Do fall additions of salmon carcasses benefit food webs in experimental streams?

Jeremy M. Cram[1,2], Peter M. Kiffney[3,4], Ryan Klett[1], Robert L. Edmonds[1]

1. University of Washington, College of Forest Resources, Seattle, WA 98195 USA

2. Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, Washington 98112, USA

3. Northwest Fisheries Science Center, Mukilteo Biological Field Station, 10 Park Avenue, Building B, Mukilteo, Washington 98275, USA

4. Hedmark University College, Department of Forestry and Wildlife Management, NO-2418 Elverum, Norway

Corresponding author: jeremycram@gmail.com

Abstract

Research showing that salmon carcasses support the productivity and biodiversity of aquatic and riparian ecosystems has been conducted over a variety of spatial and temporal scales. In some studies, carcasses were manipulated in a single pulse or loading rate or manipulations occurred during summer and early fall, rather than simulating the natural dynamic of an extended spawning period, a gradient of loading rates, or testing carcass effects in late fall-early winter when some salmon stocks in the US Pacific Northwest spawn. To address these discrepancies, we manipulated salmon carcass biomass in 16 experimental channels located in the sunlit floodplain of the Cedar River, WA, USA between mid-September and mid-December, 2006. Total carcass loads ranged from 0 – 4.0 kg/m^2 (0, 0.001, 0.01, 0.1, 0.5, 1.0, 2.0 and 4.0 kg/m^2, *n* = 2 per treatment) and were added to mimic the temporal dynamic of an extended spawning period. We found little evidence that carcasses influenced primary producer biomass or fish growth; however, nutrients and some primary consumer populations increased with loading rate. These effects varied through time, however. We hypothesize that the variable effects of carcasses were a result of ambient abiotic condition, such as light, temperature and disturbance that constrained trophic response. There was some evidence to suggest peak responses for primary producers and consumers occurred at a loading rate of ~1.0 – 2.0 kg/m^2, which was similar to other experimental studies conducted during summer.

INTRODUCTION

Pacific salmon (*Oncorhynchus* spp.) are an economically, ecologically and culturally valuable group of fishes. Recent research has highlighted the critical contributions that salmon make to the biological productivity of their natal watersheds where they release energy and nutrients accumulated at sea (Naiman et al. 2002). These energy rich resources can affect trophic productivity and fishes of freshwater ecosystems via three pathways: (1) nutrients released by carcasses can stimulate primary productivity, which leads to higher secondary production and prey availability; (2) direct consumption of carcass material by aquatic or terrestrial invertebrates, also leading to higher prey availability; and (3) juvenile fish directly consuming eggs and salmon flesh. Regardless of the pathway, all else being equal, spawning salmon can potentially confer a growth advantage to freshwater fish (Chaloner et al. 2002; Wipfli et al. 1998; Wipfli et al. 2003).

Degradation of rearing and spawning habitat, migratory barriers, harvest of adults, ocean conditions, and competition with hatchery fish have contributed to declines and extinction of many stocks of wild salmon across much of their geographic range. These losses have likely contributed to reductions in the trophic productivity of watersheds used by salmon, further contributing to population declines (Stockner et al. 2000): spawning salmon deposit less than 10% of their historic levels of carbon, nitrogen and phosphorus in the Puget Sound basin (Gresh et al. 2000). Therefore, it has been hypothesized that reductions in adult returns have resulted in lower growth and survival of juvenile salmon and other fish because of reduced trophic productivity (i.e. productivity of lower trophic levels that support juvenile salmon) leading to further reductions in adult returns (Bilby et al. 1998; Wipfli et al. 2003, 2004).

Studies linking salmon carcasses to productivity at various trophic levels have been conducted across broad spatial and temporal gradients, and with varying levels of control (Bilby et al. 1998; Claeson et al. 2006; Janetski et al. 2009; Wipfli et al. 2003). Numerous studies have examined the effects of carcasses or simulated carcasses on stream food webs in the Pacific Northwest (PNW [Washington, Oregon, Idaho]) (Bilby et al. 1998; Claeson et al. 2006; Giannico & Hinch 2007; Kohler et al. 2008), and they generally tested a single loading rate and sometimes with no replication or control of extraneous variables. The effect of carcasses on stream food webs in these studies was variable (Janetski et al. 2009) and studies examining multiple trophic levels were exclusively conducted during summer months.

It is important to quantify salmon carcass effects on freshwater ecosystems in the US PNW under controlled, ecologically relevant conditions and at multiple trophic levels to identify the mechanisms by which carcasses affect trophic productivity. Such experiments are critical from a management perspective as millions of dollars (US) are spent annually to restore Pacific salmon populations. Increasingly, restoration actions include adding carcasses into streams with little attempt to quantify appropriate loading rates, or document the ecological effects of these actions (Shaff & Compton 2009). In particular, there is a need to identify loading rates that benefit fish populations while minimizing unwanted effects such as blooms of algae that could negatively affect human use of water. To address some of these issues, we conducted a controlled experiment to expand our understanding of how carcasses affect stream productivity during fall and early winter and provide some guidance for restoration scientists considering nutrient enhancement to promote salmon populations.

We tested the hypothesis that adding salmon carcasses increases the productivity (defined as the potential of the system to produce new biomass) of experimental stream food webs during fall and early winter. We predicted that 1) total and dissolved nutrients in stream water; 2) primary producer and consumer populations; and 3) coho salmon (*Oncorhynchus kisutch*), cutthroat trout (*Oncorhynchus clarki*), and sculpin (*Cottus* spp.) growth rate and condition factor would increase as a positive function of carcass loading rate. Although we predicted that carcasses would measurably affect all trophic levels, top-down or bottom-up interactions might modulate response variables (e.g., Power 1992).

MATERIALS AND METHODS

Study site

The study was conducted at an experimental stream facility adjacent to the Cedar River, Washington near Landsburg Dam, during fall and early winter 2006 (47°38’157”N, 121°95’807”W). The climate in this region is temperate, with wet, mild winters and dry summers (mean annual air temperature = 9.7°C, mean annual precipitation = 144.5 cm, www.wrcc.dri.edu). The experimental streams were located in a 200 m^2 grassy opening in a Douglas-fir (*Pseudotsuga menziesii*) forest. Incident sunlight was high due to an unobstructed southern exposure.

