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# Influences of Lake Trout (*Salvelinus namaycush*) and *Mysis diluviana* on kokanee (*Oncorhynchus nerka*) in Lake Pend Oreille, Idaho

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**Abstract** Research on Lake Pend Oreille, Idaho, has focused on the influence of two potential limiting factors for kokanee *Oncorhynchus nerka* (Walbaum, 1792): competition for food with *Mysis diluviana* (Loven, 1862, hereafter *Mysis*) and predation by lake trout *Salvelinus namaycush* (Walbaum, 1792). Population fluctuations of *Mysis* and lake trout have resulted in substantial heterogeneity in food web conditions, apparently altering both bottom-up and top-down dynamics. Therefore, relative importance of predation and competition were evaluated as drivers of kokanee abundance, biomass, and production. A series of general linear models was used to evaluate relative influences of *Mysis* and lake trout on kokanee. Kokanee production was a density-dependent process and the collapse of *Mysis* corresponded to an increase in the modeled maximum annual production of kokanee from 224 tonnes to 408 tonnes. Lake trout also negatively influenced kokanee biomass. A *Mysis*-mediated, predator-induced kokanee biomass collapse occurred when lake trout and *Mysis* abundances were both high. Sustainable management of this fishery requires recognition that competition with *Mysis* will define the scope of kokanee production and therefore the scope of sustainable predation.

**Keywords** Density-dependence · Competition · Predation · Predator suppression · Thresholds

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## Introduction

The relative importance of top-down versus bottom-up controls represents a classic question in ecology (e.g., Power, 1994) with important implications for fisheries management (Carpenter et al., 1985; Quiròs & Boveri, 1999). Management of kokanee (the landlocked form of sockeye salmon) *Oncorhynchus nerka* is challenged by interactions between available forage (Stockner & Shortreed, 1985; Mazumder & Edmundson, 2002; Wilson et al., 2017) and predation (Beauchamp et al., 1995; Martinez et al., 2009; Ellis et al., 2011) that drive kokanee and sockeye salmon abundance and biomass. The kokanee is a middle-trophic level planktivore that often serves a dual role as a yield-oriented sportfish species and as prey for larger piscivores in trophy-oriented sport fisheries (Wydoski & Bennett, 1981; Martinez et al., 2009). Managers concerned with bottom-up limitations for kokanee and sockeye salmon have employed nutrient additions to mitigate for issues ranging from declining lentic productivity (Ashley et al., 1997; Wilson et al. 2017) to loss of marine-derived nutrients (Stockner & MacIsaac, 1996). *Mysis diluviana* (hereafter, *Mysis*), which were introduced to lakes throughout western North America for fishery enhancement, have indirectly influenced bottom-up nutrient flux to kokanee via competition for zooplankton (Northcote, 1991). *Mysis* are known to cause zooplankton community shifts (Rieman & Falter, 1981) and to regulate production of cladocerans, a preferred kokanee prey item (Caldwell et al., 2016). As for top-down limitations on kokanee, introduced lake trout *Salvelinus namaycush* are a frequently cited predator of kokanee (see Martinez et al., 2009 for review). When lake trout are at relatively low abundance in lentic waters with an abundant forage base, trophy lake trout fisheries often develop (e.g., Pate et al., 2014), but are typically unstable. Increased lake trout abundance has been implicated in kokanee population collapse in several fisheries (Bowles et al., 1991; Martinez et al., 2009; Ellis et al., 2011).

In Lake Pend Oreille, Idaho, lake trout persisted at inconsequential abundance for several decades after their 1925 introduction (Hansen et al., 2008). *Mysis* establishment in the 1970s was likely the catalyst that led to an eventual increase in the lake trout population (i.e., Bowles et al., 1991; Stafford et al., 2002). Lake trout predation on *Mysis* is likely far less efficient in Lake Pend Oreille, as compared to shallower lakes, because steep-sided deep lakes provide profundal refuge for *Mysis* during daylight hours and more diffuse scattering during low-light conditions (Schoen et al., 2015). Nonetheless, as in other waters where they were introduced, *Mysis* are an important food source for juvenile lake trout in Lake Pend Oreille (Clarke et al., 2005), which increases survival (Stafford et al., 2002; Ng et al., 2017). Increased lake trout recruitment to piscivorous life stages exacerbated predation and has been a contributor to kokanee collapse (Ellis et al., 2011). Lake trout response to *Mysis* introduction was delayed in Lake Pend Oreille relative to other waters (Martinez et al., 2009), because exponential population growth was not observed until 1999–2005 (Hansen et al., 2010). During 1995–2005, lake trout predation changed from an inconsequential component of kokanee mortality (Vidergar, 2000) to a substantial contributor that likely collapsed kokanee in Lake Pend Oreille (Hansen et al., 2010). As a result, a lake trout suppression program was initiated in 2006 that relied on a combination of incentivized angler harvest and commercial-scale gill netting and trap netting (Hansen et al., 2010). The program has successfully reduced age-8 and older lake trout by 64% from their peak abundance in 2006 (Dux et al., 2019), which likely reduced total predation on kokanee.

