

Density-Dependent Growth in Juvenile Sockeye Salmon (*Oncorhynchus Nerka*)

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Abstract: Data gathered over 77 lake-years from 4 coastal British Columbia sockeye salmon nursery lakes suggest that density-dependent growth reductions are only possible at exceptionally high fry densities. In Great Central Lake (n=33 years) and Sproat Lakes (n=30 years) there was no relationship between smolt weight and mean summer fry densities ranging from 760-3800 fry ha⁻¹. However, in two years when Sproat Lake fry densities were unusually high (1983=5183 ha⁻¹, 1996=4801 ha⁻¹) smolt weights were among the lowest recorded. In Woss and Vernon lakes (n=14 lake-years), there were significant bottom-up relationships between fall-fry weights and zooplankton biomass, but no relationships between December-fry weights and average fry densities (range 331-1361 ha⁻¹), nor were there significant top-down relationships between fry densities and average zooplankton biomass. Comparisons of zooplankton production with bioenergetic-based fry consumption, suggested that the carrying capacity for Vernon Lake which had the highest rate of zooplankton production, was 12,700 fry ha⁻¹, and for Sproat Lake which had the lowest zooplankton production, was 5200 fry ha⁻¹. We conclude that fry densities in the range commonly observed for British Columbia coastal lakes (i.e. 500-4000 ha⁻¹) cannot cause density-dependent reductions in prey biomass or fry growth rates. Further research is necessary.

Keywords: juvenile sockeye salmon, density dependence, aquatic food web, bioenergetics, zooplankton production, consumption by sockeye fry.

INTRODUCTION

It is generally assumed that growth-rates of juvenile sockeye salmon (*Oncorhynchus nerka*) are positively correlated with nursery lake productivity and negatively correlated with in-lake juvenile sockeye density. The paradigm has two parts and one corollary. (1) Increased lake productivity results in larger late-fall fry and/or smolts and (2) higher densities of juvenile sockeye are associated with smaller late-fall fry and/or smolts. Zooplankton abundance is the common factor linking the two parts of this density-dependent relationship. Higher lake "productivity" is assumed to be associated with higher abundances of zooplankton, more food and therefore faster sockeye growth-rates. Consumption of zooplankton by higher densities of sockeye is assumed to result in decreased availability of zooplankton and therefore decreased growth-rates of juvenile sockeye salmon.

Studies supporting the first proposition linking "lake productivity" and fry growth include both empirical between-lake comparisons and whole-lake fertilization manipulations. Empirical relationships based on positive correlations between lake productivity and juvenile sockeye growth have been found for nursery lakes in Alaska [1, 2] and British

Columbia [3] and have been successfully applied to the management of in-lake sockeye populations [4-6]. Comprehensive reviews of sockeye nursery-lake fertilization manipulations [7, 8] found that almost without exception, fertilization was associated with increased concentrations of chlorophyll *a*, increased zooplankton biomasses and increased late-fall-fry or smolt weights.

Studies supporting the second proposition linking increased juvenile sockeye density to reduced juvenile growth rates are all based on lake-specific observational data. Early examples come from Cultus Lake, British Columbia [9, 10], Lake Dalnee, Kamchatka [11, 12], and Babine-Nilkitkwa lakes, British Columbia [13-17]. Later examples from Alaska Department of Fish and Game (FRED) program [2] include Fraser Lake [7, 18, 19] and Coghill Lake [20]. More recent examples include the Egegik River system, Alaska [21], Quesnel, Shuswap and Chilko lakes, British Columbia [3], Wood River system, Alaska [22], Iliamna Lake, Alaska [23]. One of these studies directly links reductions in zooplankton abundance to very high densities of stocked sockeye [7], while many of the others rely on indirect measures of juvenile density and/or zooplankton biomass [2, 3, 22, 23].

On the other hand, long-term (1969-76) and detailed measures of both fish abundance and zooplankton biomass in Great Central Lake (5100 ha) [24-27] showed no relationship between juvenile sockeye density and zooplankton biomass. This is also the result from bioenergetics-based juvenile

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sockeye and kokanee studies designed to compare consumption by fish with biomass and production of their prey. In most cases, these studies have shown that age 0 sockeye or kokanee have minimal effects on prey standing stocks. In Lake Ozette, State of Washington, juvenile sockeye and juvenile kokanee consumed < 1% of the instantaneous production of their preferred prey *Daphnia pulicaria* (Forbes) [28]. In Lake Washington during March-April, age 0 sockeye consumed 5% of prey biomass per month and had no effect on standing stocks of the preferred prey *Diacyclops thomasi* (Forbes) [29]. Also in Lake Washington during April-November, juvenile sockeye plus *Neomysis mercedis* (Holmes) consumed only 10% per month of *Daphnia* biomass [29, 30]. In British Columbia's Woss and Vernon lakes on Vancouver Island, during 2000-02, juvenile sockeye salmon consumed an average of < 0.5% d⁻¹ of the zooplankton standing stock [31].

Given these very low rates of bioenergetic-based consumption by juvenile sockeye and kokanee, it is difficult to understand how density-dependent growth can be explained by top-down impacts of juvenile nerks on their zooplankton food base.

We have addressed this general problem using three data sets. (1) We used long-term data sets from Great Central Lake (33 years) and Sproat Lake (30 years) to test the hypothesis that there was a significant negative relationship between fry density and smolt weight. We also investigated the relationship between adult escapement and resulting fry density. (2) We used detailed food web data sets from Great Central and Sproat lakes to quantify the proportion of zooplankton biomass consumed by sockeye fry during the 1999 spring-fall growth period. (3) We used moderately long-term (2000-06) and detailed data sets from Woss and Vernon lakes to quantify the bottom-up relationships between lake productivity, zooplankton abundance and juvenile sockeye fall-fry lengths and weights, and also the top-down relationships between average fry density, zooplankton abundance and fall fry lengths and weights.

METHODS

Preface to Methods

Given the complexity of the three data sets noted above, we have divided the methods into four sections. The first deals with the site description and long-term data for Great Central and Sproat sockeye salmon escapement, fry and smolt weights. The second deals with the site description and experimental design used for the seven year Woss and Vernon lake experiment. The third section provides detailed descriptions of the methods used to collect and analyze the food web data collected at Woss and Vernon lakes during 2000-06 and also at Great Central and Sproat lakes during 1999. These methods are summarized in Table 1 while survey frequency and sample sizes are provided in Table 2. The fourth section deals with within and between-sample variability.

Great Central and Sproat lakes (1977-2008)

Great Central Lake (lat. 49°22' long. 125°15' lat.) (surface area 5100 ha, mean depth 212 m, average total phosphorus TP = 2.6 µg L⁻¹) and Sproat Lake (lat.

49°14' long. 125°06' lat.) (surface area 4100 ha, mean depth 59 m, average TP = 2.7 µg L⁻¹) both drain into Barkley Sound at Port Alberni, central-Vancouver Island. Over the last 35 years Great Central Lake was fertilized in all years, and Sproat was fertilized only in 1985. Sockeye escapements have averaged 190,000 y⁻¹ (Great Central) and 150,000 y⁻¹ (Sproat), and lake-wide juvenile densities have averaged 8,770,000 (Great Central) and 7,770,000 (Sproat).