Experimental design

We constructed 16 artificial channels to manipulate salmon carcass density and assess its impact on trophic ecology, while minimizing extraneous variables. Experimental streams (4.8 m long x 0.3 m wide) consisted of cinder block rows with each row or stream covered in pond liner material and partially filled with gravel (10 – 30 mm median grain size). Each stream offered

three pool (mean depth = 22 cm) and two riffle habitats. Woody debris and large cobbles (~ 64 – 100 mm median grain size) were added to pools to serve as cover for fishes; the downstream ends were partially obstructed to back up water and prevent fish emigration, while upstream ends were enclosed by a wire mesh screen to ensure that fish could not escape. Birds and mammals were excluded by 2.4 cm mesh netting which fully enclosed the channels. Although not measured, the wide openings in the mesh netting did not appear to impact incident solar radiation.

Gravity transported river water (temperature range 4.9 – 12.5 °C, mean = 8.7 °C) from above the Landsburg Diversion Dam to experimental streams. The intake pipe for river water was covered by a mesh screen (mesh opening = 1.75 cm) that prevented juvenile fishes from entering the water system but allowed the immigration of organic matter and natural populations of algae, bacteria, and stream invertebrates. Plastic pipes carried water to the primary head tank, which acted as both a settling tank for fine sediment and a reservoir. Gate valves were affixed to the inflow pipes of each stream to equalize flow at a rate of 4 $l*s^{-1}$. Plastic baskets were buried in the substrate at the top and bottom ends of each channel for the collection of invertebrates on day 90. Baskets were 15 cm wide x 15 cm long x 5 cm high and were filled with gravel, the top of which was flush with the surrounding stream substrate. Baskets were ventilated by openings on each side that allowed water, organic matter and invertebrates to pass through their walls.

Water was turned on 60 days prior to day zero (September 19, 2006) of the experiment, allowing biofilm (algae, bacteria, fungi, etc. accumulating on benthic surfaces) and invertebrates to colonize newly wetted substrate. This colonization period was deemed adequate because biofilm biomass and invertebrate abundance approached equilibrium according to preliminary sampling efforts. Cutthroat trout (mean length = 91.4 mm, mean weight = 9.6 g) and sculpin

(mean length = 77.3 mm, mean weight = 6.9 g) were collected from Cedar River tributaries (Rock and Williams creeks) above natural barriers to anadromous fishes. Coho salmon (mean length = 84.1 mm, mean weight = 7.7 g) were collected from the same location in the main stem Cedar River upstream of where most spawning has occurred (Kiffney et al. 2009). Within each taxon there were no significant among treatment differences in pre-experiment length or weight.

One fish of each species was placed into each experimental channel 30 days prior to day zero, allowing them to acclimate to their surroundings. Fish community structure (species composition and density) in channels was modeled after the Rock Creek community, where sculpin, coho, and cutthroat trout are the most abundant fish species. Cutthroat trout and coho salmon were placed at densities (0.70 fish/m^2) within the range observed in Rock Creek (Kiffney et al. 2009), while sculpin densities were higher in the natural stream (Kiffney et al. 2002). Each fish received a passive integrated transponder (PIT) tag for subsequent individual identification (model TX1400ST, Biomark, Boise, ID).

Carcass material was placed from mid-September through early December 2006 in a pattern reflecting historic run timing of sockeye salmon (*O. nerka*) in the Cedar River system, with a peak carcass placement in late-October (unpublished data, Washington Department of Fish and Wildlife). Carcass density treatments were based on current salmon spawning densities in the Cedar River above Landsburg dam between 2003 and 2005 (Kiffney et al. 2006), estimated historic levels (Gresh et al. 2000), and loading rates used for other salmon carcass related studies (Bilby et al. 1998; Wipfli et al. 2003, 2004; Wipfli et al. 1999). As a result of these data, we produced eight treatments (low = 0 and 0.001 kg/m^2, med-low = 0.01 and 0.1 kg/m^2, med-high = 0.5 and 1.0 kg/m^2, high = 2.0 and 4.0 kg/m^2), which represented the total

carcass material added to each stream replicated twice. Carcass material was added biweekly as a percentage mass of the total treatment: 10% on day 0, 15% on day 14, 25% on day 28, 30% on day 42, and 20% on day 56. Carcass material was post-spawn sockeye meat acquired from the nearby Cedar River hatchery; therefore, eggs, which are a valuable energetic resource for freshwater organisms (Schindler et al. 2003), were not added. Chunks larger than 300 g were cut and material was placed at the upstream end of each stream, where it remained anchored by its own weight.

Sample collection and processing

Every two weeks, total and dissolved nutrients, and suspended organic matter (SOM) samples were collected from the downstream end of each channel (Table 1). Total P and N were analyzed according Valderrama (1981) and dissolved nutrients (PO_4-P, NO_3-N [dissolved NO_2-N was below detection], and NH_4-N) were processed according to UNESCO (1994). Suspended organic matter samples were filtered onto pre-combusted and pre-weighed glass fiber filters (nominal pore size, 0.45 μm, Millipore), dried at 105°C for 24 h, and weighed after cooling. The filters were then ashed for 4 h at 400°C and weighed after cooling (Biggs & Kilroy 2000). The difference between the initial and final weight represents SOM (mg/L) in the sample.

Biofilm and invertebrates were collected from cobbles and unglazed terra cotta tiles (15 cm long x 7.5 cm wide x 0.5 cm high). One tile was placed in the uppermost pool and riffle of each stream beginning on day zero (first day of carcass addition - September 19, 2006). Tiles and one cobble were sampled for biofilm and invertebrates from each stream biweekly. Tiles were returned to the stream to be used at the next collection. In contrast, a different cobble was used at each sample period. Biofilm was removed from the substrate by scrubbing with a toothbrush and

rinsing with distilled water over a 355 μm sieve, which captured most invertebrates. This slurry was diluted with distilled water to 200 ml, then homogenized and split into sub-samples. These allotments were used for ash free dry mass (AFDM) and chlorophyll *a* (see Steinman et al. 2007 for more details). Subsamples for AFDM were processed in the same manner as SOM. Chlorophyll *a* subsamples were filtered onto glass fiber filters (Millipore #AP4004700) and extracted with 10 mL of 90% acetone for 22 h, and analyzed using a fluorometer (Model 10–005R, Turner Designs, Mt. View, California). Invertebrates were picked from tiles, rocks, and baskets directly or from the rinse pan, and then preserved in 90% ethanol until processing.