While the lake trout population in Lake Pend Oreille grew exponentially starting in the mid-1990s, followed by a decline with the onset of suppression in 2006 (Dux et al., 2019), *Mysis* abundance oscillated at high densities until an as-yet unexplained collapse began in 2011 (IDFG, unpublished data). These changes in both bottom-up (via competition) influences of *Mysis* and top-down influences of lake trout caused variable kokanee food web conditions since the 1990s. First, kokanee were in a high-*Mysis*, low-lake trout environment until the mid to late 1990s, when predation by lake trout was likely minimal (Vidergar, 2000). Then, in 2000–2006, *Mysis* were abundant and lake trout abundance increased exponentially. After 2006, lake trout abundance reached a peak and declined with the onset of suppression, but *Mysis* abundance remained high. Since 2011, lake trout and *Mysis* abundances have both been relatively low. Heterogeneity of these food web conditions presented an opportunity to relate variability of kokanee population dynamics to both top-down and bottom-up factors.

The goal of this study was to evaluate the relative importance of predation and competition as drivers of kokanee abundance, biomass, and production in Lake Pend Oreille, Idaho using long-term datasets for kokanee, *Mysis*, and lake trout. To achieve this goal, we addressed three objectives: (1) determine if kokanee biomass and production were inversely related to *Mysis* abundance; (2) determine if kokanee biomass and production were inversely related to lake trout abundance; and (3) quantify the relative influence of *Mysis* and lake trout on kokanee production and biomass. Our a priori expectations were (1) kokanee abundance would be inversely related to lake trout, via predation; (2) kokanee production and abundance would be inversely related to *Mysis* abundance, as a result of competition and (3) biomass, which integrates kokanee abundance and condition (weight), would be negatively influenced by both *Mysis* and lake trout.

## Study area

Lake Pend Oreille is the largest and deepest lake in Idaho, with a surface area of 38,300 ha and maximum depth of 357 m (Fig. 1). The Clark Fork River is the lake's largest tributary with an annual mean discharge of 621 $m^3$/s. Lake Pend Oreille is a temperate oligotrophic natural lake, but the upper 3.6 m of the water column is regulated by Albeni Falls Dam on the Pend Oreille River downstream. Lake elevations are typically 625.1 m in winter and 628.7 m in summer. A dam on the Clark Fork River upstream of the lake blocks passage for upstream migrating salmonids. The lake is thermally stratified in summer, typically from June through September. Shorelines are steeply sloped and littoral areas are limited in all but the northern portion of the lake.

The native fish assemblage includes bull trout *Salvelinus confluentus* (Suckley, 1859), westslope cutthroat trout *Oncorhynchus clarkii lewisi* (Richardson, 1836), northern pikeminnow *Ptychocheilus oregonensis* (Richardson, 1836), mountain whitefish *Prosopium williamsoni* (Girard, 1856), pygmy whitefish *Prosopium coulterii* (Eigenmann & Eigenmann, 1892), slimy sculpin *Cottus cognatus* (Richardson, 1836), Peamouth *Mylocheilus caurinus* (Richardson, 1836), and redside shiner *Richardonius balteatus* (Richardson, 1836). The lake is considered a conservation stronghold for bull trout, which also provide catch-and-release trophy fishing opportunities. Bull trout, lake trout, large northern pikeminnow, and introduced Gerrard-strain rainbow trout *Onchorynchus mykiss* (Walbaum, 1792) are the most abundant pelagic piscivores and kokanee are their predominant prey species (Clarke et al., 2005). Introduced smallmouth bass *Micropterus dolomieu* (Lacepède, 1802) is an abundant littoral predator,

