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Effects of Water-Level Management and Hatchery Supplementation on Kokanee Recruitment in Lake Pend Oreille, Idaho

Abstract

Resource managers have been attempting to recover the kokanee (*Oncorhynchus nerka*) 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. A bootstrap-based generalized Ricker model was used to test if wild kokanee recruitment was significantly influenced by water-level management, while accounting for error due to sampling variability and differential survival of wild- and hatchery-origin fish within age-classes. Wild kokanee exhibited a compensatory stock-recruitment relationship, whereas hatchery recruitment was positively and linearly related to stocking. The model did not identify a significant relationship between water level and wild kokanee recruitment. Density dependence and variable stocking appeared to explain the synchronized and cyclic recruitment of wild and hatchery fry.

Keywords: kokanee, spawning, recruitment, water levels

Introduction

Kokanee (*Oncorhynchus nerka*) were introduced to Lake Pend Oreille (LPO) (Figure 1) in the 1930s and rapidly became the dominant zooplanktivore in the lake. Kokanee are a semelparous Pacific salmon species that bury their eggs in gravel in streams, rivers, and lakeshores (Foerster 1968). Since their introduction into the lake, kokanee have remained both a popular sport fish and an important prey item for trophy rainbow trout (*O. mykiss*) and threatened bull trout (*Salvelinus confluentus*) in the system (Wydoski and Bennett 1981, Simpson and Wallace 1982, Clarke et al. 2005); they were also Idaho's largest recreational fishery during the 1960s and 1970s and supported a commercial fishery from 1945 to 1973 (Paragamian et al. 1992). The kokanee population began to decline in the late 1960s and has since remained at a depressed level (Bowles et al. 1991, Wahl et al. 2011). Several perturbations occurred in LPO prior to the decline, including the construction of two dams and the introduction of mysid shrimp (*Mysis diluviana*) (Bowles et al. 1991, Chipps and 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 and Elam 1993).

The Idaho Department of Fish and Game has implemented several management strategies directed at improving kokanee year-class strength over the last 30 years. The majority of kokanee spawn on the shores of the lake from early-November to the end of December each year. Agreements with hydropower operators reduced significant drawdowns after shoreline spawning began each year and prevented egg desiccation (Hoelscher 1993). Kokanee fry were stocked be-

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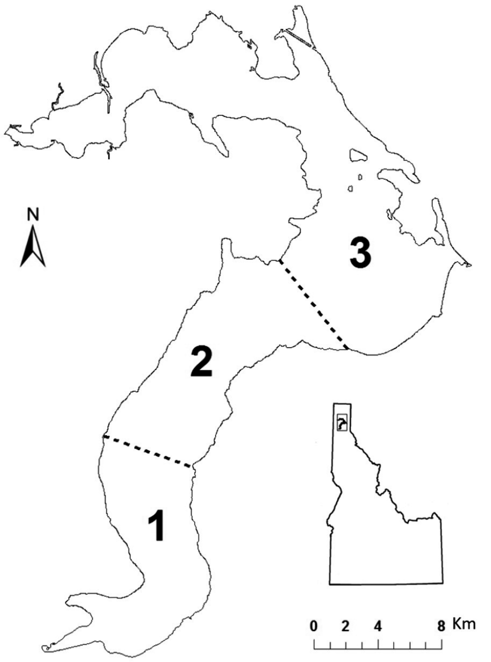

Figure 1. Map of Lake Pend Oreille, Idaho showing the three management sections (from Wahl et al. 2011).

ginning 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 and 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 and Bowles 1995). Prior to the kokanee decline, the winter water level of LPO typically 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 and 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, an increase in the winter water level would be expected to result in an 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 between the two water levels.

Recent work has indicated that the kokanee egg-to-survival estimator is an unreliable measure of the success of the water-level management strategy and that an alternative assessment method is needed (Whitlock 2013). An objective of this study was to use available data to estimate the effect of the water-level management strategy on the recruitment of kokanee. The alternative method used bootstrapping and stock-recruitment modeling to test for an effect of the water-level manipulation on the recruitment of wild-origin kokanee in the lake. Evaluation of the water-level hypothesis provided an opportunity to reassess the role of hatchery supplementation on annual recruitment. Thus, the second objective of this study was to assess the influence of hatchery supplementation by examining the relationship between stocking levels and recruitment of hatchery-origin kokanee, and between hatchery- and wild-fry abundance, and also by exploring factors that influence stocking decisions each year.