All invertebrates were identified to family using Thorp and Covich (2009). Up to 20 randomly selected individuals from Baetidae (Ephemeroptera), Heptageniidae (Ephemeroptera), and Chironomidae (Diptera) from each basket were measured for length, which was converted to biomass using length-weight regressions from Meyer (1989) for Heptageniidae, Smock (1980) for Chironomidae, and from Rosenberger (1998, unpublished) for Baetidae. Total family biomass within a basket was equal to the average individual biomass multiplied by the total number of individuals counted within the family.

Fishes were sacrificed at the end of the experiment using an overdose of MS-222 according to established protocols (www.avma.org). Each fish was weighed and measured immediately after being sacrificed. Fulton condition factor ($K = \text{weight}/\text{length}^3$) was calculated for each fish (Ricker 1975).

Data analysis

The experimental design of this study allowed us to use replicated regression to model the relationship between loading rate and ecological responses (Cottingham et al. 2005). This

approach was used rather than standard analysis of variance (ANOVA) because we wanted to determine the direction, rate of change, and shape of the relationship between the different ecological response variables and loading rate. To limit the number of statistical tests and because we expected some correlation among response variables, we examined simultaneously the response of a number of potentially correlated variables to carcass loading using multivariate linear regression and Wilks' Lambda (Khattree & Naik 1999). This model tested the multivariate response of dissolved nutrients (NH_4-N, PO_4-P), chlorophyll *a* concentration, and density of dominant insects (Baetidae, Simuliidae, Chironomidae and Heptageniidae) simultaneously within each sample period (days 15, 28, 42, 56, 73 and 90). Communities on tiles and rocks were analyzed separately. Before statistical modeling, we pooled values (e.g., biofilm AFDM) measured on tiles placed in riffles and pools within a channel on each sample day. The relationship between invertebrate biomass data collected from baskets and fish growth rate and condition factor on day 90, and carcass loading rate were also analyzed using a multivariate linear regression. Multivariate tests are relatively robust to deviations from multivariate normality especially if each response is approximately univariate normal (Quinn & Keough 2002). Therefore, we examined univariate normality of each variable separately using residual plots and the Shapiro-Wilks *W* test. If departures from normality were evident, we log-transformed these variables and then examined normality of transformed variables. If there was a positive slope between a response variable and carcass-loading rate ($p \leq 0.1$), we examined the functional form of this relationship using untransformed data. If the relationship exhibited curvature, both linear and polynomial terms were examined. The more complex model was presented if the estimated slope for both the linear and quadratic term were significantly different

from zero and the model fit (adjusted R^2) increased by > 10% relative to the model with a linear term only.

Two additional metrics were used to quantify the ecological effects of carcasses. First, we estimated a loading rate (mean ± 95% confidence interval) that was associated with an increase in trophic productivity by determining the treatment level that corresponded with the peak value for chlorophyll *a* concentration and primary consumer density on tiles and rocks within each sample day; these peak values were averaged across days (see Fig. 2). Second, nutrient budgets were calculated for each treatment by subtracting the value for total and dissolved nutrients leaving control channels from the value of outgoing water from treatment streams. We assumed that nutrient concentrations of incoming water in control steams would not differ from outgoing water. Based on this assumption, export of stream nutrients receiving carcasses would be higher than controls and that this net difference would increase with loading rate. Discharge was excluded from the calculation because each stream received equal amounts of water and groundwater was excluded. Correlation (Pearson's correlation coefficient) analysis was used within each sample day to assess bottom-up and top-down interactions on trophic level relationships (nutrient levels, biofilm biomass, and herbivore invertebrate density and biomass). The direction and magnitude of correlations were used to interpret biotic interactions and limitations on productivity (Claeson et al. 2006). Statistical analyses were conducted using R (Version 2.11.1; R program on computing) and SAS (Version 9; SAS Institute, Inc., Cary, NC).

RESULTS

Carcasses did not decay completely, but larger pieces gradually broke down over time and particles were commonly seen drifting downstream or settled in the substrate. There was

limited support for a carcass treatment effect until day 56 (Table 2); on day 56 PO_4-P (R^2 = 0.49, p = 0.002) and NH_4-N (R^2 = 0.49, p = 0.03) were positively related to loading rate (Fig. 1). While Baetidae and Heptageniidae density on tiles were also positively associated with loading rate on day 56, this relationship explained about 20% of the variation in density of these taxa (Fig. 2a-b, ~R^2 = 0.20, p = 0.08 for both taxa). The association between loading rate and Chironomidae density and total invertebrate density was stronger (Fig. 2c-d); this relationship explained about 50% of the variation in Chironomidae density.

There was also a multivariate effect of loading rate on stream rock assemblages on day 56 (Chironomidae/m^2 = 42.0 + 27.7*[loading rate, kg/ m^2], R^2 = 0.25, p = 0.05, n=16). Moreover on 73 loading rate explained 82%, 21%, 37%, and 48% of the variation in NH_4-N, PO_4-P, chlorophyll *a* concentration, and Simuliidae density, respectively. Dissolved nitrate-N showed no relationship with carcass loading rate on any sample day.

Carcass loading rate was also positively associated with Baetidae and Chironomidae biomass on the final day of the study (Fig. 3). Baetidae biomass in upstream baskets increased by 2.7 mg·basket^{-1} · kg carcass^{-1}, while Chironomidae biomass increased by 9.4 mg·basket^{-1} · kg carcass^{-1}. Interestingly, none of the three taxa (baetids, chironomids, heptageniids) sampled from downstream baskets responded to carcass loading. This pattern suggests carcass effects on invertebrates were localized. By ranking the occurrence of peak values for lower trophic levels vs. loading rate across all sample days, we were able to estimate a potential optimal loading rate for this experiment. We found that the mean loading rate associated with peak values in chlorophyll *a* concentration, density of Baetidae, Heptageniidae and Chironomidae was ~ 1.0 to 2.0 kg/m^2 (Fig. 4).

Carcass additions led to positive responses in lower trophic levels that support fishes, but evidence for increased growth or condition of fishes was minimal except for sculpins: sculpin condition factor was markedly higher at intermediate treatment levels (~1.0 – 2.0 kg/m^2, Fig. 5). This result was in agreement with our estimate of optimal loading rate from peak values. Although carcasses only contributed to increased sculpin performance, 66% of cutthroat had salmon tissue in their stomachs, as did 38% of coho and 20% of sculpin indicating fish were using this material as an energy source. Two coho salmon, two cutthroat trout, and one sculpin died or were not recovered at the conclusion of the experiment. These losses were omitted from statistical analyses.