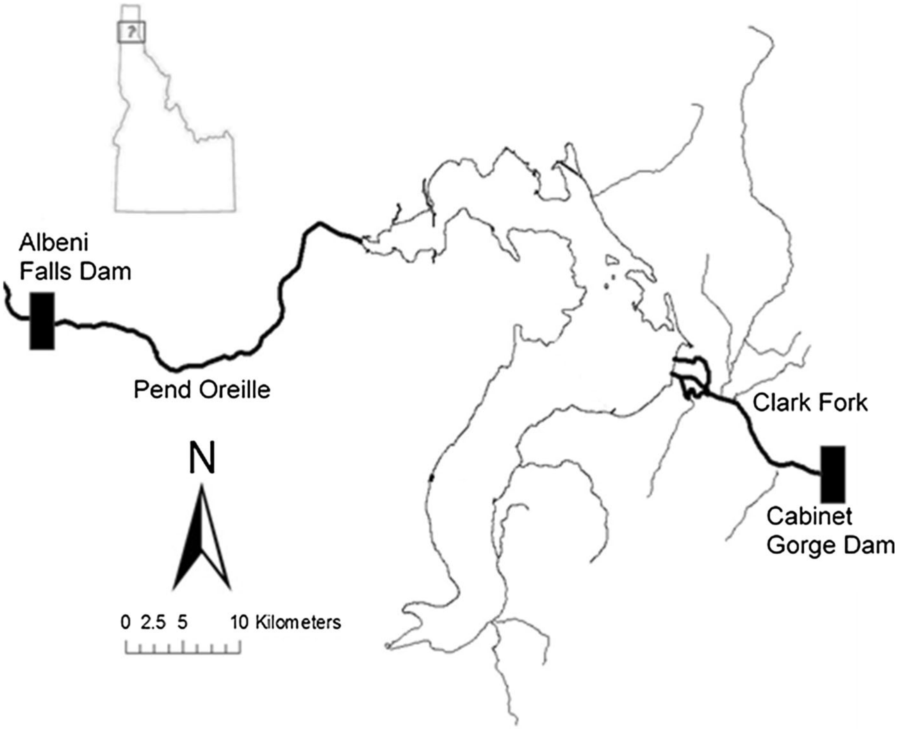

**Fig. 1** Lake Pend Oreille, Idaho

while brown trout *Salmo trutta* (Linnaeus, 1758), northern pike *Esox Lucius* (Linnaeus, 1758), and largemouth bass *Micropterus salmoides* (Lacepède, 1802) are established, less abundant, predators. Walleye *Sander vitreus* (Mitchill, 1818) is a newly established predator at low but increasing abundance that has been observed to have predation impacts on kokanee in other systems (Baldwin et al., 2003).

The kokanee population was established via immigration from Flathead Lake, Montana, through the Clark Fork River. Kokanee were abundant by the 1930s and immediately supported world-record trophy fisheries for rainbow trout and bull trout. Lake Pend Oreille supported the largest fishery in Idaho in the 1950s and 1960s. Kokanee declined in Lake Pend Oreille beginning in the late 1960s, likely due to competition with *Mysis*, predation, hydro-system management, and loss of spawning habitat. Cabinet Gorge Hatchery was constructed in 1985 to mitigate for declining kokanee abundance by helping to stabilize recruitment. Although the kokanee population is supplemented with fry from Cabinet Gorge Hatchery, recruitment of hatchery and wild fry are synchronized because egg collection depends almost entirely on within-lake broodstock collection (Whitlock et al. in press).

## Methods

### Kokanee abundance and production

Mid-water trawls at night have been used annually to evaluate kokanee population dynamics on Lake Pend Oreille. Trawl surveys during 1995–2016 occurred within one week of the August or September new moon. Trawl transects were randomly selected within three strata of comparable area (12 transects per strata). In 2003, the program converted from an otter trawl to a fixed frame trawl. The otter trawl had a 3 × 3 m opening and was 13.7 m long with graduated mesh increments from 6 to 32 mm. The fixed frame trawl had a 3 × 2.2 m opening and the net was 10.5 m long with the same net graduations as the otter trawl. During the trawling event, the vertical distribution of kokanee was first determined with a depth sounder. Fish were then sampled using a stepwise (steps defined by net height) oblique tow (1.58 m/s) through the kokanee layer and along the transect path. Four or five steps are typically needed to sample the entire kokanee layer, but occasionally three or six steps were sampled. Each step within a tow was 3 min in duration, and the time required to winch to the next step was 30–40 s. Total trawl time within the kokanee layer therefore ranged from 600 to 1280 s. We assumed all fish were captured within the identified kokanee layer.

Total length and weight were measured from all kokanee collected in the trawl. Scales were collected from 10–15 fish per centimeter length group. Two readers estimated age of fish independently and all differences in age estimates were reconciled by consensus agreement. Age-length keys were used to convert length frequencies into age frequencies.

Since 1995, production and biomass have been estimated from hydroacoustic surveys using a Simrad EK60 echosounder. These surveys were conducted at night immediately before or after trawl surveys in the same sections of Lake Pend Oreille. Six to eight uniformly spaced transects were followed from shoreline to shoreline in a zigzag pattern within each section. The starting point of the first transect within a section was randomly chosen. Transect length varied from 3.6 to 7.7 km with a boat speed of ~ 1.3 m/s. Kokanee abundance was estimated with echo integration techniques using Echoview software version 6.1.60.87483 (Echoview Software Pty Ltd, Hobart, Tasmania). This technique calculated density along each transect using the following equation (Parker-Stetter et al., 2009):

$$\rho = \left(\frac{\mathrm{NASC}}{4\pi 10^{\frac{\mathrm{TS}}{10}}}\right) 0.00292,$$

where $\rho$ is density (number of fish per ha), *NASC* is the total backscattering (m$^2$/nautical mile$^2$), and *TS* is the mean target strength in decibels in the area sampled. To estimate lake-wide kokanee abundance, mean kokanee density was estimated in each section, which was then multiplied by area to estimate abundance in each section. Finally, abundance was summed across sections to estimate total kokanee abundance.

Kokanee biomass was estimated for each year from age-specific estimates of abundance. Age-0 kokanee (< 100 mm) were separated from older age classes using Echoview software. A target-strength frequency histogram was used to identify the low point as the break between fry and larger kokanee. To separate hydroacoustic estimates of larger kokanee into age classes (age 1 through age 4), age proportions within each section from trawl surveys were applied to hydroacoustic estimates of abundance within each section. Age-specific abundance estimates within each section were summed to estimate total abundance in the lake. Kokanee biomass was then estimated by multiplying total abundance of each age class in the lake by the mean weight of kokanee in each age class. Total biomass was estimated by summing age-specific biomass estimates.