Methods

The water-level management strategy and hatchery supplementation program were evaluated using data from annual midwater trawl surveys conducted from 1983–2012. Midwater trawl data were used in this analysis because they have been conducted for more than 30 years, provide both abundance and demographic information, and the sampling protocol has changed little over time. 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 recruitment dynamics. Bootstrapping accounted for intra-annual sampling variability, and heterogeneity in the proportion of wild-origin fish as cohorts aged (Efron and Tibshirani 1993). The bootstrapping process also generated estimates of age-0, hatchery-origin fry abundance through time. These estimates were analyzed in relation to stocking levels and wild fry abundance to examine the consequences of hatchery supplementation. All bootstrap simulations and analyses were performed in the R software environment using base functions (R Development Core Team 2016); mixed-effect logistic regression models were fit using the "lme4" R package (Bates et al. 2015). Each of the components of the analysis (data set, model, bootstrap approach, and hatchery supplementation analysis) are discussed in detail in the following sections.

Midwater Trawl Data

Kokanee abundance, age structure, and wild-hatchery composition has been monitored in LPO using midwater trawl surveys since the 1970s. 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 density (Quinn and Deriso 1999). Density estimates were expanded to estimates of lake-wide abundance, based on the volume of water that kokanee are thought to occupy (i.e., [# caught / volume trawled] × total habitat volume). Another important component of the monitoring program involved estimating the contribution of hatchery kokanee to overall recruitment. Hatchery fry were identified by examining otoliths for thermal or diet-induced oxytetracycline marks (Paragamian et al. 1992, Paragamian and Bowles 1995, Volk et al. 1999).

Midwater trawling occurred annually over a span of three to five nights between 08 August and 22 September during the dark phase of the moon. Trawling stations and headings were randomly selected within each lake management section. The vertical distribution of kokanee was identified using a depth sounder. Stepwise oblique tows were 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 2012, 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 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, which remained constant across years. Information about the sex and maturity of adult kokanee was gathered by dissecting all kokanee greater than 170 mm that were captured in the trawl.

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 (Figure 1), 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). From 1992 onward, the time between trawl steps (i.e., the time required for the winch to move the trawl from one step to another) 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. Trawl surveys from 1992 to present revealed that the time between steps was relatively consistent, with a mean time between steps of 36.1 ± 3.9 s (mean ± SD). 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 abundance estimates of wild fry and mature wild kokanee, for use in a Ricker stock-recruitment model. Only wild kokanee were included in the stock-recruitment analysis because kokanee of hatchery origin primarily move into the tributaries of the lake, where their gametes are collected and used for hatchery fry production (Maiolie 1994, Wahl et al. 2011). Wild kokanee were included in the stock-recruitment analysis because they incubate in shoreline gravel and spend the earliest part of their life history in the lake. Hatchery fry are typically released in July after wild fry have been through a number of potential survival bottlenecks. The proportion of wild fry in the trawl catch 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.

Generalized Ricker Stock-Recruitment Model

Ricker (1954) introduced the first stock-recruit model, which describes a type of 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, which can be thought of as the initial slope of the curve. The β parameter is the rate at which the number of recruits decreases in relation to increasing stock size. Density dependence occurs for a variety of reasons including predation, competitive interactions, and habitat limitations (Rose et al. 2001, Greene and Guilbault 2008). The α parameter 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 and 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 and Johnston 2013); in fact, sockeye salmon (*Oncorhynchus nerka*) stock-recruitment relationships are often used as examples in texts on stock assessment (Hilborn and Walters 1992, Haddon 2011). Another reason for choosing the Ricker model was that it is flexible and can take on a dome shape as well as an asymptotic shape that is similar to the Beverton-Holt model. A model with an upper asymptote implies “compensation”, in which increases in spawners are offset by decreases in the number of recruits per spawner. A model with the dome-shaped curve implies overcompensation, in which the decrease in recruits per spawner overwhelms the effect of increasing the number of spawners, leading to a reduction in the number of total recruits beyond a particular spawner level (Bjorkstedt 2000). There are several explanations for why overcompensation might be expected in LPO, including scramble competition among newly hatched fry, redd superimposition on the part of spawners, or concurrent density dependence, where fry compete for forage with older age classes of kokanee (Bjorkstedt 2000, Green and Guilbault 2008). Finally, 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. 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 α parameter 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.