Correlation analysis revealed instances where trophic level abundance and biomass were potentially limited by both bottom-up and top-down factors. For example, on day 28 there was a positive correlation between biofilm chlorophyll *a* and Heptageniidae density on rocks ($r = 0.53$, $p = 0.05$). In contrast, on days 15 and 90 density of Baetidae ($r = -0.54$, $p = 0.04$) and Heptageniidae ($r = -0.85$, $p = 0.001$) on tiles was negatively correlated with biofilm AFDM.

Nutrient export values varied among days and treatments (Fig. 6). Each nutrient showed both net positive and negative values in relation to carcass treatment over the course of the experiment. Overall, grand means for each nutrient species were not different from zero, indicating that carcass loading had little overall impact on nutrient export.

We speculate that the dynamics of this experiment were affected by a major storm event. On November 6, 2006 (prior to day 56) there was a large flood, which affected the operation of our water source. Due to concern about debris entering the Landsburg Diversion dam, water flow was shut off causing channels to be partially dewatered for ~18 hours. During this event two

coho salmon died. Perhaps the most important consequence of this event was the influx of fine sediment, which covered a portion of the benthos of each stream by about 2 cm. Despite this disturbance, there was evidence that nutrients and lower trophic levels recovered: chironomid, baetid and heptageniid densities on day 56 were positively associated with carcass loads.

DISCUSSION

Water chemistry

Concentrations of biologically important elements increased as a function of carcass loading rate, but this relationship was not consistent over the course of the experiment. Dissolved PO_4-P and NH_4-N were the most responsive nutrient species to carcass treatment, consistent with other studies (Chaloner et al. 2007; Claeson et al. 2006), while NO_3-N exhibited little pattern with loading rate. For example, on days 56 and 73 NH_4-N concentrations were about 6-8× higher in the highest carcass treatment (4.0 kg/m^2) compared to controls. Claeson et al. (2006) documented approximately a 4× increase in ammonium that peaked eight weeks after carcass additions, which was similar to our study. Chaloner et al. (2007) observed maximum dissolved NH_4-N levels of 200 μg/L and PO_4-P of 18 μg/L during peak spawning (July-August) in Alaska streams, which were 41× and 14× higher than background concentrations, respectively. These concentrations were more than double the maximum values achieved in our study, despite carcass amounts that were higher than those in Chaloner et al. (2007) (~0.6 – 0.8 kg/m^2). Higher nutrient levels in the Alaskan study may reflect warmer water temperatures and higher light levels during summer stimulating carcass breakdown and nutrient release, fish excretion of nutrients, egg release and decomposition, and wildlife activity (Naiman et al. 2002; Schindler et al. 2003).

Although carcasses increased surface water nutrient levels in our study, concentrations were consistently below levels that would pose a threat to drinking water quality (e.g., www.ecy.wa.gov) or which might promote harmful algal blooms downstream (Dodds 2007). Furthermore, the relationship between carcass load and stream water nutrients was variable across dates, which resulted in negative net nutrient export on some days. This result was unexpected and we partially attribute to complex trophic interactions. We hypothesize that nutrients were adsorbed onto sediments or assimilated by stream biota prior to reaching the end of the channels thereby limiting the amount of nutrients exported from the system (Bilby et al. 1996). Our experimental streams were closed systems relative to natural streams as there was no interaction with groundwater, riparian habitats or terrestrial scavengers; so, we might expect higher export of nutrients than natural streams because there were fewer routes for nutrient uptake or storage. Alternatively, changes in nutrient concentrations as a result of spawning migrations may be more pronounced in natural streams due to excretion and physical disturbance associated with spawning fish (Janetski et al. 2009). Identifying factors or processes that affect how salmon influence nutrient cycling and ultimately stream and riparian food webs, will provide greater insight into the ecological role of these organisms in their natal ecosystems.

Biofilm

The only significant effect of carcasses on algal biomass or biofilm was observed in December, despite relatively cold water and low ambient light. Previous studies have found strong bottom-up effects of carcasses on biofilm chlorophyll *a* and AFDM (Chaloner et al. 2007; Wipfli et al. 1998; Wipfli et al. 1999), but these studies were conducted in summer when incident light and water temperature were relatively high. Claeson et al. (2006) also did not

detect a biofilm increase with carcass additions, which they suspected was due to increased grazing pressure by stream invertebrates. In other words, invertebrate consumption outpaced biofilm growth thereby limiting primary producer biomass accrual.

The limited effect of carcasses on primary producers we observed may have also been partially a result of invertebrate grazers consuming excess algal biomass. For example, on two of six sampling dates there was a negative correlation between primary consumer density and biofilm biomass. Alternatively, or in addition to high invertebrate consumption, fungal growth on carcasses may have absorbed limiting nutrients making them unavailable for primary producers (Mackenzie 2001). We observed an abundance of this fungus in channels receiving high (2.0 – 4.0 kg/m^2) amounts of carcass material. Compton et al. (2006) suggested that nutrients released from salmon carcasses in the fall might not stimulate primary production unless they are retained in the substrate until the following spring. Our results suggest that high rates of invertebrate consumption may not result in increased algal biomass and competition with fungi may limit the effects of nutrients released from carcasses on biofilm communities.

Invertebrates

In our study, we observed that some invertebrate taxa increased on tiles, rocks and baskets in response to carcass loading, but effects were variable over time. Claeson et al. (2006) measured increases of over 200% in the density of Heptageniidae and Chironomidae after carcass placement. Other studies have shown strong numerical responses in terms of abundance and biomass of Chironomidae, but negative responses from Baetidae and/or Heptageniidae (Lessard & Merritt 2006; Wipfli et al. 1999). We found that chironomids showed a positive response to carcass treatment in both density and biomass, indicating that they were able to

exploit increased primary productivity as a response to carcass placement or consume the carcass particles directly (Chaloner & Wipfli 2002; Minakawa 1997). Baetidae, Heptageniidae and Simuliidae density also increased with loading rate, but only on one sample date. Furthermore, we observed that Baetidae biomass in baskets increased with loading rate on day 90. Interestingly, effects of carcasses on insect biomass were localized, with positive effects occurring in baskets closest to salmon carcasses. Claeson et al. (2006) observed the largest increase in insect populations at transects closest (10 m) to carcasses compared to those more distant (50- 250 m). These results indicate that the benefits of salmon carcass additions on primary consumers are highly localized, and vary across species and time.

