STREAM-ASSOCIATED AMPHIBIAN RESPONSE TO MANIPULATION OF FOREST CANOPY SHADING

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Abstract: We reduced vegetation cover along a 50-m reach of 25 headwater streams in northwest Oregon and western Washington. Vegetation removal began directly over the stream and moved outward until attaining the treatments of 0%, 30%, and 70% cover (hereafter; no-, low-, and intermediate-shade levels). Each treated reach was paired to an upstream reference reach where cover averaged 92-97%. Using a replicated BACI design, we documented pre- versus post-treatment changes (two years each) in light levels, water temperature, stream periphyton, stream drift, and the abundance, body condition, and growth rates of six stream associated amphibians. Treatments resulted in a roughly three-fold gradient of photosynthetically active radiation at stream surfaces (267[35 SE] to 682[75] umols/m^2/sec). At the greatest light levels, heterotrophic streams dominated by allochtonous inputs shifted toward autotrophy as revealed by declines in stream detritus, increases in maximum water temperatures, and increases in periphyton accumulation. At higher trophic levels, responses to treatments were inconsistent, complex, and in some cases, appeared to be overridden by site-specific

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characteristics. However, many response variables exhibited patterns that agreed with a major prediction of the light:nutrient hypothesis: i.e., herbivore growth rates are maximized at moderate (low- and intermediate-shading) light levels. Specifically, drift of macroinvertebrate-gathering collectors generally increased and was greatest at intermediate-shade levels. Counts of amphibians increased from pre- to post-treatment periods in all reaches, including references, except for Olympic torrent salamanders (*Rhyacotriton olympicus*). Increased counts of amphibians following shade reductions were most often greatest at intermediate-shade levels. However, after adjusting counts for concurrent increases in reference reaches, only giant salamanders (*Dicamptodon* spp.), Cascade torrent salamanders (*R. cascadae*) and Olympic torrent salamanders increased post-treatment and only in the no- and intermediate-shade retention reaches ($P = 0.06$-0.10). Estimates of amphibian body condition did not exhibit any consistent patterns among taxa, but some species/development stages had greater condition in reaches exposed to the greater levels of sunlight, e.g. tailed frog (*Ascaphus truei*) larvae. The same generalization applies to estimates of amphibian growth rates, except that Cascade torrent salamander growth increased only at the intermediate level of shading. Except for macroinvertebrate shredders, which declined at the lowest shade level, reductions in vegetation shading either had little effect on the other response variables ($P > 0.10$) or the effects were primarily positive ($P \leq 0.10$, 22 of 36 contrasts). Although amphibian responses were taxon-specific, our data suggest that incorporating spatially and temporally periodic canopy openings, similar to our moderate light retention levels, as part of riparian management may benefit most stream amphibian taxa as long as other potential stressors (fine sediment delivery or water temperature) are not limiting. This claim should hold for areas at latitudes similar to this study.

Overall, the intermediate-shading treatment resulted in the most positive responses and the smallest increase in water temperature.

INTRODUCTION

Concern about the status of amphibians globally has increased the level of scrutiny that a multiplicity of environmental factors may have on amphibians (Stuart et al. 2004). One arena of concern is forestry practices, which has been the focus of numerous studies over the last three decades (deMaynadier and Hunter 1995, Kroll 2009 and references therein). A number of these studies have examined the effects of timber harvest on a suite of stream-associated amphibians (SAAs) endemic to the Pacific Northwest (PNW); including tailed frogs (*Ascaphus truei*), giant salamanders (*Dicamptodon* spp.), and torrent salamanders (*Rhyacotrition* spp.) (Murphy and Hall 1981; Bury and Corn 1988; Corn and Bury 1989; Bury et al. 1991; Kelsey 1995; Bull and Carter 1996; Diller and Wallace 1996, 1999; Wilkins and Peterson 2000; Wahbe and Bunnell 2003; Steele et al. 2002, 2003; Russell et al. 2004, 2005; Jackson et al. 2007; Kiffney and Roni 2007; Kroll et al. 2008; Leuthold et al. 2012). Despite this substantial number of studies, their collective results seem contradictory, generating uncertainty (Kroll 2009), and preclude development of guidelines on how to manage for SAAs when implementing harvests. Though diverse factors contribute to these seemingly contradictory results, the most important are likely (1) the confounding effects of regional variation in physical features (parent geology, topography, altitude, latitude) because most SAAs have relatively broad distributions, (2) studies were not designed to examine interactions between harvest effects and abiotic factors, and (3) we have little understanding of how much the probability of detecting SAAs varies with diverse habitat conditions and sampling methods (Kroll 2009).

