	UCL
α	145.88	97.10	235.92
β	-1.24×10^{-5}	-1.60×10^{-5}	-9.79×10^{-6}
γ	-0.40	-0.93	0.06

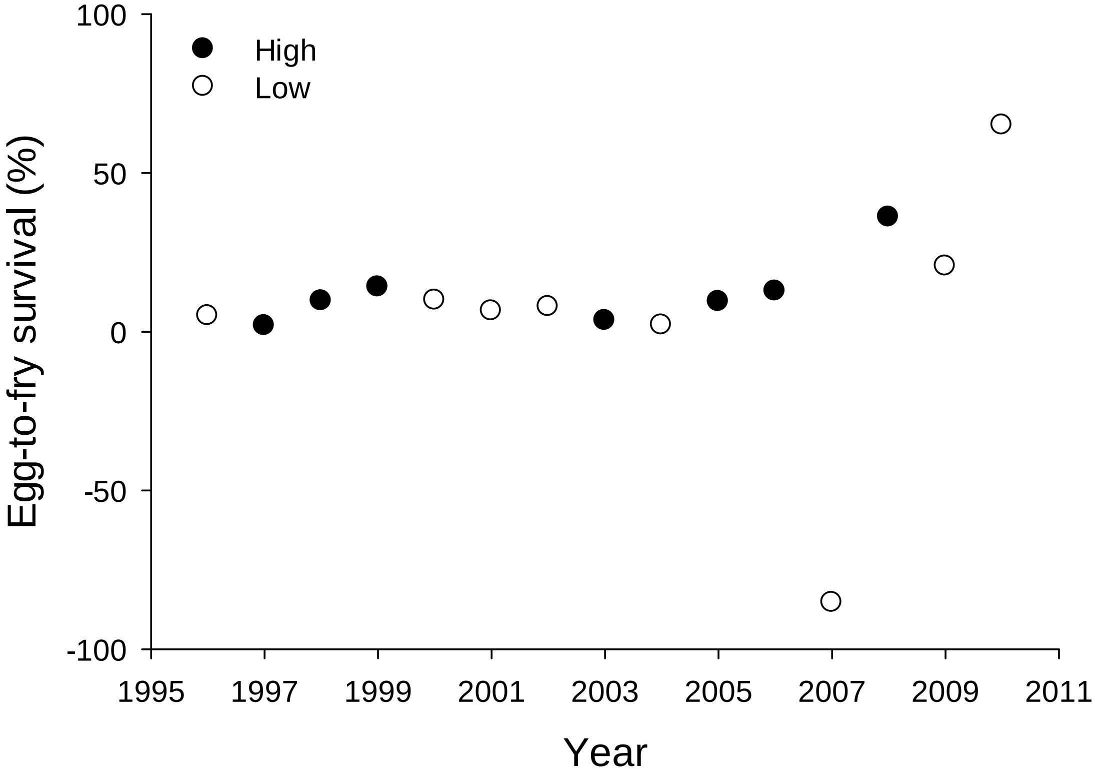

Figure 4.1. Egg-to-fry survival estimates of kokanee used to evaluate a recruitment response to low and high minimum winter water-levels in Lake Pend Oreille, Idaho.