A number of studies have shown that chironomids respond positively to carcass additions (Claeson et al. 2006, Wipfli et al. 1999). Therefore, chironomids, which were represented by the collector-gatherer functional feeding group in our study (Merritt & Cummins 1996), appeared to be most the successful taxon at exploiting the resources provided by salmon carcasses. We hypothesize that this success is due to a number of factors including an opportunistic feeding behavior, propensity to drift allowing them to search and respond to food-rich patches, and fast generation times. The mixed response of other invertebrates may reflect variation in morphology, behavior, life history, or interactions with other species. For instance, the morphology of the mouthparts of the Heptageniidae may limit them to scraping thin layers of biofilm off rocks (Merritt & Cummins 1996), thereby preventing them from benefiting from the food resources provided by carcasses.

Fish

By adding energy and nutrients in the form of salmon carcass material to channels, we predicted a positive response in growth and condition factor of each fish species as carcass loading increased (Bilby et al. 1998; Wipfli et al. 2003, 2004). For instance, Bilby et al. (1998) observed a transient positive effect of adding salmon carcasses on the condition factor of juvenile coho salmon and steelhead trout (*Oncorhynchus mykiss*) during winter in two Western Washington streams. In contrast, we found no evidence to support the hypothesis that increased salmon carcass load caused faster growth or improved condition of juvenile cutthroat trout or coho salmon despite observing that carcass flesh was abundant in fish diets. Our data did indicate, however, that sculpin condition factor peaked at intermediate carcass treatments (~1.0 – 2.0 kg/m^2).

Fish growth in our channels may have been limited due to physiological or behavioral constraints. For example, limited effects of carcasses on fish growth may have been due to low water temperatures (Wilzbach et al. 2005) limiting metabolism or the exclusion of eggs, which typically serve as energy rich food items for resident fishes during salmon spawning (Hicks et al. 2005). Limiting fish movement may have also contributed to the minimal carcass effects we observed. Kahler et al (2001) found that some juvenile coho exhibited a high propensity to move, and these 'movers' had higher growth rates than 'non-movers'. Based on these observations, we might predict a stronger response of juvenile salmon to carcasses if they were able to consume eggs and to move freely enabling them to select habitat characteristics that provide the highest fitness benefits.

CONCLUSION

The seasonal timing and graduated loading scheme used in this study were somewhat unique from other experimental studies, potentially increasing our understanding of how salmon carcasses affect productivity during the fall spawning period typical of western Washington, Oregon, and southwestern British Columbia. This study also contributes to the growing body of literature suggesting that adult salmon provide ecologically important sources of energy and nutrients even during fall and winter. Overall, we found carcasses can affect the trophic ecology of streams during this time period but these effects were: (1) primarily limited to nutrients and primary consumers, (2) transient, and, (3) in some cases, localized.

Additional research on the trophic effects of adult salmon are needed across a range of ambient conditions including more study of temporal dynamics and how spawning salmon interact with other factors such as disturbance regime, gradient, ambient nutrient conditions, light input or habitat heterogeneity. It should also be recognized that salmon are not just sources of energy and nutrients, but can cause profound ecosystem-level affects via nest building and nutrient excretion (Moore et al. 2007). Restoration efforts using carcass addition may result in beneficial conditions for fishes, but responses from these additions will not reflect how a natural spawning run affects freshwater and riparian ecosystems. Furthermore, the localized effects of carcasses on invertebrate biomass in the experimental streams suggests that transfer of energy and nutrients may be more successful when carcasses are scattered broadly across a treatment area rather than released at high densities in a few locations.

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Tables

Table 1. Sample types are shown according to days they were collected and what they were sampled for. Water, tiles, and rocks were sampled biweekly for a variety of responses, while basket invertebrates and fish were only collected at the end of the experiment.

Sample type	Days sampled	Sampled for
Water	0, 15, 28, 42, 56, 73, 90	Water chemistry, TOM, nutrient budget
Tiles	0, 15, 28, 42, 56, 73, 90	biofilm biomass, invertebrate density
Rocks	0, 15, 28, 42, 56, 73, 90	biofilm biomass, invertebrate density
Baskets	90	Invertebrate biomass
Fish	0, 90	Growth

Table 2. Results from multivariate linear regression and Wilks' Lambda modeling the relationship between dissolved PO_4-P and NH_4-N, and density of Baetidae, Simuliidae, Heptageniidae and Chironomidae on unglazed ceramic tiles and natural rocks and carcass treatment (kg/m^2, n = 16 total samples per day) relative to days after treatment initiation on 9/19/2006 (***: $\alpha = 0.01$, **: $\alpha = 0.05$, *: $\alpha = 0.1$).

Day	Multivariate *p-value*	
	Tiles	Rocks
15	0.1	0.5
28	0.8	0.5
42	0.2	0.8
56	0.02**	0.08*
73	0.002***	<0.001***
90	0.3	0.3

Figure legends

Fig. 1. The relationship between carcass treatment and dissolved a) PO_4-P (μg/L = 2.9 + 0.60*(carcass loading [kg/m^2]), R^2 = 0.49, p = 0.002, n = 16) and b) NH_4-N (μg/L = 279 + 9.7*(carcass loading [kg/m^2]), R^2 = 0.30, p = 0.03, n = 16) concentration in water samples taken on day 56.

Fig. 2. The relationship between carcass treatment and density of a) Baetidae (individuals/m^2 = 19.8 + 21.5*(carcass loading[kg/m^2]), R^2 = 0.20, p = 0.08, n = 16), b) Heptageniidae (individuals/m^2 = 65.0 + 21.3*(carcass loading[kg/m^2]), R^2 = 0.21, p = 0.08, n = 16), c) Chironomidae (individuals/m^2 = 29.3 + 37.8*(carcass loading[kg/m^2]), R^2 = 0.50, p = 0.002) and d) total invertebrates (individuals/m^2 = 200 + 82.7*(carcass loading[kg/m^2]), R^2 = 0.40, p = 0.009, n = 16), n = 16) measured on tiles on day 56.

Fig. 3. The relationship between carcass treatment and biomass of a) Baetidae (mg/basket = 7.6 + 2.7*(carcass loading [kg/m^2]), R^2 = 0.26, p = 0.06, n = 14), and b) Chironomidae (mg/basket = 7.4 + 9.4*(carcass loading [kg/m^2]), R^2 = 0.60, p = 0.001, n = 14).