Notwithstanding these complications, these studies agree in that timber harvest has two immediate primary physical effects: 1) reduced vegetation cover and 2) increased fine sediments to streams. Because parent geology, aspect, and stream gradient can either diminish or exacerbate these effects, we expect that the relative magnitude of their impact on SAAs will vary with local conditions. For example, Murphy and Hall (1981) and Hawkins et al. (1983) found that the positive effects of removal of riparian vegetation (increased primary productivity) could mask a potentially detrimental sedimentation effect; and Murphy and Hall (1981) and Diller and Wallace (1996) found that steep stream gradients reduced the potential negative effects of increased sediments. Hence, to really understand the impact of these physical effects on SAAs, it is essential to examine them independently, i.e., under conditions where one or the other are absent or nearly so. In this study, we examine the impacts of reducing vegetation cover on SAAs while keeping sediment influx to a minimum.

In forested ecosystems of the PNW, headwater stream autochtonous productivity is limited due primarily to interception of sunlight by dense cover of vegetation from the low-shrub layer to the forest canopy (Gregory et al. 1987, Murphy 1998, Kiffney et al. 2004). In general, energy inputs to these streams are from allochtonous sources and the streams are heterotrophic (Lagrue et al. 2011, Marcarelli et al. 2011). These characteristics shape stream communities at all trophic levels (Hall et al. 2000, Baxter et al. 2005, Lagrue et al. 2011). Reductions in vegetation cover can change these fundamental relationships by shifting stream segments from heterotrophic systems to autotrophy where autochtonous energy sources dominate and stream community composition or structure changes (Feminella and Hawkins 1995, Lagrue et al. 2011, Hill et al. 2010, 2011a, 2011b; Lange et al. 2011, Ohta et al. 2011).

Many studies have shown that reduced canopy cover has positive effects on abundance, species richness, survival, growth, and development of several species of pond breeding anurans and some caudates (see review in Earl et al. 2011 and references therein). However, Earl et al. (2011) found a differential response to pond shading between two ambystomatid salamanders and three anurans as well as within the anuran community they analyzed. Although that study was conducted in lotic environments and with different taxa, we suggest that such a dichotomy could be universal based on the energy subsidies of shaded vs. open waters, macroinvertebrate differences, and the trophic position of anuran (grazers) and caudate (predators) larvae. These fundamental relationships may also be applicable to headwater stream communities in the PNW.

A number of studies in the PNW have indicated that a reduction in vegetation cover increases stream primary productivity (Hansmann and Phinney 1973) which often results in greater production at higher trophic levels (Murphy and Hall 1981, Hawkins et al. 1983, Bisson and Sedell 1984, Bilby and Bisson 1987, Holtby and Scrivener 1989, Fuch et al. 2003, Kiffney et al. 2004, Wilzbach et al. 2005, Mallory and Richardson 2005). Inconsistent conversion of the increase in primary production to higher trophic levels may reflect the confounding and negative effects of increased sedimentation (e.g., Murphy and Hall 1981) or temperature (e.g., Leach et al. 2011). Moreover, inconsistencies may also arise because light saturation for algal production occurs at less than full sunlight (Murphy 1998), which suggests a threshold at which further reductions in shade will not increase productivity, a pattern that may vary with latitude. In addition, the light:nutrient hypothesis predicts that herbivore growth rates are maximized at moderate (low to intermediate) light levels because greater carbon assimilation at high light levels reduces the quality of algae to grazers, and at low light levels herbivores are limited by the available mass of algae (Sterner et al. 1997). This relationship could also affect secondary consumers because herbivores experiencing optimum growth rates should result in greater foraging efficiency by predators (Charnov 1976).