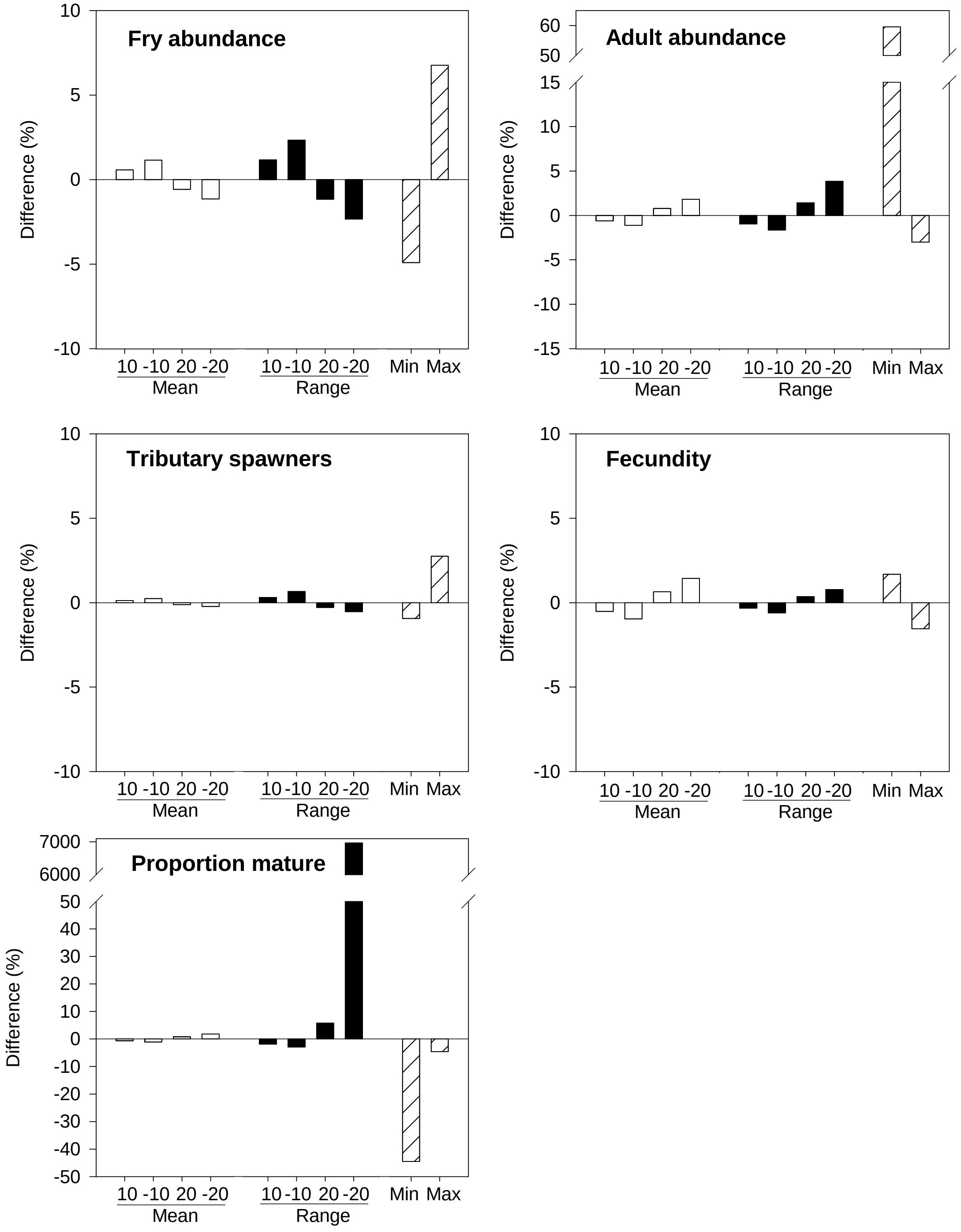

Figure 4.2. Results of a piecewise sensitivity analysis used to evaluate a kokanee egg-to-fry survival estimator in Lake Pend Oreille, Idaho from 1996 to 2010. Each sub-estimate was evaluated by inserting ±10% and ±20% of the mean, ±10% and ±20% of the range, and the maximum and minimum of each sub-estimate's distribution into the estimator and calculating the difference from the baseline.