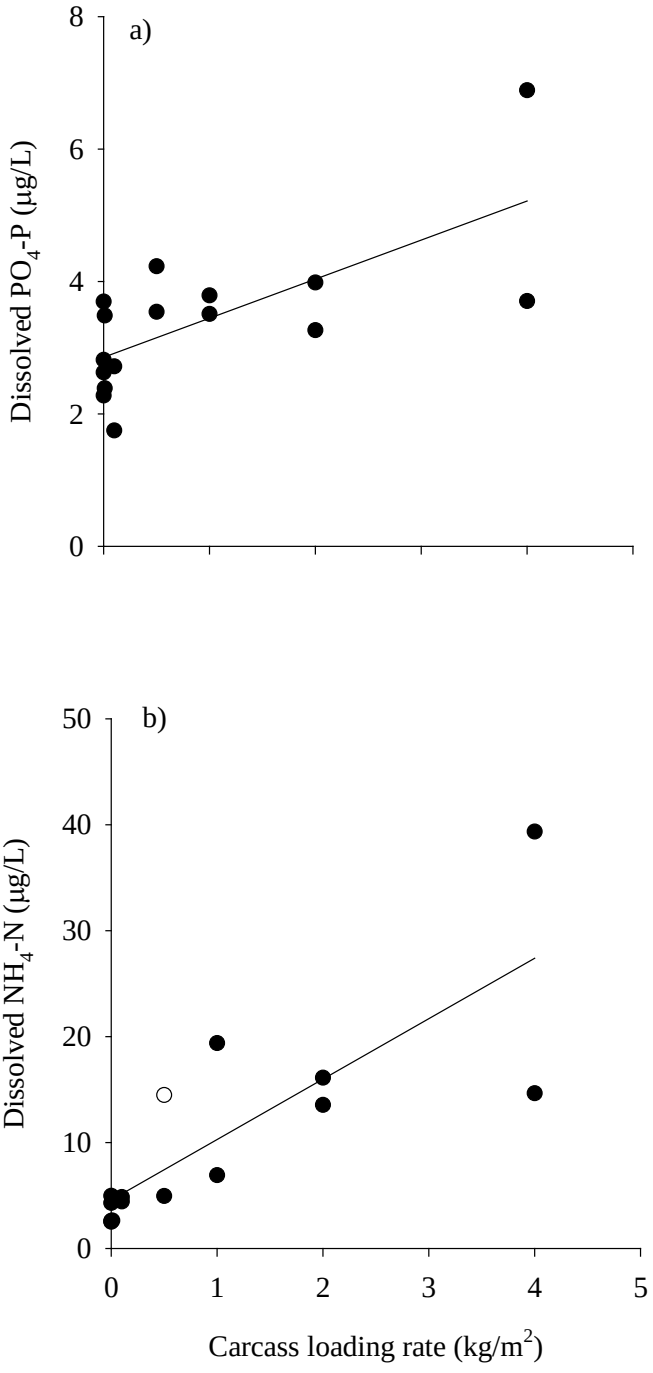
Fig. 4. Mean (± 95% CI) loading rate where peak values occurred for chlorophyll *a* biomass, Simuliidae, Baetidae, Heptageniidae and Chironomidae density on tiles and rocks averaged across the six sample dates.

Fig. 5. The relationship between carcass treatment and sculpin condition factor (length/weight^3 = 1.3 + 0.14*(carcass loading [kg/m^2] – 0.06*(carcass loading [kg/m^2])^2), R^2 = 0.40, p = 0.01 for linear and 0.03 for quadratic terms, n = 15) on day 90.

Figure 6. Mean (+ 1 SD) net nutrient export by treatment bin (low = 0 and 0.001 kg/m^2, med-low = 0.01 and 0.1 kg/m^2, med-high = 0.5 and 1.0 kg/m^2, and high = 2.0 and 4.0 kg/m^2) for each nutrient on all sampling days, with grand means (GM) also represented. Total and dissolved nutrient export was calculated as outgoing treatment nutrient concentration (μg/L) – outgoing control nutrient concentration (μg/L), where control streams were those receiving no carcass material. A positive export number indicates more nutrients were leaving treatment channels relative to nutrients entering control channels.