Over 33 years in Great Central Lake and 30 years in Sproat Lake, juvenile sockeye densities, fry sizes and associated smolt weights were systematically measured using in-lake echosounding, mid-water trawling (fry) and trap-netting at the lake outlets (smolts). Pelagic fish (principally juvenile sockeye) densities were estimated at night using one of four echosounders. Between 1977 and 1982 we used a Furuno FM-22, 200kHz, single beam echo sounder with 100 W of power output, a pulse width of 1.0 ms and a custom designed Time Varied Gain (TVG) to control for attenuation losses due to increasing target depth. Between 1982 and 2001, we used a Simrad EY-M, 70 kHz, single beam echosounder with 75 W of power output, pulse width 0.6 ms and a TVG circuit. From 2002 to 2005 we used a Simrad EY-500, single beam, 70 KHz sounder with 50 W power output with pulse width at 0.2 ms and a TVG circuit. After 2006 we used a split-beam Biosonics DT-X, 200kHz sounder with 300 W power, pulse width at 4 ms and a 6.6° transducer. Cross calibration of the Furuno and Simrad EY-M echosounders is documented by Gjernes *et al.* [32]. Cross-calibration of the two Simrad machines showed that they produce similar results when configured appropriately (P. Rankin, unpublished data). Cross-calibrations of the Simrad and Biosonics echosounders were based on survey data collected on 13 sampling dates spread among four B.C. sockeye nursery lakes. During each sampling date, complete lake surveys were conducted simultaneously by two survey crews following identical survey transects. Total density estimates ranged from 300-4000 fish ha⁻¹. The relationship between total densities derived from Simrad vs. Biosonics was Simrad = 111+0.9*Biosonics (n = 13, R² = 0.94). From this we concluded that density estimates from the two machines were similar. Details regarding survey design and counting methods (for the single beam echosounders) follow Hyatt and colleagues [32-34] and methods (Sonar 5 Pro) for the split-beam (Biosonics) echosounder are described by Balk and Lindem [35].

Smolt samples were collected from outlet streams using a 2x2m trawl net suspended in the main channel. Sampling generally started during the last week of April and was completed by the end of May. The peak migration period usually occurred between the last week of April and first week of May. After each trawl set, fish were immediately removed from the net, and preserved in 10% buffered formalin or 70% ethanol. Weights were corrected for preservative effects and expressed as fresh standardized weight (g). Detailed smolt sampling procedures are described by Hyatt *et al.* [33].

Woss and Vernon Lakes (2000-06)

Woss Lake (50°7' long. 126°36' lat.) (surface area 1366 ha, mean depth 65 m, average TP = 3.5 µg L⁻¹) drains into the Nimpkish River and then into Broughton Strait, north-Vancouver Island. Vernon Lake (50°2' long. 126° 25' lat.)

Table 1. Summary Linking Results to Methods. Column 1- Lake. Lake Abbreviations are W = Woss, V = Vernon, G = Great Central and S = Sproat. Where Years are not Shown the Summaries Apply to Woss and Vernon 2000-06, Great Central and Sproat 1999. Smolt and in-Lake Acoustic Estimates are for Great Central and Sproat 1977-2008. Column 2 - The “Result” Used to Draw Subsequent Conclusions, Column 3- Method Used to Collect Field Data, Column 4 – Method Used to Derive Result. Refer to Table 2 for Numbers of Samples Per Season. Detailed Methods are Provided in the Methods Section

β	Parameter or Result	Method Used in the Field	Method Used to Estimate Parameter
W,V	Phytoplankton species biomass	integrated samples, 1,3,5 m	Utermöhl (1958) counts
W,V,G,S	Zooplankton species biomass	30 m vertical hauls, metered	volume-weighted combined samples; species, length-weight, egg counts
W,V,G,S	Zooplankton productivity	as above	egg-ratio production models
W,V,G,S	Fish density	acoustic	echo-integration
W,V,G,S	Fish vertical migration	acoustic	as above
W,V,G,S	Fish, length, weight, stomachs	2x2 m trawl net	length-weights; stomach contents
W,V,G,S	Rates consumption by fish	density, growth, stomachs, migration, water temperature	fish bioenergetics model
G,S	Fish density (1977-2008)	acoustic	echo-integration analysis
G,S	Smolt weight (1977-2008)	2x2 m fyke net	length-weights, age
G,S	Adult escapement (1977-2008)	electronic fish-way counts	resistivity counter

Table 2. Woss and Vernon Lakes 2000-2006; and Great Central (GCL) and Sproat Lakes 1999. Fertilizer Treatment and Sample Size

	Fertilizer kg P ha ⁻¹	Fertilizer kg N ha ⁻¹	No. Algal Samples	No. Zooplankton Samples	No. Fish Biosamples	Total No. Fish Sampled	Total No. Fish Stomachs	No. Fish Acoustic Samples
Woss								
2000	0.4	5.9	7	8	5	376	120	4
2001	0.5	7.2	8	9	5	357	101	5
2002	0.7	9.7	8	9	7	808	109	7
2003	0.5	9.9	5	8	4	462	0	4
2004	0.0	0.0	7	7	3	284	108	5
2005	1.1	10.0	7	8	4	629	57	3
2006	1.0	8.8	6	7	3	313	97	4
Vernon								
2000	0.0	0.0	7	8	4	277	120	3
2001	0.0	0.0	7	8	4	175	97	4
2002	0.0	0.0	8	9	7	423	114	7
2003	0.0	0.0	4	4	3	209	0	3
2004	1.1	10.0	7	6	3	278	86	5
2005	1.1	10.0	7	8	4	364	55	3
2006	1.2	8.1	6	7	3	265	87	3
GCL 1999	0.6	8.5	0	9	5	871	159	3
Sproat 1999	0.0	0.0	0	7	4	303	116	3

(surface area of 837 ha, mean depth 62 m, average TP = 2.9 $\mu\text{g L}^{-1}$) drains into the Sebalhal River which also flows into the Nimpkish River [31]. The Woss River system produces approximately 25% of total Nimpkish system sockeye salmon. Vernon Lake and the Sebalhal River produce approximately 20% of total Nimpkish sockeye salmon [36].

During 2000-06, the “productivity” of both Woss and Vernon lakes was altered through the addition of various concentrations of fertilizer (Table 2) and during the same period, fish density was altered through natural year-to-year variation in recruitment. For Woss and Vernon lakes, our research plan was to use the power of fertilization to increase

lake productivity and zooplankton biomass while still holding all other parameters (i.e. morphometry, species composition) steady. This gave us the opportunity to isolate top-down effects of sockeye on a wider range of treatment-induced zooplankton densities.

Food web analysis Woss and Vernon 2000-06; Great Central and Sproat 1999

The goal of the intensive 2000-06 analysis in Woss and Vernon lakes and the 1999 analysis in Great Central and Sproat lakes, was to calculate zooplankton consumption by the fish as a percentage of production by each prey species-type. When consumption exceeded production we expected to see the zooplankton population decline and at that point we could assume that the "sockeye salmon production capacity" of the lake had been reached or exceeded. During each lake-year, we measured species-specific zooplankton densities, lengths, weights, biomasses and estimated their production. We also measured *O. nerka* densities, lengths, weights, biomasses, stomach contents and estimated their prey-specific rates of consumption. We then calculated prey consumption by nerkids as percent daily species-specific zooplankton production to draw inferences about whether consumption exceeded production [31]. This allowed us to simulate the effects of changing planktivorous fish numbers and to calculate the density threshold at which consumption by fish > production of their zooplankton prey.