Production was estimated using the increment summation method (see Eq. 8.45 in Hayes et al., 2007) and was defined as the change in weight of the kokanee population from one year to the next, regardless of the fate of individual fish at the end of each year (Ricker, 1975). The increase in mean weight of a cohort from one year to the next was calculated and multiplied by the average cohort abundance for the 2 years. Cohort-specific production estimates were then summed across cohorts to estimate total production in the lake.

## Mysis density estimation

Density of adult (excluding age-0) *Mysis* was evaluated in Lake Pend Oreille during 1995–2016. *Mysis* were sampled at night within one week of the new moon in June to estimate density. A stratified random sampling design used the same three lake strata (sections) as described above for kokanee sampling. Sampling intensity varied over time, with 10 sample sites per strata in 1995–2003, 15 sample sites per strata in 2004–2006, and 8 sample sites per strata in 2007–2016. *Mysis* were collected using a 1 m conical net with 1000 μm mesh and 500 μm mesh on the collection bucket. The net was lowered to a depth of 45.7 m, which is below the *Mysis* nocturnal scattering layer as identified on a depth sounder, allowed to settle for 10–15 s, and raised with an electric winch to the surface at a rate of 0.5 m/s. Collections were preserved in 50% ethanol.

In the laboratory, *Mysis* were sorted into age classes using length frequency (Caldwell & Wilhelm, 2011) and adult *Mysis* were counted in each collection and divided by the area of the net opening (0.817 $m^2$). Adult *Mysis* densities were averaged across all collections within sections and section averages were multiplied by area of each section to estimate total adult abundance. Finally, total adult abundance was divided by total lake surface area to estimate population density (*Mysis*/$m^2$).

## Lake trout abundance estimation

Lake trout have been the focus of several studies and management programs on Lake Pend Oreille, and several abundance estimation approaches were integrated to develop a time series of directly or indirectly obtained abundance estimates. Mark–recapture studies were used to estimate the abundance of age-8 and older lake trout in 1999 using a combination of angling and electrofishing (see Vidergar, 2000 for detailed methods), and again in 2003 and 2005 using trap nets to mark fish and randomly set gillnets to sample the marked fraction of the population (Hansen et al., 2008). An exponential growth model was fit to abundance estimates to describe growth of the lake trout population during 1995–2005:

$$N_{\mathrm{t}+1} = N_0 e^{rt}.$$

In the exponential growth model, $N_{\mathrm{t}}$ is total abundance in year $t$, $N_0$ is starting abundance, and $r$ is the intrinsic rate of population change during the period (Quinn & Deriso, 1999). For years with no abundance estimate in 1995–2005, parameters of the fitted model ($N_t = 737$, $r = 0.3008$) were used to estimate abundance. For the period 2006–2016, cohort analysis was used to estimate abundance (Dux et al., 2019). To account for methodological bias of abundance estimates in the two periods, the average ratio of cohort analysis abundance to mark–recapture abundance in 2007, 2008, and 2011, when additional mark–recapture surveys were completed as described by Hansen et al. (2008), was used to scale mark–recapture estimates in 1995–2005.

## Kokanee biomass model

We evaluated concurrent influences of *Mysis* density and lake trout abundance on kokanee biomass. Bivariate relationships between biomass and covariates indicated exponential functions would best describe patterns, so all variables were $\log_e$ transformed in a linear regression model:

$$\log(B_t) = \beta_0 + \beta_1 \log(\mathrm{Mys}_t) + \beta_3 \log(\mathrm{LKT}_t),$$

where $B_t$ is the kokanee biomass in year $t$, $\mathrm{Mys}_t$ is the *Mysis* density in year $t$, $\mathrm{LKT}_t$ is the lake trout abundance in year $t$.

### Kokanee production/biomass model

Density-dependent kokanee population dynamics were modeled with a production–biomass model to evaluate joint influences of *Mysis* and lake trout on kokanee abundance and biomass. The model was updated from the version described by Hansen et al. (2010) to predict kokanee production from the relationship between biomass in 1 year $\beta_{t-1}$ to production in the next year $P_t$:

$$P_t = \alpha B_{t-1}\left(e^{-\beta B_{t-1}}\right)e^{\varepsilon}.$$

In the production–biomass model, $\alpha$ is the production ($P_\mathrm{t}$)/biomass ($B_{\mathrm{t}-1}$) at low biomass, $\beta$ is the instantaneous rate at which production/biomass declines with biomass, and $\varepsilon$ is the multiplicative process error. Maximum production was defined as $P_{\max} = \alpha/\beta e$ (Ricker, 1975). A $\log_\mathrm{e}$-transformed version of the model was used to facilitate general linear modeling (GLM):

$$\log_e\left(\frac{P_t}{B_{t-1}}\right) = \log_e(\alpha) - \beta B_{t-1} + \varepsilon.$$

Additional models of this general form included adult *Mysis* density and lake trout abundance as potential explanatory variables affecting production and biomass of kokanee. Given that these are density-dependent models for kokanee, and *Mysis* are expected to reduce food availability (and thus capacity) for kokanee, our a priori expectation was that candidate models including interactions between *Mysis* and kokanee biomass would have the most support. Kokanee biomass was included in all candidate models. Due to the small number of covariate combinations, candidate models included all combinations of *Mysis* density, lake trout abundance, and their interactions. Relative fit of the candidate models was weighted using corrected AIC values (AICc) for small sample sizes (Burnham & Anderson, 2003). Models were determined to be equally plausible if they were within 2.0 ΔAICc of the top model (Burnham & Anderson, 2003).