1 **Figures**

Figure 1



2

Figure 2

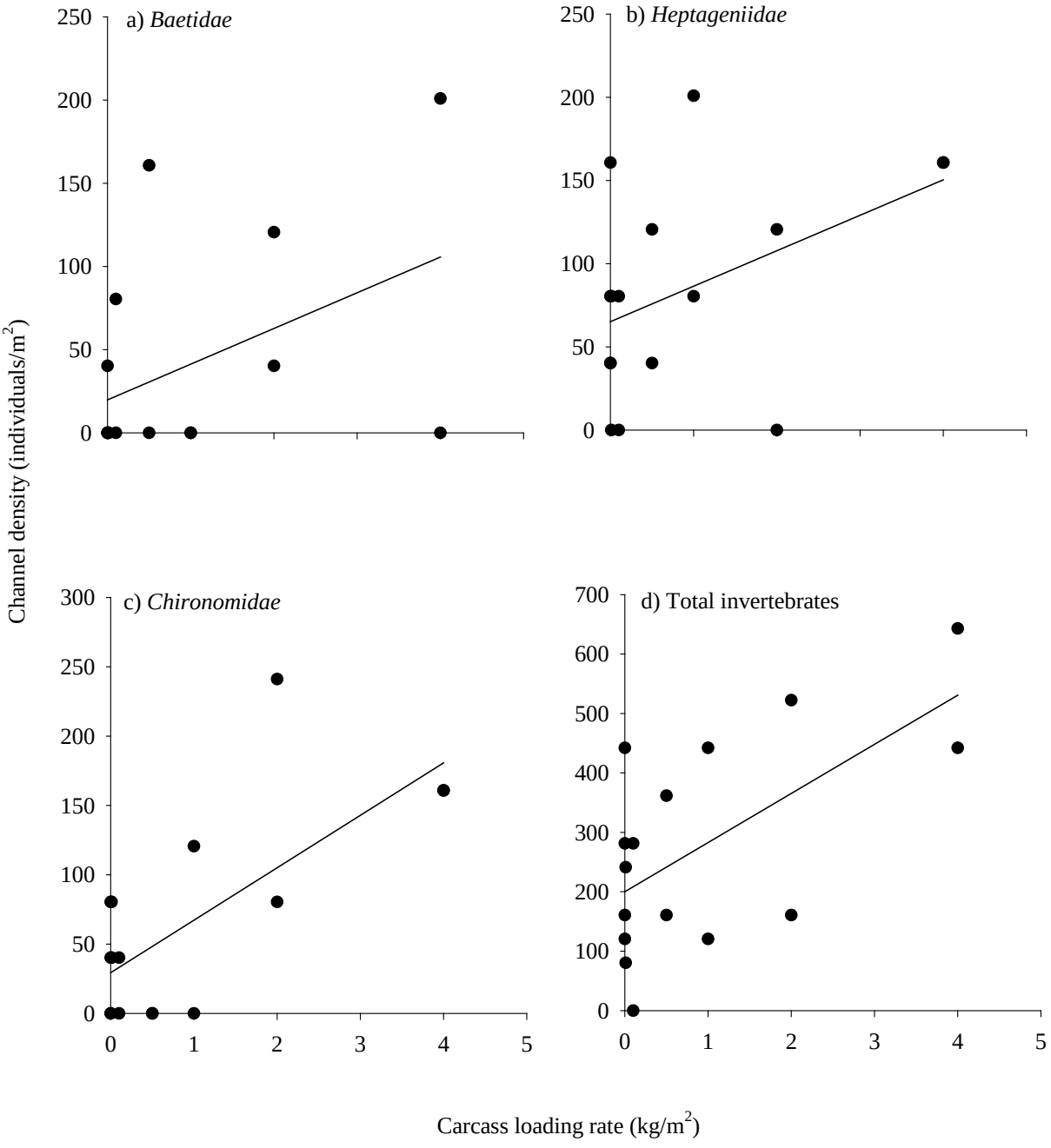
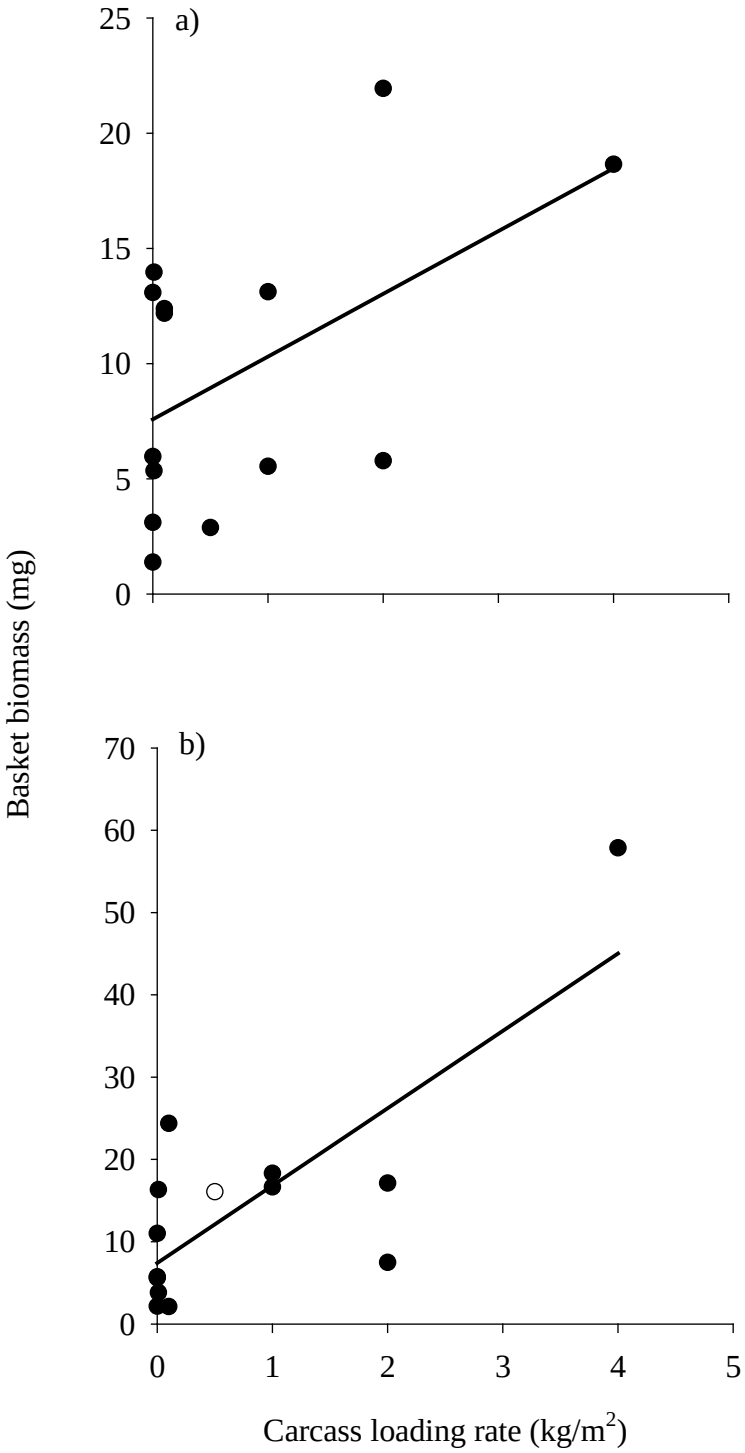
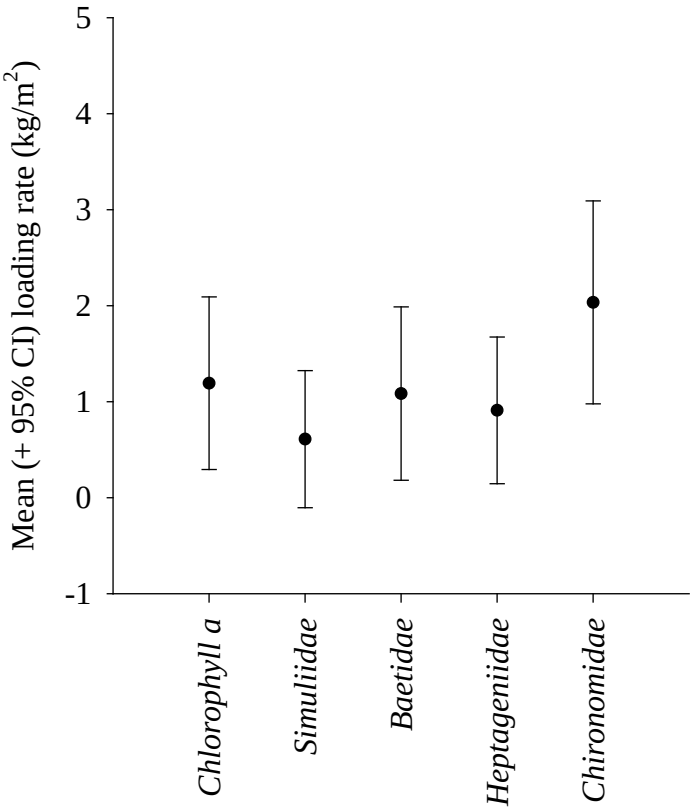

a) *Baetidae*
b) *Heptageniidae*
c) *Chironomidae*
d) Total invertebrates
Channel density (individuals/m^2)
Carcass loading rate (kg/m^2)
0
50
100
150
200
250
300
400
500
600
700
1
2
3
4
5