At Woss and Vernon Lakes, during 2000-06, phytoplankton was collected approximately every 3 weeks from each of two stations in each lake (Table 1, 2). At the laboratory, each lake-date pair was combined and processed using the Utermöhl technique [37]. Cells were identified (genus level) measured and biomasses were recorded as $\text{mm}^3 \text{m}^{-3}$ (approximates $1 \mu\text{g}$ wet weight L^{-1}). The objective of the phytoplankton procedure was to assess biomasses of edible and non-edible algae. We quantified "edibility" based on size, toxicity and digestibility. Single cells or colonies < 30 μm width or length were considered edible [38, 39] unless they were classified as being either "toxic" or "digestion-resistant" (defined below). *Microcystis* was always classified as being "toxic". Other genera were assumed to be non-toxic. Algae with gelatinous sheaths [40] were classified as digestion-resistant (not edible).

Zooplankton samples (Rigosha™ metered, 30 x 30 cm square net, 100 μm mesh, 0-25 m vertical haul) were collected approximately every 3 weeks at each of 4 stations in Woss, Great Central and Sproat lakes and 3 stations in Vernon Lake. Samples were washed out of the plankton net with carbon-dioxide saturated water and were then preserved in 4% buffered and sugared formalin. Sample frequency, number of sampling sites and net metering followed protocols suggested by Yan *et al.* [41-43]. At the laboratory, combined volume-weighted samples were created and used to estimate species-specific densities, lengths and weights. For each combined count, 300-500 individual zooplankton [44] were identified, measured and their eggs counted. Length-weight regressions were used to calculate dry-weight biomass for each individual [45, 46]. Our goal was to estimate species-specific prey biomasses available to pelagic fish and to estimate daily rates of prey replacement resulting from

species-specific production. Zooplankton production was estimated using the egg ratio method [47, 48].

During June-December, pelagic fish densities were surveyed 3-7 times (Table 2) using 11 transects in Woss, 7 transects in Vernon, 6 transects in Great Central and 11 transects in Sproat lakes. The acoustic methods used to estimate fish density are summarized above for Great Central and Sproat lakes. Limnetic fish samples were collected 3-7 times (Table 2) using a mid-water trawl net (2 m x 2 m mouth opening x 7.5 m long). Trawl depths were based on echo-sounding results. Fish were processed for lengths, weights and stomach contents. Survey protocols including stomach content analysis are described in McQueen *et al.* [31]. Our goal was to calculate June-October rates of consumption by the fish as a percentage of biomass and production by each species of zooplankton prey. For Woss and Vernon lakes (2000-06) and Great Central and Sproat lakes (1999), Wisconsin Model 3 parameters CA and CB [49] were adjusted so that simulated fry growth rates matched rates observed in the field (Appendix A). Model fry densities were based on curves of best fit from field samples (Table 2, Appendix A). The model was used to estimate daily consumption from mid-June to end-November for Great Central and Sproat lakes and from mid-June to end October for Woss and Vernon lakes (Tables 1, 2). In all four lakes, diel migration studies [31, 50] showed that fry fed in both the epilimnion and hypolimnion and therefore model temperatures were based on 0-40 m average water temperatures. Energy densities ($\text{J}\cdot\text{g}^{-1}$ wet weight) were set at $5233 \text{ J}\cdot\text{g}^{-1}$ for sockeye and kokanee, at $3000 \text{ J}\cdot\text{g}^{-1}$ for copepods and $2500 \text{ J}\cdot\text{g}^{-1}$ for cladocerans.

For all four lakes, the calculation of "carrying capacity" was based on field estimates of average daily species-specific zooplankton production and daily species-specific consumption by limnetic fish. Simulated fish densities were then increased. When consumption by fry > production of their prey, we assumed that carrying capacity had been reached. In the Great Central and Sproat lake cases, prey production and simulated consumption by fry were based on field estimates from 1999. In the Woss and Vernon lake cases, production and simulated consumption were based on data averaged over several survey years (2000-06) except 2003 when fish stomachs were not sampled.

Within-year variability

Throughout we used seasonal averages to facilitate between-year comparisons for Woss and Vernon phytoplankton, zooplankton, fish density and fish weight-at-age data. Because the averages were all derived from samples collected through the growing season, there was no meaningful way to summarize within-year variability. We have therefore provided original seasonal data for zooplankton and fish (Appendices A and B).

RESULTS

Great Central and Sproat Lakes: Long-Term Results

Smolt weights and fry densities in Great Central Lake were recorded over 33 years (1976-2008). During 31 lake years, sockeye fry densities varied from $735\text{-}3503 \text{ ha}^{-1}$ (mean 1718 ha^{-1}) and average smolt weights ranged between 2.0-5.0 g (mean 3.1 g). Over this density range there was no rela-

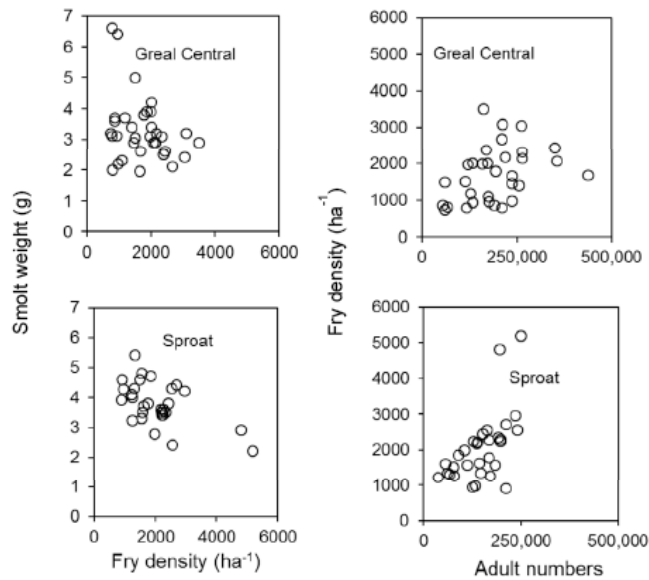


Fig. (1). Great Central Lake and Sproat Lake smolt weights (left side panels) with respect to average (June–November) fry densities. Mean summer (June–November) fry densities (right panels) with respect to the number of spawning adults.

tionship between average in-lake fry density and average smolt weight (Pearson $R^2 = 0.013$, $n = 31$, $p = 0.548$) (Fig. 1). During two years (1986, 1990) fry densities averaged $<1000 \text{ ha}^{-1}$ and smolt weights were exceptionally high (6.6, 6.4 g respectively), but during eight other years when fry densities $<1000 \text{ ha}^{-1}$, smolt weights ranged between 2–4 g ha^{-1} . Including the two outliers failed to yield a significant relationship between fry density and smolt weight (Pearson $R^2 = 0.088$, $n = 31$, $p = 0.093$). At Sproat Lake during 28 of 30 lake years (1978–2007), sockeye fry densities ranged from 934–2962 ha^{-1} (mean 1845 ha^{-1}) and annual-average smolt weights ranged between 2.4–5.4 g (mean 3.8 g). Over this density range there was no relationship between average in-lake fry density and average smolt weight (Pearson $R^2 = 0.107$, $n = 28$, $p = 0.089$) (Fig. 1). During two of the 30 lake-years (1983, 1996), fry densities were exceptionally high (5183 and 4801 ha^{-1}) and smolt weights were among the lowest recorded (2.2 and 2.9 g respectively). Including the two outliers, produced a significant relationship (Pearson $R^2 = 0.310$, $n = 30$, $p = 0.001$) between fry density and smolt weight.

Spawner numbers and associated average fry densities were recorded over 32 years in Great Central Lake and 31 years in Sproat Lake (Fig. 1). In Great Central Lake at high adult densities, there may have been density-dependent mortality, perhaps due to events on the spawning beds. In Sproat Lake, there was no evidence of density-dependent mortality.