To directly test the role of *Mysis* collapse on this density-dependent relationship, a linear production/biomass model was also fit with a categorical variable for *Mysis* (high, low) and the interaction between this categorical variable and kokanee biomass to test for equal slopes and intercepts in an ANCOVA framework. Separate models without covariates were fit to the production and biomass data before and after *Mysis* collapse. Goodness of fit of these models was then compared to an equivalent model fit to the 1995–2016 time series.

## Results

Hydroacoustic-trawl-estimated abundance of all kokanee ranged from 6,995,000 fish in 2006 to 25,310,000 fish in 2016 during 1995–2016 (mean = 13,980,000, SD = 4,780,000, Fig. 2). Kokanee biomass ranged from 74 metric tonnes in 2007 to 626 metric tonnes in 2013 (mean = 226 metric tonnes, SD = 124). Kokanee production peaked at 518 metric tonnes in 2012 and was lowest at 174 metric tonnes in 2009 (mean = 256 metric tonnes, SD = 88). *Mysis* density oscillated between 200 and 400 individuals/m$^2$ during 1995–2010, but fell to 7 individuals/m$^2$ in 2013 (Fig. 2). Lake trout abundance (age-8 +) was 2003 fish in 1995, peaked at 43,349 fish in 2005, and declined thereafter (Fig. 2; Dux et al., 2019).

Kokanee biomass was significantly related to both lake trout abundance and *Mysis* density ($F_{2,19} = 18.63$, $P < 0.001$), collectively explaining 66% of inter-annual variation in kokanee biomass (Fig. 3, top panel). Kokanee biomass was negatively affected by both *Mysis* density ($\beta_1 = -0.347$, $t = -4.848$, $df = 19$, $P < 0.001$) and lake trout abundance ($\beta_2 = -0.346$, $t = -3.818$, $df = 19$, $P = 0.001$). The response surface (Fig. 3, bottom panel) of the biomass model illustrated that kokanee biomass was (1) intermediate when either lake trout or *Mysis* density were low, (2) high when lake trout abundance and *Mysis* density were both low, and (3) low when lake trout abundance and *Mysis* density were both high.

Lake trout was not included in the top fitting kokanee production-biomass model (Table 1). The best fitting model (Akaike $w = 0.44$) included kokanee biomass and *Mysis* density. The next best fitting model ($\Delta$ AIC$_\mathrm{c} = 0.38$, Akaike $w = 0.37$) included kokanee biomass, *Mysis* density, and an interaction between the two. No other models were within 2.0 Δ