Bootstrapping

Point-estimates of wild kokanee fry and wild mature kokanee abundance alone could be used to 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 obscure relationships and produce misleading parameter estimates in stock-recruitment models (Ludwig and Walters 1981, Walters and Ludwig 1981). Given the potential for measurement errors to interfere with parameter estimation, a combination of nonparametric and parametric bootstrap techniques were used to propagate the sampling-related uncertainty into Ricker model parameter estimates (Efron and Tibshirani 1993, Haddon 2011). Nonparametric bootstrapping does not make distributional assumptions, except that the empirical distribution function of the data approximates the true distribution and involves iteratively sampling independent observations with replacement to approximate the sampling distribution of a given statistic. Alternatively, parametric bootstrapping involves randomly drawing samples from specified probability distributions. For this analysis, nonparametric bootstrapping provided a representation of the sampling error in abundance calculations, whereas parametric bootstrapping was used to propagate uncertainty in the estimated proportion of wild-origin kokanee for a given year and age class.

A rescaled nonparametric bootstrap was applied to counts of age-0 kokanee and mature adult kokanee for each lake section and year in the time series. A rescaled form of the nonparametric bootstrap was used because naïve nonparametric bootstrap methods underestimate variance for data from complex sample surveys (Rao and 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). In this study, the nonparametric bootstrap produced distributions of counts for fry and mature kokanee in each lake section, which were then used to calculate a sampling distribution of lake-wide abundance for each year. The abundance of wild-origin fry and mature fish in a given year was then calculated by combining total abundance data, with simulated sampling distributions for the proportion of wild-origin kokanee in each year and age class.

Prior to generating sampling distributions for natal origin estimates, several analyses were performed to determine the parameter values that would be used in the parametric bootstrap. Parametric bootstrapping was used instead of nonparametric because the raw data used to estimate the proportion of wild fry in a sample or an age class were unavailable for some years in the dataset. This issue was addressed by "borrowing information" regarding annual sampling variability (intra-annual; σ_{year}) and variability in the proportion of natal origin as a cohort ages (intra-cohort; σ_{cohort}) from subsets of survey years where these data were available. Intra-annual error was estimated using a mixed-effect logistic regression model that contained data from 26 years of the time series, and which contained section-specific counts of wild fry and total fry (Hosmer et al. 2013). The model contained a fixed effect for year as well as an observation-level random effect to account for overdispersion (Warton and Hui 2011). The overall estimate of intra-annual error (σ_{year}) was calculated by summing the error in the overdispersion term and the mean standard error of annual means.

A similar mixed logistic regression model was used to estimate intra-cohort error for the proportion of wild-origin kokanee (σ_{cohort}). It was necessary to estimate the intra-cohort error because, for the first 17 years of the time series, only the natal origin of fry was measured and it was unrealistic to assume that the proportion of wild-origin kokanee in a year class remains constant through time. The intra-cohort model was fit using data from surveys between 1999 and 2012 when thermal marks were used to estimate the origin of older age classes in addition to fry (Wahl et al. 2011). A total of 10 complete (i.e., age-0 through age-5) cohorts was included in the model, representing brood years 1998- 2007. The model consisted of a fixed effect for cohort and an observation-level random effect to account for overdispersion. Similar to the previous model, the intra-cohort error (σ_{cohort}) was calculated by summing the error in the overdispersion term and the average error of the cohort means.

The parametric bootstrap that produced sampling distributions for the proportion of wild-origin kokanee across ages and years, involved several steps. First, the sampling distribution for the proportion of wild-origin age-0 kokanee in a given year was calculated by transforming point-estimates of the proportion of wild-origin fry ($\hat{p}_{y,0}$) into a value on the real number line ($\mu_{y,0}$) using the logit function:

$$\mu_{y,0} = \text{logit}(\hat{p}_{y,0})$$

Simulated proportions of wild-origin age-0 kokanee ($\tilde{p}_{y,0}$) were then calculated by adding random intra-annual error (ε_y) to $\mu_{y,0}$ and back transforming:

$$\tilde{p}_{y,0} = \text{logit}^{-1}(\mu_{y,0} + \varepsilon_y)$$

where $\varepsilon_y \sim Normal(0, \sigma_{year})$. Similarly, simulated proportions of wild-origin kokanee ages 1-5 were calculated by adding intra-annual error (ε_y) and also intra-cohort error (τ_j) to the logit-transformed wild-origin proportion when the cohort was age 0:

$$\tilde{p}_{y,j} = \text{logit}^{-1}(\mu_{y-j,0} + \varepsilon_y + \tau_j)$$

where j is an index for the cohort age, $j = 1{:}5$, and $\tau_j \sim Normal(0, \sigma_{cohort})$.