Great Central and Sproat Lakes: 1999

In Great Central Lake during June–November 1999, fry densities declined as the fry grew and gained weight (22 June density = 3239, mean weight = 0.21 g; 25 November density = 1457, mean weight = 1.88 g). Total 1999 zooplankton biomass gradually increased through the season averaging $13.95 \mu\text{g L}^{-1}$ dry weight and $>95\%$ of that biomass comprised only three species (*Holopedium gibberum*, *Diacy-*

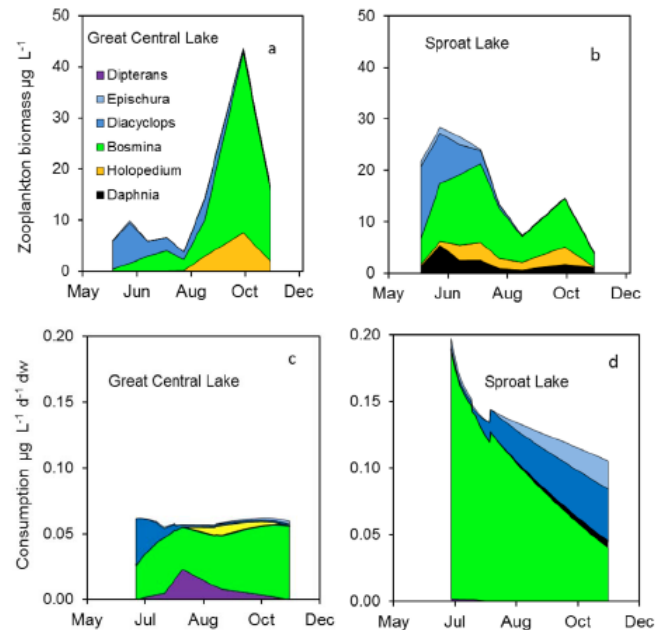


Fig. (2). Great Central and Sproat lake (panels a, b) zooplankton biomass and (panels c, d) daily rates of consumption by juvenile sockeye.

clops bicuspidatus, *Bosmina longispina*) (Fig. 2a). The other 5% included 2 copepods (*Epischura nevadensis*, *Skistodiatomus oregonensis*) and 5 cladocerans (*Daphnia longiremis*, *Daphnia pulex*, *Bosmina longispina*, *Bosmina longirostris*, and *Polyphemus pediculus*). Throughout the summer–fall, daily prey consumption by juvenile sockeye averaged $0.05 \mu\text{g L}^{-1} \text{d}^{-1} \text{dw}$ (Fig. 2c) which translates to 0.4% d^{-1} of total zooplankton standing stock biomass. Percent zooplankton standing stock and production consumed by juvenile sockeye varied through the summer–fall, but never exceeded 100% of daily species-specific production.

In Sproat Lake during June–November 1999, fry densities apparently increased (27 June density = 1426, mean weight = 0.73 g; 18 November density = 2240, mean weight = 2.67 g). In contrast to Great Central Lake, total 1999 Sproat Lake zooplankton biomass decreased through the season averaging $18 \mu\text{g L}^{-1}$ dry weight. More than 95% of total zooplankton biomass comprised 5 species (*Epischura nevadensis*, *Holopedium gibberum*, *Diacyclops bicuspidatus*, *Bosmina longispina* and *Daphnia longiremis*) (Fig. 2b). The other 5% included *Daphnia pulex*, *Bosmina longirostris*, and *Polyphemus pediculus*. Throughout the summer–fall, daily consumption by juvenile sockeye averaged $1.2 \mu\text{g L}^{-1} \text{d}^{-1} \text{dw}$ (Fig. 2d), which translates to 0.7% d^{-1} of total standing stock biomass. Percent zooplankton standing stock and production consumed by juvenile sockeye varied through the summer–fall, but never exceeded 100% of daily species-specific production of zooplankton

Woss and Vernon Lakes 2000–06 Standing Stocks

In Woss Lake during all years except 2005, more than half of the phytoplankton biomass comprised large, inedible diatoms *Rhizosolenia eriensis* and *R. longiseta*. During 2005, more than half of the phytoplankton biomass comprised *Lep tocyllindrus sp.*, a small, highly edible, coiled and flattened

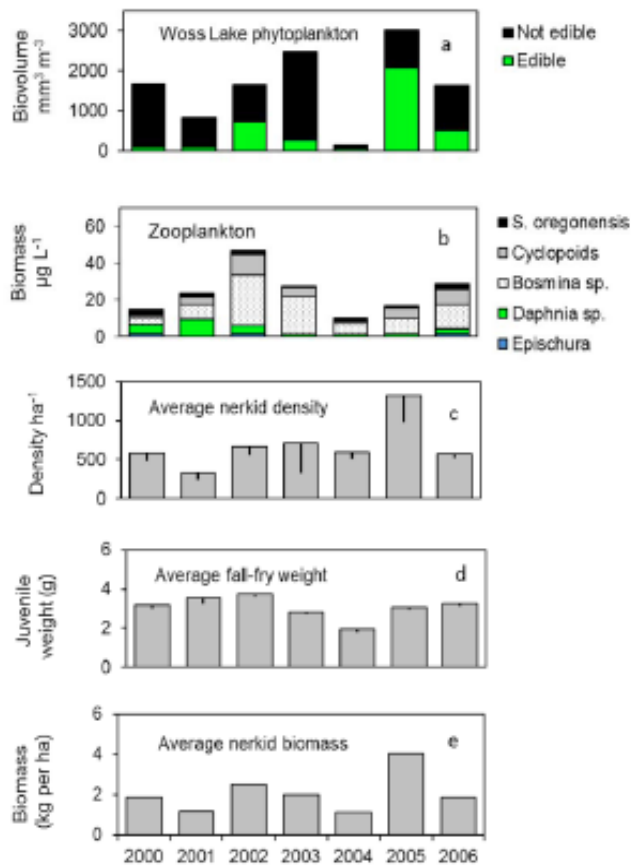


Fig. (3). Woss Lake 2000-2006 average (June-November) phytoplankton biovolumes, zooplankton biomasses, and nerkid densities, fall weights and biomasses. 95% CI error bars are shown in panels c and d. Detailed zooplankton biomasses are plotted in Appendix B.

cylinder, measuring approximately $20 \times 8 \times 3 \mu\text{m}$ (Fig. 3a). The Woss Lake zooplankton community included *Daphnia ambigua*, *Bosmina longirostris*, *Holopedium gibberum*, *Polyphemus pediculus*, *Diacyclops thomasi*, *Epischura nevadensis* and *Skistodiaptomus oregonensis* (Appendix B, Fig. 3b). Population biomasses increased with warming spring-summer water temperatures and declined with cooling fall temperatures. Electivity-based prey preference by juvenile sockeye salmon was *Epischura*>*Daphnia*>*Bosmina*>*Diacyclops*. During 2000-06, a total of 3358 *O. nerka* were sampled with the 3x2m trawl net (Table 2) and 28 (0.8%) were age-1 hold-over sockeye. Mean seasonal densities of juvenile sockeye in Woss Lake (Appendix A, Fig. 3c) varied with escapement and average fall weights (Appendix A, Fig. 3d) varied with zooplankton biomass (Fig. 5e, f).