Of the studies that have examined higher trophic level responses to shading, few have addressed SAAs (Hawkins et al. 1983, MacCracken 2002, Kiffney et al. 2004, Mallory and Richardson 2005, Kiffney and Roni 2007). Hawkins et al. (1983) detected no differences in the density and overall mass (g/m^2) of coastal giant salamanders (*D. tenebrosus*) in stream reaches between adjacent or paired clearcut and unharvested stands in western Oregon, but Kiffney and Roni (2007) found that shading had an effect, because the interaction between light and stream gradient best explained *D. tenebrosus* abundance at their coastal Oregon sites. In a riparian hardwood conversion study in southwestern Washington, MacCracken (2002) found body condition (based on the residuals index) of Columbia torrent salamanders (*R. kezeri*) to be greater, albeit at lower densities, in streams where the surrounding tree canopy was reduced by 30-50%. In addition, though Wahbe and Bunnell (2003) found no statistically significant differences in density or mass of coastal tailed frog larvae among streams in clearcut, second-growth, and old-growth stands; larval mass averaged highest in clearcuts, suggesting a biologically significant effect in terms of better foraging in those streams for this algae grazer. However, two manipulative experiments have demonstrated that *A. truei* larvae can show marked responses to variation in light levels. Using experimental channels that were artificially shaded to create four levels of photosynthetically active radiation (PAR) reaching streams (2%, 10%, 22%, and 100% of full exposure), Kiffney et al. (2004) found that larvae lost mass in the two treatments with the lowest light levels, whereas larval growth rates were seven-times greater in the 100% versus the 22% treatment. Light level was also strongly related ($R^2 = 0.96$) to the proportion of larvae surviving at the end of the study. Using in-stream experimental enclosures, Mallory and Richardson (2005) showed that *A. truei* larvae had relative growth rates that were14% higher in the less shaded treatments, which presumably reflected the 30-40% greater periphyton mass in those treatments when contrasted with the more shaded treatments. Collectively, these studies imply that shade reductions will translate to SAA responses (trophic cascade hypothesis [Paine 1980]) that are manifest as an improved body condition, growth or survival of primary consumers (e.g., tailed frog larvae) and increased body condition and population density of secondary consumers (e.g., salamanders). Nonetheless, confidence in the applicability of these results is limited due to the retrospective and correlative nature of all studies except the latter two. Moreover, how the pattern that the latter studies found might change with latitude or influence secondary consumers is not known; tailed frog was the only SAA addressed in their experiments and they worked in a system lacking SAA secondary consumers. Furthermore, the response to reduced shade appears to be linear, contrary to the light:nutrient hypothesis, but few of these studies sampled along a complete gradient of light intensity and thus have limited utility in assessing the predictions of that hypothesis.

The combination of the limited scope of past studies in terms of the SAA community, the light levels examined, and geographic extent led us to undertake a reach-level manipulative experiment to examine SAA response. The overarching objective of this experiment was to assess the effects of shade reductions on SAAs, and examine some possible causal mechanisms as well as the applicability of both the trophic cascade and light:nutrient hypotheses at primary and secondary consumer levels. We studied six SAA species, one of which (*A. truei*) is a primary consumer during its larvae stage and has been the focus of previous studies (Wahbe and Bunnell 2003, Kiffney et al. 2004, Mallory and Richardson 2005), and the remaining species, all salamanders (*D. tenebrosus*, *D. copei*, *R. cascadae*, *R. kezeri*, and *R. olympicus*), are secondary consumers during their in-stream larval stages (Nussbaum et al. 1983). Coastal tailed frog and the torrent salamanders were part of the seven target SAAs considered during the development of headwater stream protection strategies for private and state lands managed for timber production in Washington (Forests and Fish Report 2000) and later adopted under the Forest Practices Habitat Conservation Plan (Washington Department of Natural Resources 2005). We focused on SAA abundance, body condition, and growth rates, as response variables based on their use in previous studies and our belief that a change in body condition or growth rate would likely be the most rapid response evident from shade manipulations. We also measured water temperature and light, and estimated periphyton accumulation and macroinvertebrate abundance to enable linking SAA responses to any treatment effects on those key variables.