Bootstrap-based sampling distributions describing the abundance of wild age-0 and mature kokanee were used to fit a generalized Ricker stock-recruitment model which incorporated process error as well as sampling variability. The model bootstrapping process required four steps:

1. A distribution of 10 000 bootstrap abundance estimates was generated for both age-0 and mature spawners for each brood year, based on recommendations by Smith (1997).
2. Estimates of wild age-0 and wild mature kokanee were calculated by combining total abundance estimates with another 10 000 randomly drawn estimates of the proportion of wild kokanee in each year and age class.
3. Distributions of these estimates were sampled with replacement and used to fit separate stock-recruitment models.
4. 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 and Tibshirani 1993). Intervals containing zero indicate that a parameter does not differ significantly from zero at the $\alpha = 0.05$ level (Fox and 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. 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 informed managers about how many fish should be stocked each year, so stocking levels were examined in relation to the abundance of age-3 to age-5 kokanee during the previous year.

Results

The generalized Ricker model appeared to describe 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 2). The Ricker model provided a reasonable fit to the data

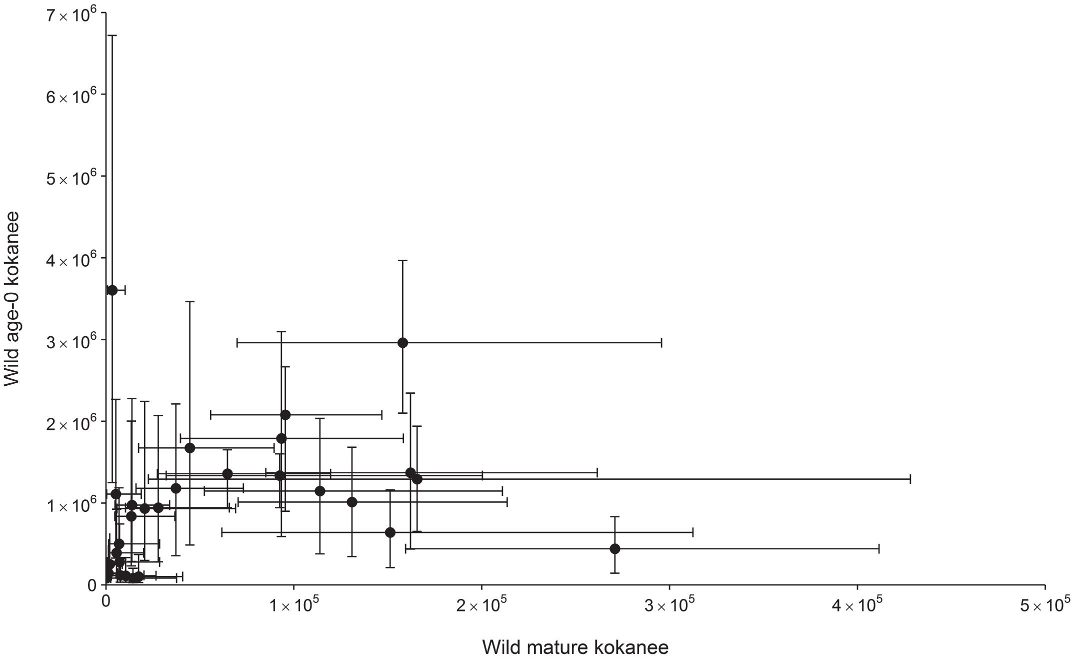

Figure 2. Wild age-0 kokanee abundance from 1983 to 2011 versus wild mature abundance of kokanee from the previous year in Lake Pend Oreille, Idaho. Abundances and demographic information were estimated using midwater trawling. Error bars denote 95% bias-corrected and accelerated confidence intervals.

because recruitment showed a pattern of increase until 1 $\times 10^5$ spawners was reached, followed by a more gradual decrease as wild mature kokanee abundance increased (Figure 3). Bootstrap distributions of wild fry and wild mature kokanee estimates appeared normal based on histograms and quantile 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, suggesting overcompensation. Although the point-estimate for the water-level parameter was positive, confidence intervals for the water-level parameter spanned zero, indicating that years of higher water-level did not significantly affect the α parameter (Table 1). The positive direction of the water-level effect was found to be highly influenced by the estimate of wild recruitment in the year 2011, thus the bootstrapped model was fitted with and without including 2011.