Vernon Lake phytoplankton biomass was greatest during 2005-06 when the lake was fertilized and lowest during 2000-03 when it was not (Fig. 4a). During most years, most of the phytoplankton biomass comprised non-edible diatoms. The Vernon Lake zooplankton community was the same as for Woss Lake, except that *Hesperodiaptomus kenai* replaced *S. oregonensis* and *E. nevadensis* was absent. Prey preference by juvenile sockeye salmon was *Hesperodiaptomus*>*Daphnia*>*Bosmina*>*Diacyclops* (Appendix B, Fig. 4b). In Vernon Lake during 2000-06, a total of 2103 *O. nerka* were sampled with the trawl net (Table 2), 94.3% were

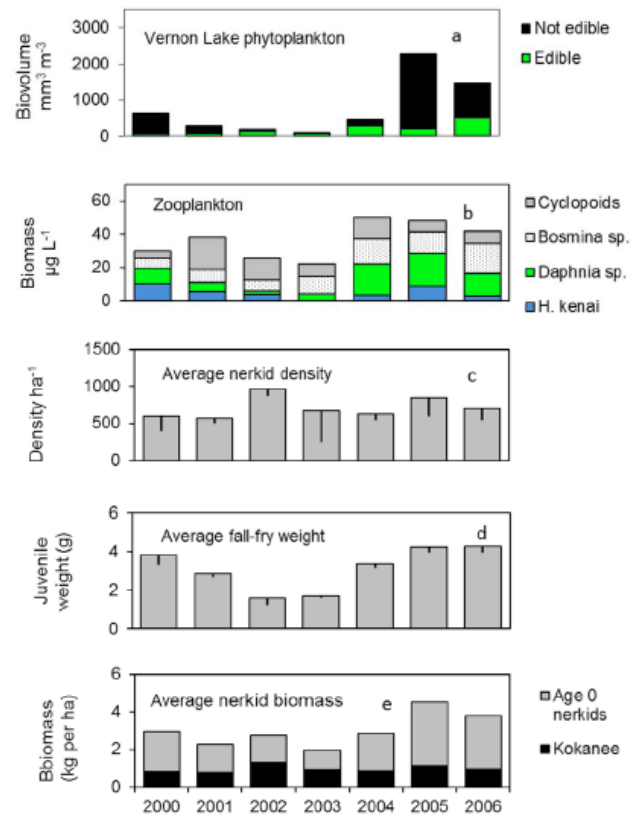


Fig. (4). Vernon Lake 2000-2006 average (June-November) phytoplankton biovolumes, zooplankton biomasses, and nerkid densities, fall weights and biomasses. 95% CI error bars are shown in panels c and d. Detailed zooplankton biomasses are plotted in Appendix B.

juveniles 1.9% were age-1 and 3.8% were older. We assumed that all fish older than age-0 (total of 121) were kokanee. During 2000-06, total numbers in this “kokanee sample” group were 0, 24, 18, 13, 5, 40, 21 per lake-year, and their average weights during 2001-06 were 29, 20, 11, 29, 27, 21 g wet weight respectively. Although kokanee numbers were small (average 6% of total density), each fish was relatively large and together they represented about 32% of the total *O. nerka* biomass in Vernon Lake (Fig. 4c, d, e). Mean seasonal densities of juvenile sockeye in Vernon lake (Appendix A, Fig. 4c) varied with escapement while average fall weights (Appendix A, Fig. 4d) varied with zooplankton biomass (Fig. 5e, f).

For both lakes, there was a significant positive correlation between fertilizer load and mean June-October biovolume total algae (Pearson $R^2 = 0.602$, $n = 14$, $p < 0.01$) (Fig. 5a). In both lakes, the relationships between the total biomass of zooplankton and total biovolume of phytoplankton was not statistically significant (Pearson $R^2 = 0.073$, $n = 14$, $p = 0.34$) (Fig. 5b), nor was the relationship between total biomass of zooplankton and biovolume of edible algae (Pearson $R^2 = 0.073$, $n = 14$, $p = 0.36$) (Fig. 5c). The outlier was Woss Lake 2005 (red symbol Fig. 5b, c). During that year, phytoplankton biomasses were very high, zooplankton biomasses were low and juvenile sockeye density and biomass were the highest on record (Fig. 3). When Woss Lake 2005 was removed from the analysis, total zooplankton biomass was correlated with edible phytoplankton biomass

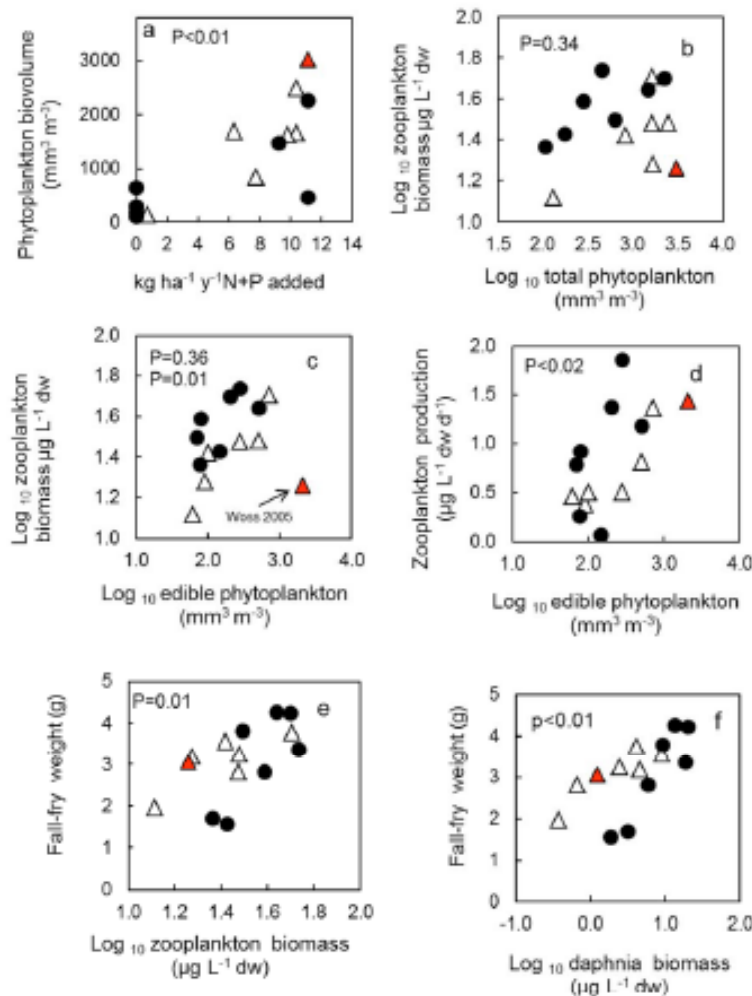


Fig. (5). Woss (Δ) and Vernon (O) lake (2000-2006) bottom-up correlations based on summer (June-November) averages for adjacent trophic-levels. The red symbols are for Woss Lake 2005.

(Pearson $R^2 = 0.422$, $n = 13$, $p = 0.01$) (Fig. 5c). In both lakes there was a positive and significant correlation between rates of zooplankton production and edible phytoplankton biomass (Pearson $R^2 = 0.372$, $n = 14$, $p < 0.02$) (Fig. 5d), and a stronger correlation (Pearson $R^2 = 0.689$, $n = 14$, $p < 0.01$) between Woss Lake zooplankton production and the biomass of edible *Leptocylindrus sp.* (data not shown). For both lakes, there was a significant positive relationship between mean weights of fall-fry and zooplankton biomass (Pearson $R^2 = 0.372$, $n = 14$, $p = 0.01$) (Fig. 5e) and a significant positive relationship between mean weights of fall-fry and one of their most preferred prey, *Daphnia* (Pearson $R^2 = 0.462$, $n = 14$, $p < 0.01$) (Fig. 5f). In Vernon Lake, the relationship between mean weights of fall-fry and the two most preferred prey, *Daphnia* + *Hesperodiptomus*, was even stronger (Pearson $R^2 = 0.757$, $n = 7$, $p < 0.01$, two tail, data not shown).