Figure 3


a)
b)
Basket biomass (mg)
Carcass loading rate (kg/m2)
0
5
10
15
20
25
30
40
50
60
70
1
2
3
4

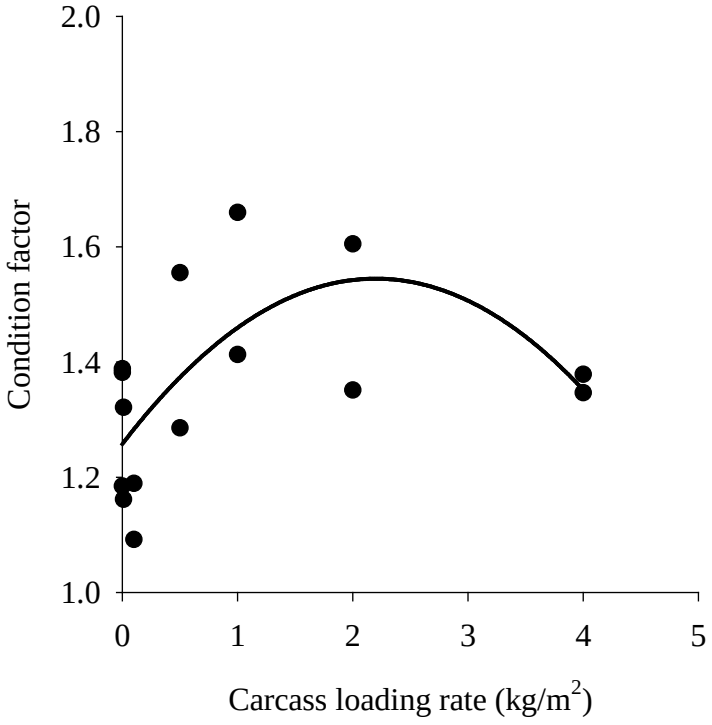
1

Figure 4


Mean (+ 95% CI) loading rate (kg/m2)
5
4
3
2
1
0
-1
Chlorophyll a
Simuliidae
Baetidae
Heptageniidae
Chironomidae

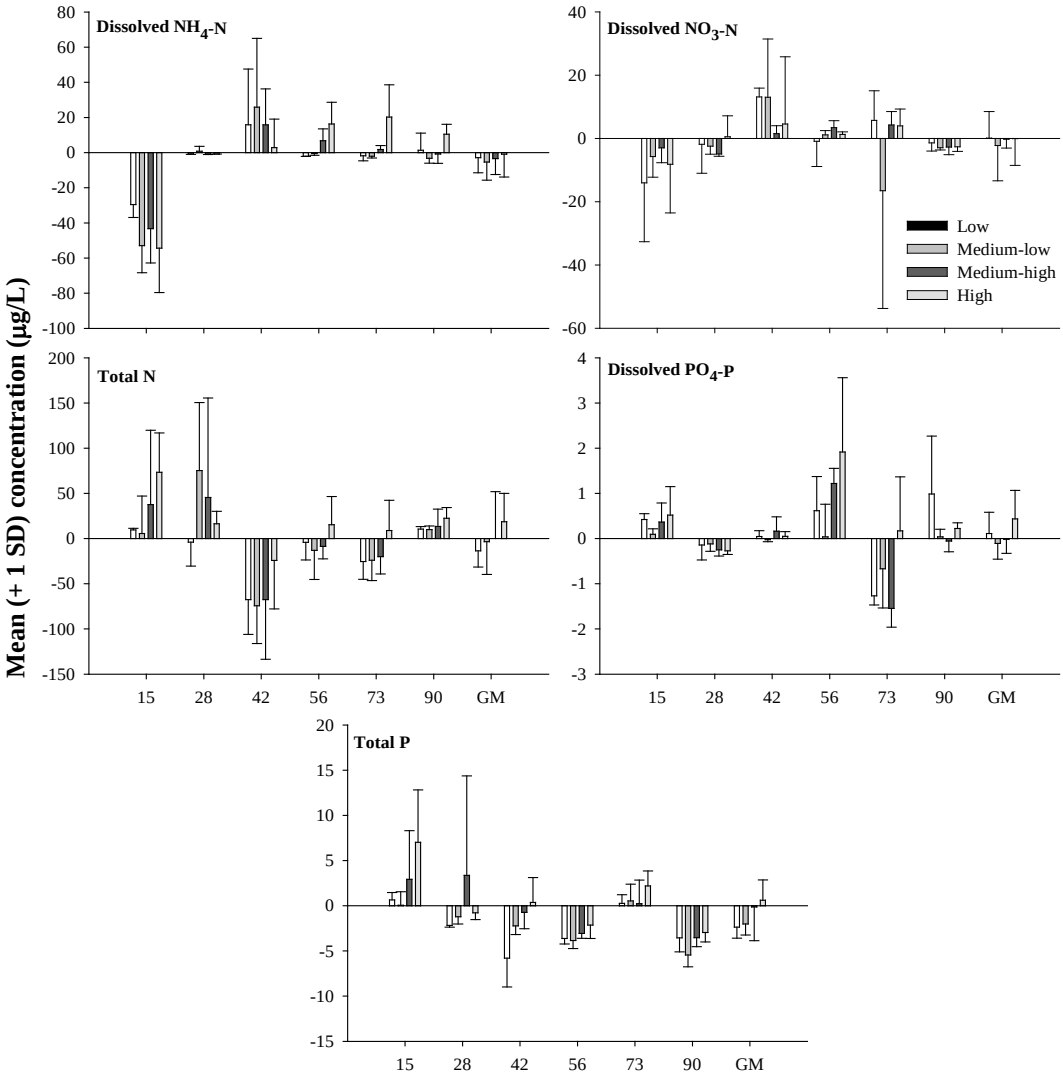
2

Figure 5


2.0
1.8
1.6
1.4
1.2
1.0
Condition factor
0
1
2
3
4
5
Carcass loading rate (kg/m2)

1

1 Figure 6


Dissolved NH4-N
Dissolved NO3-N
Total N
Dissolved PO4-P
Total P
Low
Medium-low
Medium-high
High
Mean (+ 1 SD) concentration (µg/L)
15
28
42
56
73
90
GM
Sample days and grand mean

2