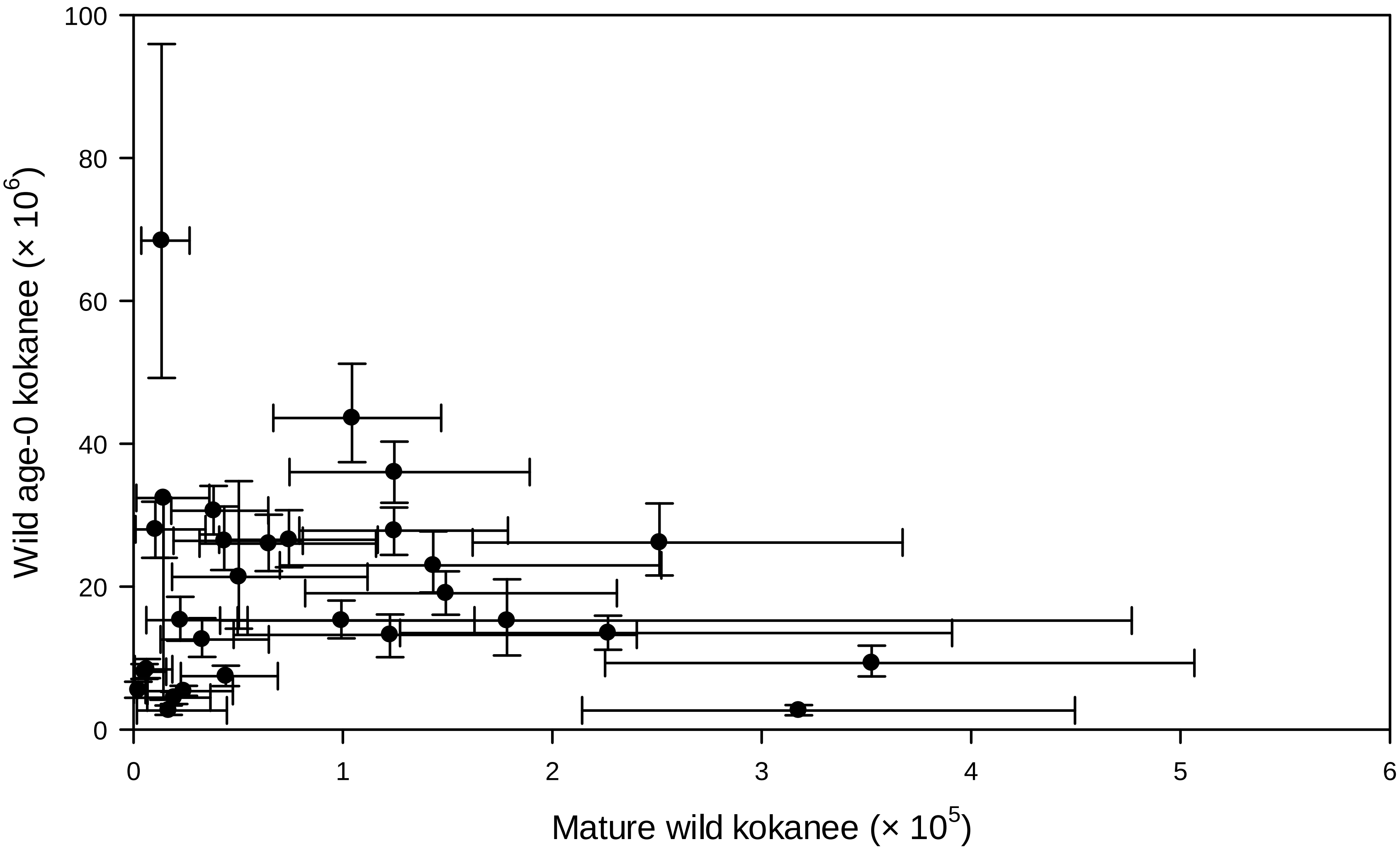

Figure 4.3. Wild age-0 kokanee abundance from 1983 to 2011 versus wild mature abundance of kokanee from the previous year in Lake Pend Oreille, Idaho. Abundances and demographic information were estimated using midwater trawling. Error bars denote 95% bias-corrected and accelerated confidence intervals.