There was no evidence of a density-dependent relationship between average June-October fish density and fall-fry weight (Pearson $R^2 = -0.019$, $n = 14$, $p = 0.64$, two tail)(Fig. 6a). There was also no top-down relationship between fish density and zooplankton biomass (Pearson $R^2 = -0.016$, $n = 14$, $p = 0.67$, two tail)(Fig. 6b). The relationship between fish biomass and zooplankton biomass was positive and not

significant when Woss 2005 was included (Pearson $R^2 = 0.214$, $n = 14$, $p = 0.10$, two tail) and significant when Woss 2005 was excluded (Pearson $R^2 = 0.506$, $n = 13$, $p = 0.01$, two tail) (Fig. 6c). All of these results are contrary to density-dependent predictions.

In Woss Lake, *Daphnia* were the preferred prey (Fig. 7a). During 2000-02, *Daphnia* biomasses were relatively high (Fig. 3), declined in 2003 and remained low in 2004-06. During the high biomass years, the proportion of *Daphnia* biomass consumed per day was slightly lower than later when *Daphnia* biomasses declined, but in all years percent biomass consumed per day was near 1% or less (Fig. 7a). In Vernon Lake, *H. kenai* was the most preferred prey (Fig. 7b). From year-to-year, the biomass of *H. kenai* varied (Fig. 4), but it remained the dominant prey and consumption by fish never accounted for more than 1.3% of *H. kenai* biomass per day.

In both Woss and Vernon lakes, daily bioenergetics-based consumption by all pelagic *O. nerka* ($\mu\text{g L}^{-1} \text{d}^{-1}$ dry weight) divided by daily zooplankton production ($\mu\text{g L}^{-1} \text{d}^{-1}$ dry weight) (*i.e.* C/P) gradually increased as the fish became larger, but seldom exceeded 100% (Fig. 7c,d). In both lakes, *Daphnia* were among the most preferred prey and the expect-

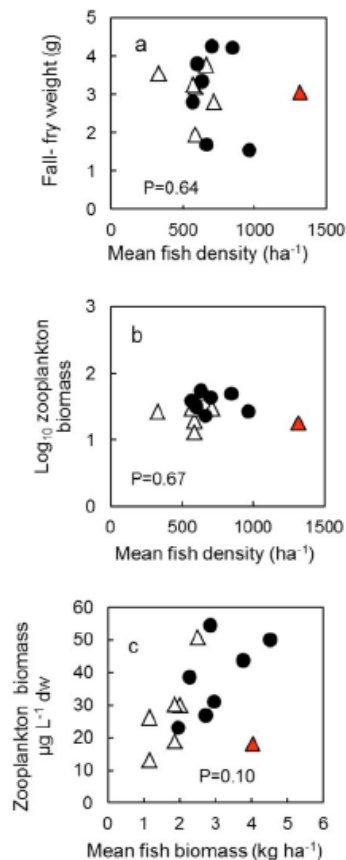


Fig. (6). Woss (Δ) and Vernon (O) lake (2000-2006) top-down correlations based on summer (June-November) averages for adjacent trophic-levels. The red symbols are for Woss Lake 2005.

tation was that *Daphnia* should be the species most affected by top-down predation. However in both lakes, C/P for *Daphnia* was $>100\%$ on only 9 of 78 lake-days, and C/biomass+production was $>10\% \text{ d}^{-1}$ on only 1 of 78 lake-days.

DISCUSSION

It is generally accepted that growth rates of juvenile sockeye salmon are regulated by nursery-lake water temperature and zooplankton biomass [26]. It is also generally accepted that nursery-lakes with more algae and higher rates of primary production, have more zooplankton and higher juvenile sockeye carrying capacities [1, 3]. Early work [9-12, 15] has led to the assumption that there is an inverse density-dependent relationship between juvenile sockeye density and growth rate [17]. However, with the exception of high-density stocking experiments, there are few supporting studies involving direct in-lake measures of natural fry densities and associated zooplankton biomasses. In fact, data-intensive studies such as those conducted at Great Central Lake (5100 ha) [24-27] show no effect of sockeye on their food, and virtually all bioenergetics-based food web studies show that natural densities of age 0 sockeye and age 0 kokanee cannot possibly consume enough prey to negatively impact zooplankton standing stocks [28-31, 51, 52]. That is the dilemma faced by the density-dependent growth hypothesis, and it is the subject of our analysis of data from Great Central, Sproat, Woss and Vernon lakes. Our goal was to use

multi-year data sets to evaluate the hypotheses that (1) increased lake “productivity” is associated with higher abundances of zooplankton, more food for juvenile sockeye and therefore faster rates of growth and that (2) consumption by juvenile sockeye can reduce zooplankton biomasses to levels that are low enough to cause reduced sockeye growth-rates.

Do More Productive Lakes Produce Larger Juvenile Sockeye?

Both empirical and lake manipulation studies strongly support the generalization that increased nursery-lake productivity is associated with higher biomasses of zooplankton and larger fall-fry and/or smolts [1, 3-8, 20]. We also found exceptions that emphasized the importance of phytoplankton and zooplankton species composition. In Woss and Vernon lakes, fertilizer quantity was always correlated with phytoplankton biovolume, but there was no clear relationship between total phytoplankton biovolume and total zooplankton biomass (Fig. 5b). During some years, fertilizer additions stimulated the growth of large non-edible diatoms including *Rhizosolenia* and zooplankton abundance was lower than expected. During other years, fertilization stimulated edible phytoplankton including *Leptocylindrus* and zooplankton biomass was higher than expected (Fig. 5c, d). We also found that while there was always a significant positive relationship between zooplankton biomass and mean weights of fall-fry (Fig. 5e), these relationships were even stronger when zooplankton species composition favoured large-bodied taxa such as *Hesperodiptomus* and *Daphnia* (Fig. 5f).

What is the Evidence for Density-Dependent Growth Regulation?

The usual explanation for apparent density-dependent growth of nursery-lake sockeye is that increased consumption of zooplankton by higher densities of sockeye reduces availability of zooplankton and therefore limits growth-rates. However, when the supporting evidence is re-examined, this explanation becomes less compelling. Classic observational studies at Cultus Lake, British Columbia [9-10] used ratios of zooplankton biomass/sockeye density to conclude that growth was density-dependent. Reanalysis of the original data shows that in Cultus Lake, there was no relationship between fish density and zooplankton biomass. Data from another classic British Columbia nursery lake study has also been cited in support of the density-dependent hypothesis. At Babine-Nilkitkwa (475 km²) [13-16], sockeye density was estimated 17 times during 08 August and late October 1956, 57, 58. Juvenile sockeye were captured using a 1 m diameter trawl net deployed at seven stations arrayed down the long axis of the lake. Densities were estimated from swept volume and a survival curve based on the literature was then applied to make all of the density data conform to the same theoretical August 21-25 sample period. It was assumed that over a three month period, the fish remained at specific sections of the lake, did not mix with fish from other locations and consumed zooplankton populations that also remained in specific sections of the lake for three months in each year. Given all of these assumptions, we suggest that it is impossible to conclude much, if anything, about relationships between sockeye density and zooplankton biomass. Also, because the Babine-Nilkitkwa study became the primary data