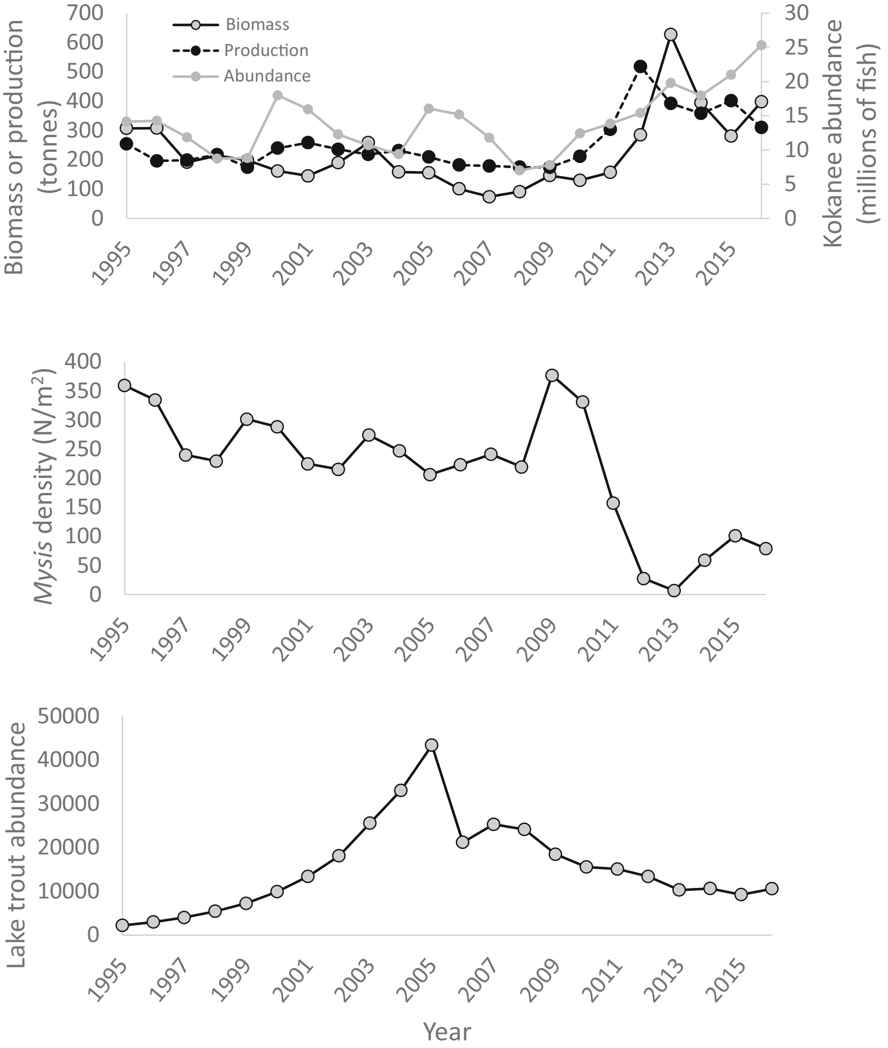

**Fig. 2** Kokanee biomass, production, and abundance (top panel), *Mysis* density (center panel), and age-8 + lake trout abundance (bottom panel) in Lake Pend Oreille, Idaho, during 1995–2016

AIC$_c$ of the top model (Table 1). The two top models had $R^2$ values of 0.83 and 0.86, respectively.

The production–biomass model for 1995–2010, before *Mysis* collapsed, differed significantly from a model for 2011–2016, after *Mysis* collapsed (Fig. 4; ANCOVA interaction; $F_{3,18} = 9.58$, $P < 0.01$). The 1995–2010 model was:

$$P_t = 3.21B_{t-1}\left(e^{-0.0053B_{t-1}}\right)$$

and the 2011–2016 model was

$$P_t = 3.27B_{t-1}\left(e^{-0.0029B_{t-1}}\right).$$

The combined goodness of fit of separate models of kokanee production and biomass before and after the *Mysis* collapse was more than three times higher (combined $R^2 = 0.76$) than a single model over both periods ($R^2 = 0.21$). Between 1995–2010 and 2011–2016, production per unit biomass at low biomass ($\alpha$) remained essentially the same, but the strength of density dependence ($\beta$) declined by 46%. Maximum annual production ($P_{\max}$) increased from 224 tonnes for 1995–2010 to 408 tonnes for 2011–2016.

## Discussion

We found that inter-annual variation in kokanee biomass and production in Lake Pend Oreille were correlated with lake trout abundance and adult *Mysis*

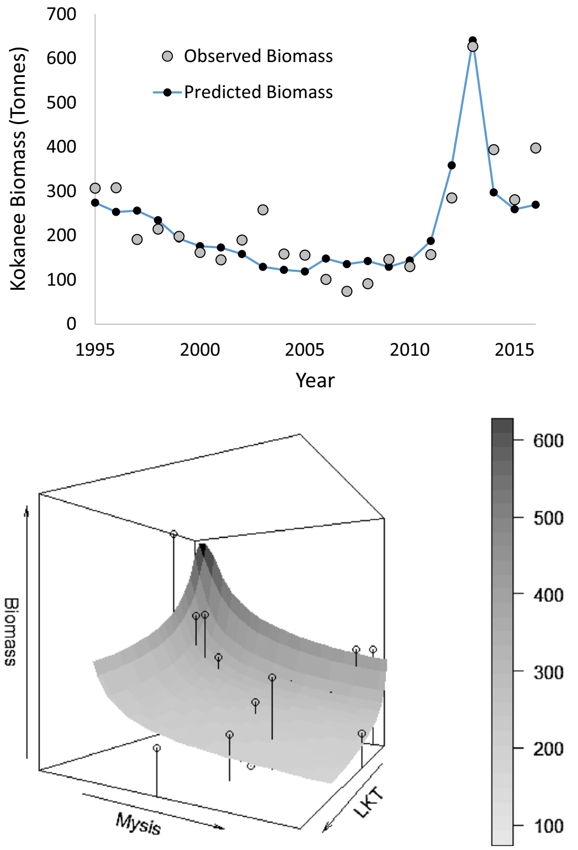

**Fig. 3** Observed and expected kokanee biomass (top panel) in Lake Pend Oreille, Idaho, during 1995–2016. Expected biomass was estimated using kokanee biomass as a function of lake trout (LKT) abundance and *Mysis* density. The response surface (bottom panel) depicts the expected biomass with darker shading = higher biomass and lighter shading = lower biomass. Circles on stems are observed data points

density in patterns consistent with predation and both inter- and intraspecific competition. Managing top-down control of kokanee through predator suppression has driven fishery management in Lake Pend Oreille (see Hansen et al., 2010; Dux et al., 2019; Hansen et al., 2019), but this study indicates *Mysis* may be just as important for regulating kokanee abundance. To pinpoint processes connecting *Mysis* to a kokanee bottleneck, net-pen experiments showed that reducing autumn zooplankton abundance reduced age-0 kokanee growth and biomass (Clarke & Bennett, 2002). Further, low cladoceran prey abundance was attributed to *Mysis* in spring and autumn when Lake Pend Oreille was not stratified and *Mysis* overlapped with their prey (Chipps & Bennett, 2000; Caldwell et al., 2016). Consumption of cladocerans by *Mysis* was estimated to be four times higher than kokanee in Lake Pend Oreille in 1995–1996 (Chipps & Bennett, 2000). These studies demonstrate some of the potential mechanisms influencing the change in the production–biomass relationship after *Mysis* collapsed. The production–biomass model demonstrated not only the powerful regulating influence of *Mysis* in Lake Pend Oreille, but also strong intraspecific density-dependent regulation of kokanee, which influences life-history characteristics, such as growth and age at maturity (Grover, 2005).