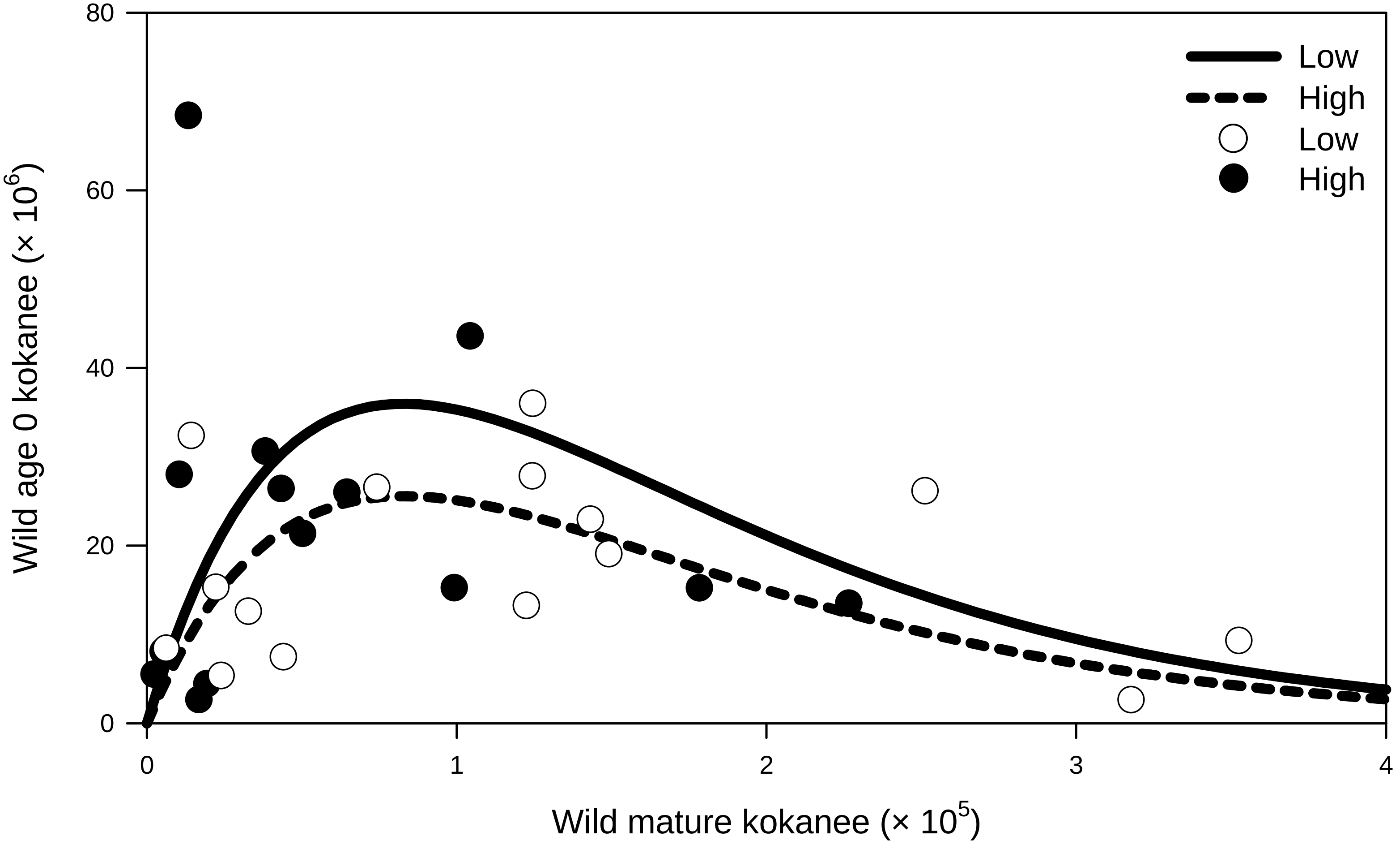

Figure 4.4. Wild age-0 kokanee abundance from 1983 to 2011 versus abundance of wild mature kokanee from the previous year in Lake Pend Oreille, Idaho, estimated using midwater trawling. Lines depicted fitted values for years of high (>626 m) and low (<626 m) water levels from a bootstrap-based generalized Ricker stock-recruitment model.