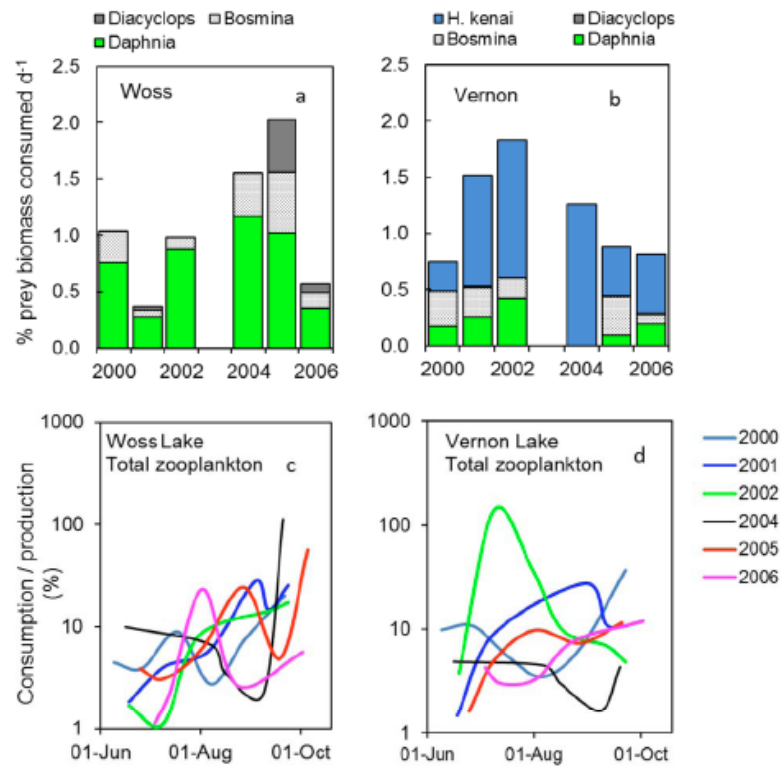


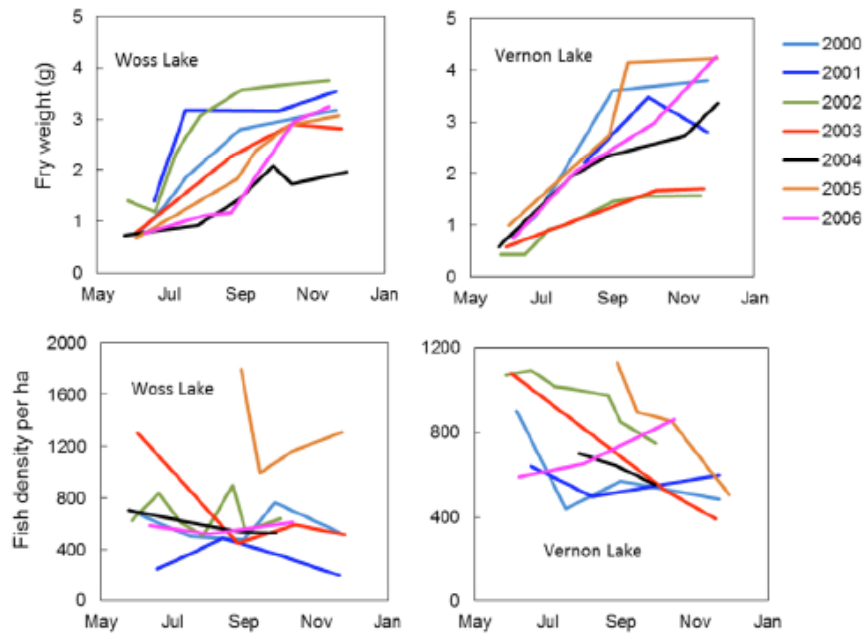
Fig. (7). Woss and Vernon Lake (panels a, b) percentage of mean summer zooplankton standing stock consumed per day by fish, (panels c, d) consumption / production expressed as a percentage.

source for the influential theoretical analysis by [17] Brocksen *et al.*, we suggest that compelling conclusions drawn from that work, are now highly questionable. More recent studies in British Columbia [3] and Alaska [3, 21-23] employed much more sophisticated field and analytical techniques, but all relied on indirect measures of either juvenile sockeye density or zooplankton biomass. In fact, only very high-density fry stocking trials in relatively small, oligotrophic Alaskan lakes provide strong evidence for density-dependent regulation of zooplankton biomass by juvenile sockeye [7]. For example, when Esther Pass Lake (surface area 0.2 km²) was stocked for two years (1988-89) with approximately 7,700 fry ha⁻¹, zooplankton biomasses declined from 402 to 65 mg m⁻² dw and when stocking was halted (1990), zooplankton biomass rebounded to 184 mg m⁻². When Pass Lake (surface area 0.5 Km²) was stocked for two years (1988-89) with approximately 12,000 fry ha⁻¹, mean summer zooplankton biomasses declined from 783 mg m⁻² dw during the control year (1985) to only 13 mg m⁻² dw during the stocked year (1989). When stocking was halted and fertilizers applied (1990), zooplankton biomass remained depressed at 10 mg m⁻². Can these results be extended to natural sockeye nursery lakes? We suggest that over the normal sockeye fry density range (500-4000 ha⁻¹) commonly observed in coastal sockeye nursery lakes, the answer is no.

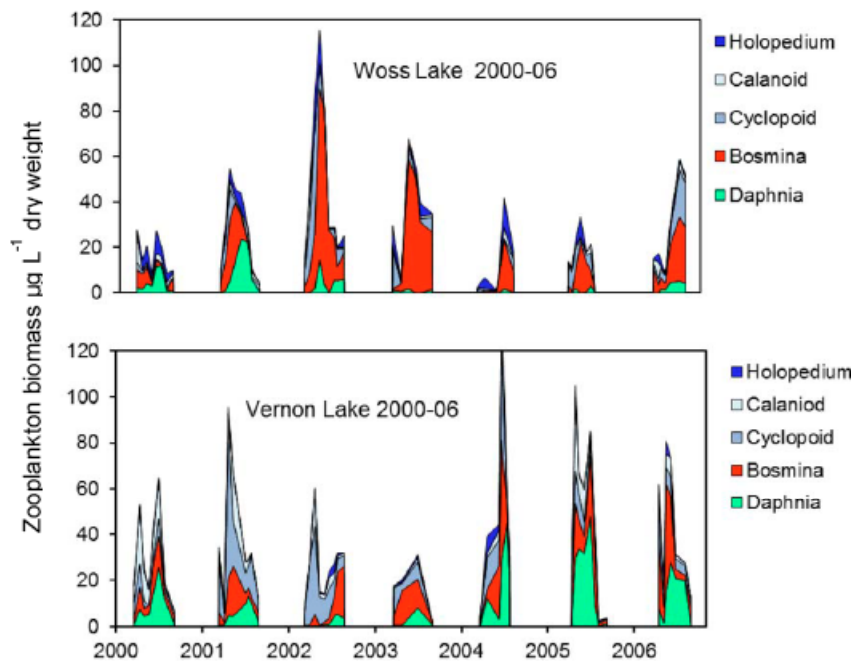
Woss Lake 2005

Woss Lake 2005 was the lake-year most likely to show top-down impacts of sockeye on zooplankton. During that year, edible algal biomass was the highest recorded, zooplankton biomass among the lowest and both fish density and biomass were the highest recorded (Fig. 3). The Woss