We found that kokanee production was a density-dependent process and that the collapse of *Mysis* corresponded to a shift in the expression of that process. While we did not model the influence of environmental factors, which may influence inter-annual variability in the strength of competition between *Mysis* and kokanee (Schoen et al., 2015), our models nonetheless suggest *Mysis* are an influential driver of kokanee productive capacity in Lake Pend Oreille. The kokanee production–biomass relationship since 2011 illustrated the conditions required to sustain the extraordinary production that historically supported kokanee harvests exceeding one million fish annually in the 1950s and 1960s. *Mysis* have been implicated in food web shifts (e.g., Rieman & Falter, 1981), so not surprisingly, *Mysis* is correlated with production, which was expected to be driven by bottom-up factors (Downing & Plante, 1993). Observed changes in the stock–recruitment relationship for one species caused by interactions with another species are not unique to *Mysis*-kokanee systems. A similar shift was observed in the stock–recruitment relationship for yellow perch *Perca flavescens* (Mitchill, 1814) in the western basin of Lake Erie when environmental changes caused by introduced zebra mussel *Dreissena polymorpha* (Pallas, 1771) improved conditions for recruitment (Zhang et al., 2017). Shifts in the production–biomass relationship have also been observed in Barents Sea capelin *Mallotus villosus* (Müller, 1776) where herring *Clupea harengus* (Linnaeus, 1758) overlapped (Gjøsæter & Bogstad, 1998). In that system, the stock–recruit relationship fit poorly ($R^2 = 0.36$) until herring were included ($R^2 = 0.72$). Similarly, this phenomenon also drives recruitment dynamics for cod *Gadus morhua* (Linnaeus, 1758), which primarily feed on capelin (Hjermann et al., 2007).

**Table 1** Akaike Information Criterion (AIC) results for each of the candidate models in the kokanee production–biomass analysis for Lake Pend Oreille, Idaho, during 1995–2016. Models were ranked by their ΔAICc values, likelihood of being the best model given the data (RL), and Akaike weights (w) (LogL is the log-likelihood and K is the number of parameters in each model). Model variables included kokanee biomass (Bio), *Mysis* (Mys), and lake trout (LKT)

| Model | LogL | K | AIC | AICc | $\Delta AIC_c$ | RL | *w* |
|---|---|---|---|---|---|---|---|
| Bio + Mys | 9.99 | 4 | − 11.97 | − 9.62 | 0.00 | 1.00 | 0.44 |
| Bio × Mys | 11.50 | 5 | − 12.99 | − 9.24 | 0.38 | 0.83 | 0.37 |
| Bio + LKT + Mys | 9.99 | 5 | − 9.98 | − 6.23 | 3.39 | 0.18 | 0.08 |
| Bio + + Mys × LKT | 11.67 | 6 | − 11.35 | − 5.75 | 3.87 | 0.14 | 0.06 |
| Mys + Bio × LKT | 10.83 | 6 | − 9.67 | − 4.07 | 5.55 | 0.06 | 0.03 |
| LKT + Bio × Mys | 10.07 | 6 | − 8.13 | − 2.53 | 7.09 | 0.03 | 0.01 |
| Bio × Mys × LKT | 16.52 | 9 | − 15.05 | − 0.05 | 9.57 | 0.01 | 0.00 |
| Bio | − 0.64 | 3 | 7.29 | 8.62 | 18.24 | 0.00 | 0.00 |
| Bio + LKT | − 0.03 | 4 | 8.06 | 10.41 | 20.03 | 0.00 | 0.00 |
| Bio × LKT | 0.02 | 5 | 9.95 | 13.70 | 23.32 | 0.00 | 0.00 |

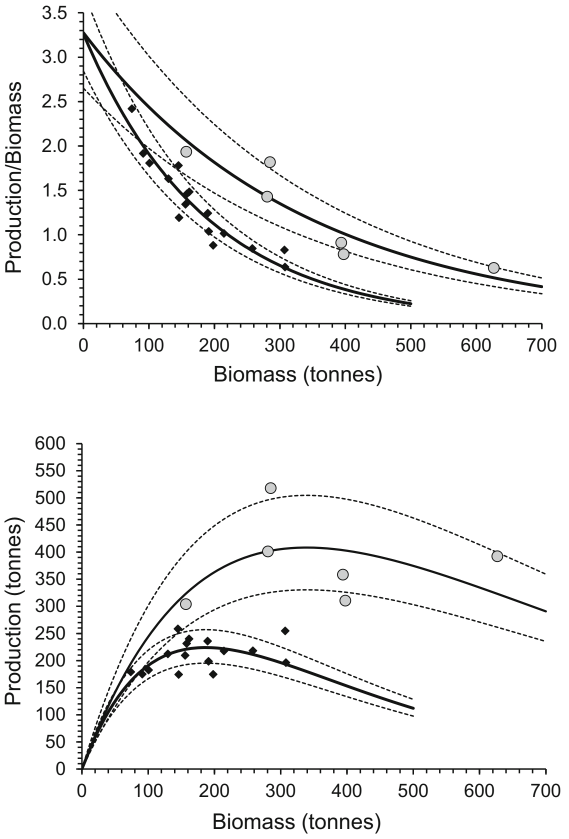

**Fig. 4** Per-capita (top panel) and total (bottom panel) kokanee production in relation to biomass density in Lake Pend Oreille, Idaho, during 1995–2016. Black diamonds are before *Mysis* collapse during 1995–2010. Gray circles are after *Mysis* collapse during 2011–2016