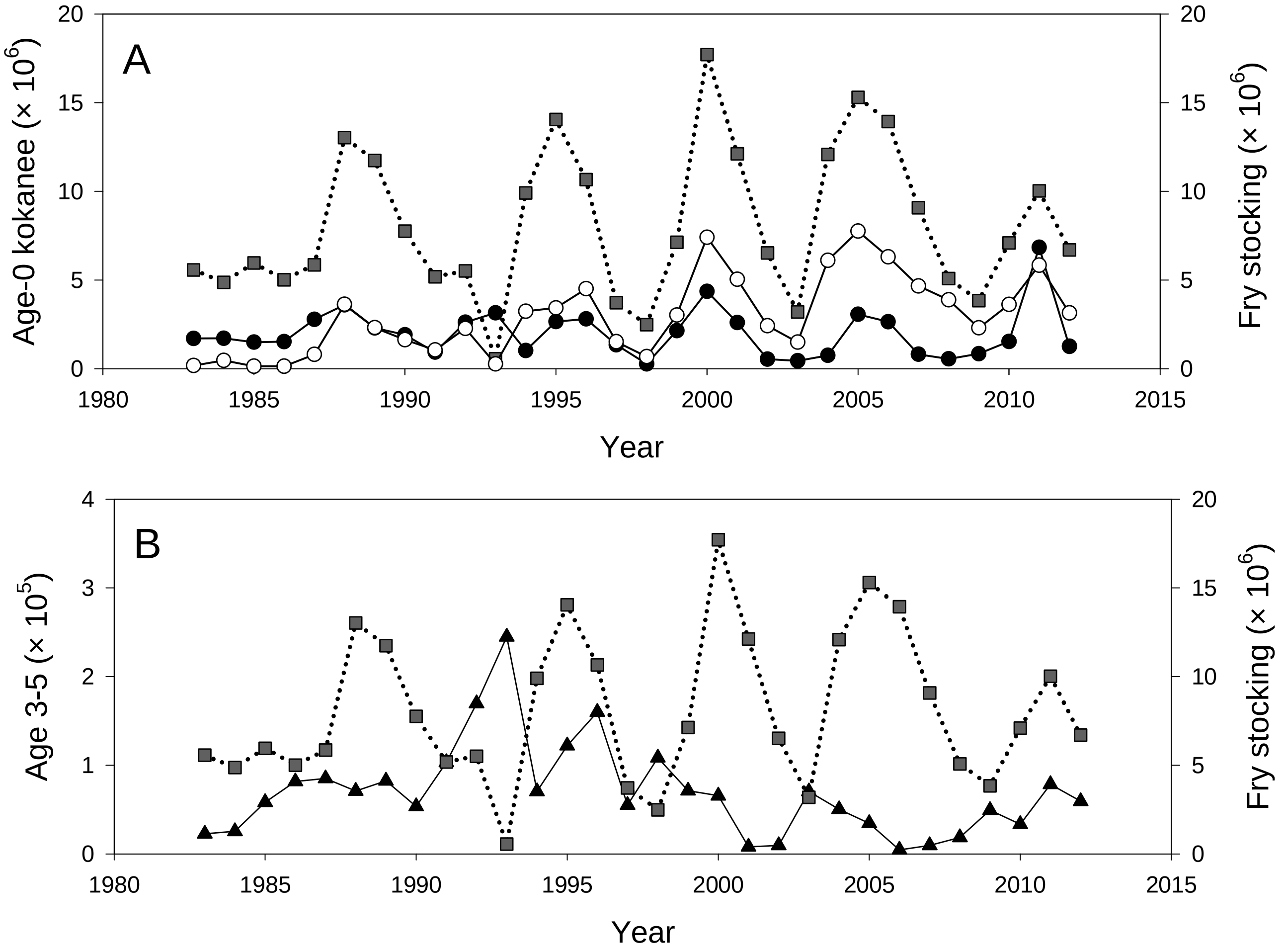

Figure 4.5. Kokanee abundance and stocking in Lake Pend Oreille, Idaho. Plot **A** depicts the number of fry stocked annually in June or July (··■··) and the abundance of wild (—●—) and hatchery (—○—) fry sampled by trawling in August-September of the same year (1983 to 2012). Plot **B** describes the number of fry stocked and abundance of age 3-5 kokanee (—▲—) in the previous year (1984 to 2012).

CHAPTER 5: GENERAL CONCLUSIONS

This thesis contributed to the current understanding of kokanee *Oncorhynchus nerka* shoreline spawning ecology while addressing an important management question. A broad goal of this research was to contribute to the currently limited understanding of the habitat requirements of shore-spawning salmonids. The management-related goal of this thesis was to evaluate whether the recruitment of shoreline spawning kokanee was adversely affected by the water-level regime set by hydropower operations in LPO. Laboratory and *in situ e*gg-box investigations examined the relationship between habitat and incubation success and measured survival in preexisting habitat and that made available by an experimental increase in water level. Existing data were also used to test whether kokanee recruitment was affected by water levels across a 30-year time series.

These chapters contributed to the understanding of shoreline spawning conditions on incubation success in a number of ways. The laboratory incubation experiment was the first salmonid incubation experiment to simulate shoreline conditions. Egg-box investigations revealed that substrate composition was a poor predictor of survival under the incubation conditions that were evaluated. *In situ* studies also revealed that in some cases eggs deposited at depths in excess of 10 m had greater survival than those in shallow water. Downwelling areas produced intragravel survival that was three times that of random areas. These areas also appeared to be selected by spawners, providing evidence that downwelling habitats likely contribute substantially to kokanee recruitment.

The influence of water-level management on kokanee intragravel survival and recruitment was evaluated across broad spatial and temporal scales. One of the *in situ* studies evaluated the water-level hypothesis by directly and representatively sampling the shoreline of LPO and comparing survival and substrate conditions above and below the low water level. A stock-recruitment model used resampling methods to test for an effect of water level on recruitment, while accounting for intra-annual sampling variability. Neither the egg box investigations nor the stock-recruitment model found evidence that kokanee recruitment was enhanced by higher water levels. In fact, both incubation studies suggested that shoreline spawning habitat in LPO is not as limited as was previously thought. It is clear from this work that water-level management is not an effective strategy for kokanee recovery and that future efforts should consider limiting factors outside of the intragravel life history stage.