2005 observation was almost always the outlier in correlation plots involving phytoplankton, zooplankton or fish (red symbol Figs. 5, 6). Static measures of average biomass and density certainly suggest that during 2005, high fish density and biomass should have caused a trophic cascade (*i.e.* high fish biomass → high rates of zooplankton consumption → reduced zooplankton biomass → reduced grazing rates → high algal biomasses). However, dynamic estimates of production and consumption lead to a different conclusion. Total consumption by all fish was slightly higher than the six year average, average consumption per fish was slightly lower and fall-fry weight was equal to the average for all years. During 2005, consumption by fish averaged 15% d⁻¹ of total zooplankton production, 49% d⁻¹ of production by the most preferred prey (*Daphnia*), but only 0.8% d⁻¹ of *Daphnia* biomass+production. *Daphnia* production averaged 5% of biomass, so that the loss to predation was negligible. These data suggest that even in 2005, top-down regulation of zooplankton biomass was impossible and that Woss Lake fish likely had little difficulty finding their prey. Because *Daphnia* biomasses were relatively low, fish consumed *Daphnia* + *Bosmina* + *Diacyclops* (Fig. 7). Assuming that the fish consumed average sized prey, bioenergetics analysis suggested that the average fish required approximately 1000 *Daphnia*, 3000 *Bosmina*, and 1000 *Diacyclops* to meet the daily energy demand required to support their observed growth. Total prey density was 5.3 individuals L⁻¹. We know it's very likely that juvenile sockeye can detect all prey within a hemisphere having a radius of at least 5 cm, (*i.e.* can see prey up to 5 cm distant from the eye) in clear water [53] which means a fish would need to swim about 25 cm (cylinder 10 cm diameter and 25 cm long = $(12.8 * \pi 5^2) = 1000$



Appendix A. Woss and Vernon (2000-06), fry weight-at-age based on trawl samples and fish density per ha based on acoustic sampling.



Appendix B. Zooplankton biomasses $\mu\text{g L}^{-1}$ for Woss and Vernon lakes 2000-06. Sample sizes are summarized in Table 2. Daily counts are based on combined samples from 4 stations in Woss Lake and 3 stations in Vernon Lake.

$\text{cm}^3 \approx 1 \text{ L}$) in order to encounter 5 prey. Assuming a mean fish length of 3 cm and an average swimming speed of 2 body lengths per second, 36 minutes of swim time plus handling time would be required to encounter 5000 prey. Of course the fish would very likely select larger than average prey. This would require additional swim time, but less prey would be needed to meet metabolic demands. Diel migration studies [31] showed that Woss Lake fish remained in the upper water column from dusk to dawn, and therefore it was probably quite easy for the average fish to satisfy daily energy demands. During 2005, Woss Lake fish densities were

the highest recorded in the study and each fish occupied an average volume of 190 m^3 which was also occupied by 92,000 *Daphnia*. Since the average fish consumed $<1000 \text{ Daphnia d}^{-1}$, it seems unlikely that predation by fish could influence *Daphnia* densities and even more unlikely that consumption by fish could influence the densities of other more numerous zooplankton species.

Lake Carrying-Capacity

Simulated increases in fish density showed that zooplankton community resilience to changes in fish density

was different in each of our four lakes. As simulated fish densities were increased, zooplankton biomasses remained unaltered until consumption > production. Beyond that point, there was a rapid decrease in zooplankton biomass. For our lakes, these trigger points varied from 12,798 fry ha⁻¹ in Vernon Lake, to 9,500 fry ha⁻¹ in Great Central Lake, 7,980 fry ha⁻¹ in Woss Lake, and 5,200 fry ha⁻¹ in Sproat Lake. A number of potential errors are associated with these estimates of carrying-capacity. (1) Our simulations were based on the assumption that all zooplankton mortality is due to increased predation by fish. Zooplankton die for many reasons including predation by invertebrates and changes in food supply and water temperatures. We have attempted to account for some of this “unexplained” mortality and associated loss of production capacity, by using production data derived directly from field samples. For both Woss and Vernon lakes, our production estimates are based on six lake years and are likely relatively robust. For Great Central and Sproat lakes, we had field estimates from only one year, and our conclusions are more tentative. (2) A second important assumption is that prey selection remains static at all levels of predation. The prey selection data used to parameterize the bioenergetics model were gathered at fry densities averaging 300-1400 ha⁻¹ in Woss and Vernon lakes and 1700-2300 in Great Central and Sproat lakes, and prey electivity was assumed to remain constant at all simulated predator densities. As actual field densities increase, it is likely that the largest and most edible zooplankton species would be preferentially reduced, thus increasing the energy required for hunting thus decreasing sockeye growth rates. Although this will inevitably have consequences at very high predator densities, it is likely that the effects will be minimal at low and medium levels of sockeye abundance. Field data collected during 2005 from Woss Lake show that in the relative absence of the preferred prey species (*Daphnia*), the fish switched to alternatives (*Bosmina* and *Diacyclops*) with no loss in growth rate. Also, in all four of our lakes, production/consumption for vulnerable prey such as *Daphnia*, was relatively low averaging 14% d⁻¹ in Vernon Lake, 33% d⁻¹ in Woss Lake, 11% d⁻¹ in Sproat Lake and 18 % d⁻¹ in Great Central Lake. This suggests that substantial increases of predator densities would be needed to significantly change prey species composition during most of the spring-summer interval. The antidote to both of these potential errors is more emphasis on detailed field work for lakes having important ecological and economic importance. Future research should include field measurements of prey switching under various intensities of predation by juvenile sockeye salmon and the application of more sophisticated, dynamic production and consumption models. (3) Finally, our simulations are based on data gathered during the summer to early fall. There is no doubt that during the early spring and late fall when cool water is associated with substantially reduced rates of Cladoceran egg production, consumption by sockeye fry exceeds Cladoceran production. However, low temperatures are also associated with low metabolic rates, and the sockeye in our four lakes survive at these times on a diet made up almost exclusively of *Diacyclops*.

Two factors strongly influenced the carrying capacities estimated for our four lakes. (1) Lakes with higher areal rates of zooplankton production supported higher juvenile sockeye

growth rates (Pearson R² = 0.339, n = 16, p = 0.01). (2) Phytoplankton and zooplankton species composition mediated zooplankton production and ultimately fish growth rates. In Woss and Vernon Lakes, periodic blooms of inedible and edible algae were associated with changes in zooplankton production (Fig. 6d) and also with changes in fish growth rates (Fig. 6e, f). In Vernon Lake during 2000-01, high biomasses of the large copepod, *Hesperodiaptomus*, were associated with unusually high sockeye growth rates. In Great Central and Sproat lakes during 1999, nutrient concentrations, phytoplankton species compositions and biomasses of zooplankton were all very similar, yet Sproat Lake fish grew more quickly than Great Central Lake fish and Sproat Lake fish biomasses were more than twice as large. The single recorded difference was that Sproat Lake had higher concentrations of calcium and much higher biomasses of *Daphnia* (2.028 vs. 0.039 µg L⁻¹ dw), the most preferred prey in both lakes.

In summary our data suggest that over the range of densities commonly found in Coastal British Columbia sockeye nursery lakes (500-4000 ha⁻¹), there was no evidence of density-dependent growth suppression of juvenile sockeye and even less evidence that consumption by sockeye was high enough to significantly reduce zooplankton biomasses. Over the last 20 years, several models have been used to estimate carrying capacities in sockeye nursery lakes [1, 3-5]. All are based on indirect or direct estimates of primary production and all provide only general levels of precision for specific lakes. Some British Columbia nursery lakes are large (>1000 ha) and individually may support commercial catches of adult sockeye valued at millions of dollars per year. Our study suggests that for important sockeye nursery lakes, 2-4 lake-years of detailed observations of zooplankton and fish production may be used in bioenergetics-based consumption analyses to produce more precise estimates of lake-specific carrying capacities for juvenile sockeye. The expense of establishing reliable carrying capacities to inform production limits for fisheries management would seem to represent money well spent.

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