We found that lake trout was correlated with kokanee production and biomass in Lake Pend Oreille, but only in conjunction with *Mysis*, likely because of two related mechanisms. First, *Mysis* simultaneously decrease available prey for kokanee and increase lake trout recruitment to piscivorous size classes (Ellis et al., 2011). Second, the presence of *Mysis* appeared to reduce the productive capacity of the kokanee population sufficiently to create an imbalance between total predation and kokanee production (Hansen et al., 2010). Recovery of the kokanee population beginning in the late 2000 s was apparently facilitated by the simultaneous collapse of *Mysis* and suppression of lake trout. This observation is essentially a reversion of the phenomenon observed in Priest Lake, Idaho (Bowles et al., 1991), Lake Granby, Colorado (Martinez et al., 2009), and Flathead Lake, Montana (Ellis et al., 2011), where competition from *Mysis*, combined with unchecked growth of the lake trout population led to rapid, and continued, collapse of kokanee.

Top-down influences of predation are likely important regardless of the presence of *Mysis* in Lake Pend Oreille. High kokanee abundances were observed in the mid-1990s before the lake trout population expanded and the lowest observed kokanee abundances (in 2001 and 2006) occurred during a period when lake trout abundances were markedly increasing. Mysis densities were high during the entirety of that time. Predation by lake trout in the absence of

*Mysis* has been implicated as a limiting factor contributing to the decline of kokanee in Blue Mesa Reservoir, Colorado (Hardiman et al., 2004; Pate et al., 2014), which supports the assertion of top-down control of kokanee without apparent competition from *Mysis*. Similarly, predation by cutthroat trout and northern pikeminnow was identified as a primary limiting factor for kokanee and sockeye salmon populations in Lake Ozette, Washington (Beauchamp et al., 1995). Top-down control of pelagic planktivores has been described in other fish assemblages, such as the regulation of alewife populations by salmonid predators in Lake Michigan (Stewart & Ibarra, 1991), and population expansions of macroinvertebrates and small pelagic fishes in the Scotian Shelf ecosystem of the Atlantic Ocean following collapse of cod stocks (Frank et al., 2005). While the influence of top-down predation by lake trout on kokanee in Lake Pend Oreille cannot be demonstrated independently from *Mysis*, it is undoubtedly important.

The biomass model provided a framework by which we demonstrated concurrent regulation of kokanee production by *Mysis* and lake trout. Kokanee existed at moderate biomass in the presence of *Mysis*, but before the lake trout population expanded. The precipitous slope of the response surface as lake trout abundance increased suggests that total predation exceeded production at a reduced carrying capacity (moderate-to-high *Mysis* densities). Evidently, the kokanee population in Lake Pend Oreille exists near a predation-induced collapse threshold when *Mysis* density is high. As lake trout became abundant, consumption began to exceed production by 2006 and the kokanee population was expected to collapse without predator suppression (Hansen et al., 2010). A similar dynamic was observed in Lake Chelan, where predation by a newly abundant lake trout population exceeded kokanee production with *Mysis* present (Schoen et al., 2012). *Mysis* likely relax the numerical response of lake trout to reduced kokanee abundance (Ng et al., 2017), although the functional response may still be density dependent at very low prey densities (Eby et al., 1995). Such a model could explain why kokanee continued to persist at low abundance in waters where *Mysis* and lake trout facilitated their collapse (e.g., Priest Lake, Idaho, and Granby Reservoir, Colorado, Martinez et al., 2009). However, a stable, low abundance kokanee population is not a tenable management goal and the results of the production–biomass model presented here suggests that *Mysis* mediate the threshold for predator-induced collapse.

Continued management of Lake Pend Oreille as a yield fishery for kokanee, a trophy fishery for pelagic predators, and an important bull trout conservation population will depend on the interplay between top-down and bottom-up influences on kokanee. We do not know if *Mysis*, which recovered from all-time low abundance in 2012 to 38% of their long-term average, will return to high densities observed before 2011 and again limit kokanee production in Lake Pend Oreille. The difference between kokanee production and total predator consumption in Lake Pend Oreille will define the scope for management (Hansen et al., 2010). Further, because feasible management options for regulating *Mysis* are currently limited (Martinez & Bergersen, 1989), maintenance of the fishery will require continued management of kokanee predators. Lake trout have been the focus of a successful suppression program (see Dux et al., 2019). Management resources are not inexhaustible, and suppression and maintenance of desired lake trout population objectives, while feasible (see Hansen et al., 2019), could come at an opportunity cost for managing other kokanee predators in the lake. Ironically, long-term maintenance of Lake Pend Oreille as a diverse fishery for trophy predatory fish, including bull trout, rainbow trout, lake trout, and walleye will only be possible if managers can continue to avoid predation in excess of production.

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