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 4A). Hatchery stocking and hatchery abundance were positively and linearly related to stocking rate (r = 0.81 ; $R^2 = 0.66$; $P < 0.01$) and the abundance of wild fry ($r = 0.38$; $R^2 = 0.15$; $P = 0.02$). Stocking appeared to be negatively related to the estimated abundance of age-3 to age-5 kokanee estimated from midwater trawling during the previous year (Figure 4B). Although there was a similar pattern of recruitment between wild- and hatchery-origin kokanee, the composition of age-0 kokanee in the trawl shifted throughout the time series. In the mid-1980s, wild-origin fry dominated the trawl catch, then there was a shift to a relatively even mix of hatchery- and wild-origin through 2000,

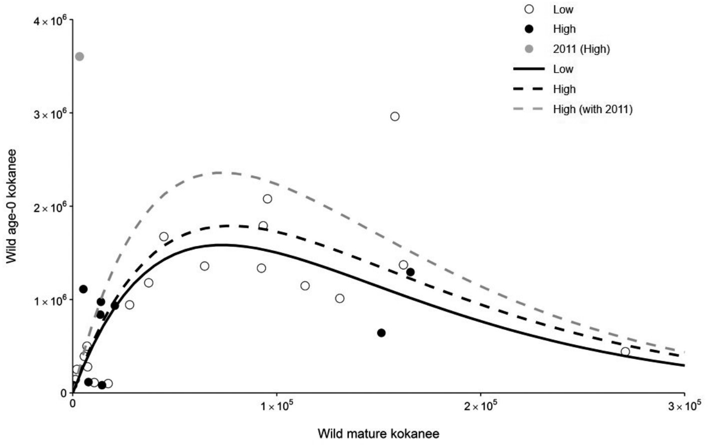

Figure 3. Wild age-0 kokanee abundance from 1983 to 2011 versus abundance of wild mature kokanee from the previous year in Lake Pend Oreille, Idaho, estimated using midwater trawling. Lines depict fitted values for years of high (> 626 m) and low (< 626 m) water levels from a bootstrap-based generalized Ricker stock-recruitment model. Fitted regression lines for the two water levels are shown despite the fact that water level was not a significant predictor of recruitment.

finally shifting to predominantly hatchery-origin up until present.

Discussion

The analysis failed to identify a significant relationship between the water-level management strategy and recruitment of wild-origin kokanee in LPO. The analytical approach was useful for not only assessing the water-level management strategy, but propagating uncertainty due to sampling and changes in the proportion of wild- and hatchery-origin fish through time. The Ricker model appeared to adequately describe wild kokanee recruitment patterns over the previous 30 years. Recruitment estimates for hatchery and wild-origin kokanee indicated that the two groups were synchronized.

The bootstrap-based modeling approach used in this study has a number of advantages and can be applied to many management questions besides stock-recruitment modeling (Dixon 2001). The main benefits of bootstrap-based modeling approaches are that they facilitate the creation of models that integrate multiple data sources, appropriately propagate uncertainty, and are more intuitive than other equally flexible modeling approaches (e.g., maximum likelihood estimation or Bayesian modeling; Haddon 2011). In this study, bootstrapping enabled uncertainty in the proportion of wild-origin kokanee for a cohort to be combined with sampling-related uncertainty in trawling data. The only other way to combine this information would have been to optimize a customized likelihood function or define a Bayesian model and sample posterior distributions using a Markov Chain Monte Carlo algorithm, both of which require specialized knowledge and substantially more programing skill.

Findings from this analysis of water-level management effects 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). The water-level hypothesis in LPO is unique because it is the only known case in which spawning habitat quality is thought be the primary 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 (Decker-Hess and Clancey 1990, Modde et al. 1997). 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 and Bodaly 1984, Gafny et al. 1992). There are several reasons why an effect of water-level may not have been

TABLE 1. 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
	All years		
α	58.79	34.64	101.53
β	–1.36 × 10-5	–1.91 × 10-5	–0.98 × 10-5
γ	0.40	-0.31	1.09
	2011 Excluded		
α	55.95	32.98	97.17
β	–1.29 × 10-5	–1.83 × 10-5	–0.91 × 10-5
γ	0.12	–0.59	0.86

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 3). 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. Furthermore, a field study in LPO suggested that kokanee incubation success is not enhanced in substrates made available during years with higher water levels (Whitlock et al. 2014).

The model results may have been influenced by the low detection probability of mature fish, which indicates that a 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*) predation (Hansen et al. 2008, 2010). 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 and Falter 1981). Since the mid-1970s, the presence of mysid shrimp has been considered to be a factor restricting kokanee recruitment (Rieman and Falter 1981, Bowles et al. 1991, Chipps and 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.

Synchrony appeared to exist between the recruitment of wild and hatchery fry over much of the 30-year time series. 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. One possibility is that otolith readers failed to detect oxytetracycline or thermal marks on some hatchery fish. If this is not the case, then another explanation for the correlation between age-0 hatchery and wild kokanee might be related to a lack of awareness 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. Peaks in overall recruitment may have 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 stock-recruitment relationship. The compensatory 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 number 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

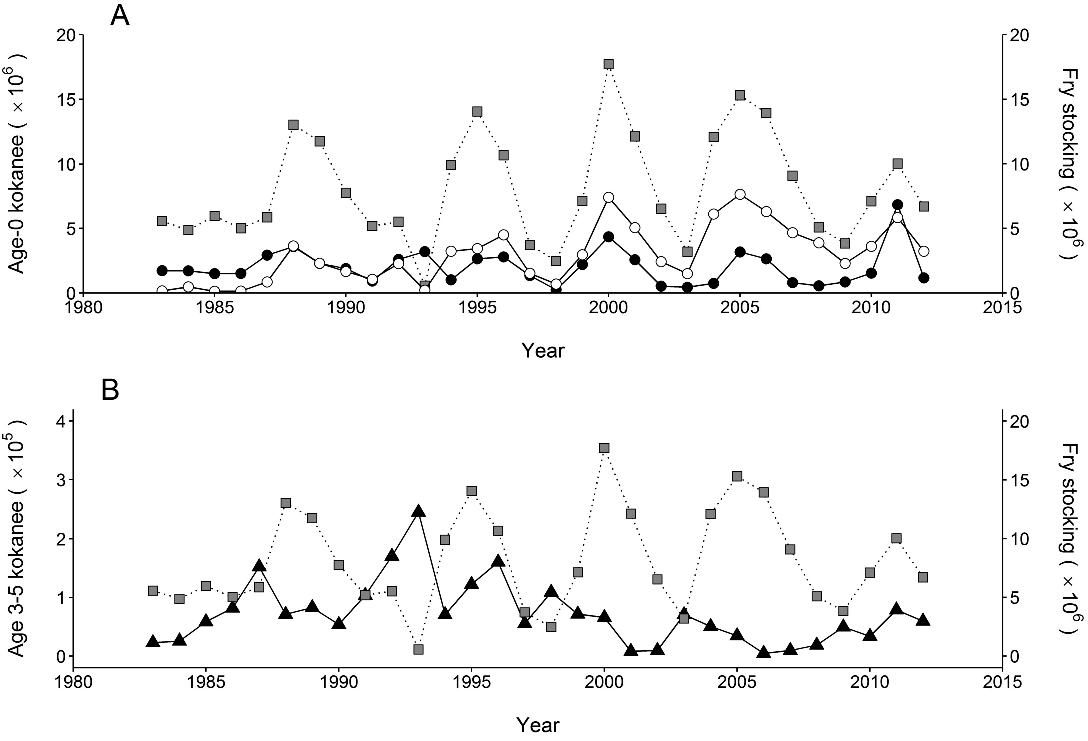

Figure 4. Kokanee abundance and stocking in Lake Pend Oreille, Idaho. Plot A depicts the number of fry stocked annually in June or July (■) and the abundance of wild (-●-) and hatchery (-○-) fry sampled by trawling in August-September of the same year (1983 to 2012). Plot B describes the number of fry stocked and abundance of age 3-5 kokanee (-▲-) in the previous year (1984 to 2012).

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 and 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 affected by density-dependent growth, which often influences survival, age-at-maturity, and fecundity (Rieman and 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 the kokanee population in LPO 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.

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