To evaluate the applicability of the trophic cascade and light:nutrient hypotheses effectively, we examined mutually exclusive, testable predictions for each. For the trophic cascadae hypothesis, less shade is expected to result in greater periphyton accumulation and increased macroinvertebrate abundance. Further, the abundance of macroinvertebrate functional feeding groups should shift from pre-treatment patterns to greater dominance by scrapers or collectors (filterers and gatherers) because of the dependence of these groups on periphyton and the close association of shredders with leaf litter inputs (Hawkins et al. 1982, Cummins et al. 1989, Quinn et al. 1997, Kiffney et al. 2003, 2004, Leberfinger et al. 2011). We also hypothesized that SAA primary consumers, larval *A. truei*, will show some form of a positive response to less shade (Kiffney et al. 2004, Mallory and Richardson 2005). Lastly, we expect the salamanders to show a response to less shade if their typical prey is part of the macroinvertebrate assemblage that either increase or decline with changes in light regimes. For the light:nutrient hypothesis, which predicts that an intermediate level of shading is optimal (Sterner et al. 1997, Murphy 1998), we would expect SAAs to exhibit a non-linear response to shade levels. That non-linear relationship could either be an asymptote with a response plateau, or quadratic, where the response declines beyond a peak level. The latter may depend either on whether high light levels actually decrease periphyton quality as food for both tailed frog larvae and macroinvertebrates eaten by salamanders (based on the light:nutrient hypothesis), whether higher temperatures that may occur at high light levels compromise assimilation efficiency (bioenergetics hypothesis, Brett et al. 1969, Railsback and Rose, 1999, Leach et al. 2011), or both.

METHODS

Site Selection: We selected small SAA-occupied streams with a mostly south-facing aspect (135˚- 235˚) because the effect of shade removal due to increased solar radiation was expected to be greatest in such streams (Risley 2003, Moore 2005). We also constrained sites to competent lithologies because greater SAA abundance on such lithologies (versus less competent ones; Wilkins and Peterson 2000, Jackson et al. 2007) increased the likelihood of identifying a shade-reduction effect. Lastly, we selected sites from over a relatively broad area where the target SAA genera co-occur, namely from northwest Oregon to the Olympic Peninsula and from the Coast Ranges to the Cascade Mountains (Jones et al. 2005). This greatly increased the geographic and ecoregion scope of inference for our results.

Site Description: We used 25 streams located in two general areas: an east-west-oriented area defined by the Columbia River and a second area along the east side of the Olympic Peninsula. Fifteen of the 18 streams near the Columbia River were on Longview Timberlands LLC ownership in Clatsop County, Oregon; and Cowlitz, Skamania, and Wahkiakum Counties in Washington (Fig. 1, Appendix 1). The remaining three Columbia River-proximate sites were a stream in Wahkiakum County on The Campbell Group ownership and two in Skamania County on Washington Department of Natural Resources (DNR) lands. All seven streams on the Olympic Peninsula were on DNR lands in Mason County (Fig. 1).

All streams were on lands intensively managed for timber production within second-growth coniferous forest. Variation existed in managed stand composition; managed forest at most sites was primarily Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*), but three mid-elevation sites in Skamania County had noble fir (*Abies procera*). Riparian stands bordering streams varied as well; red alder (*Alnus rubra*) and western hemlock were often dominant, and Douglas-fir, western red cedar (*Thuja plicata*) and big-leaf maple (*Acer macrophyllum*) were regularly to infrequently important (Appendix 1). Understory was dominated by one or more of vine maple (*Acer circinatum*), salmonberry (*Rubus spectabilis*), stink currant (*Ribes bracteosum*), and devils club (*Oplopanax horridus*) in the shrub layer, and diverse forbs and mosses in the ground layer. Combined canopy and shrub layers often resulted in pre-treatment vegetation cover over streams in excess of 100%.

General silviculture on all ownerships involved clearcut logging and one of three modes of site preparation (broadcast burning of slash, piling and burning of slash, or piling with or without burning and chemical treatment) followed by planting of site-adapted seedlings. However, a mix of clearcut logging and selective logging was used at mid-elevation sites. Study streams were located either in rotation-age second-growth or had a ≥30- m buffer left on both sides of the stream during the most recent harvest, between four and 10 years prior to initiation of the study. At one site, adjacent stands were harvested during the fall following treatment

Figure 1. Location of study sites within three ecoregions of western Washington and northwest Oregon.

implementation. In that case, we worked closely with the harvest operators to ensure that the treatment specified (no-shade) for this study site was maintained and the reference reach was not impacted.

The study design included eight blocks (Fig. 1), each of which had three streams; one additional stream in the Olympics was also included (Jorsted Cr, intermediate-shade retention). Streams within blocks were located within the same 3rd- or 4th-order watershed (*sensu* Strahler 1957) except in the Olympics, where five of the seven streams were located in adjacent 3rd- or 4th-order watersheds. Actual study reaches were 1st- or 2nd-order except for one 3rd-order stream in the Olympics. Two of the three SAA genera, *Ascaphus* and *Rhyacotriton*, were represented in all streams, but *Dicamptodon* occurred only in the six blocks in northwest Oregon and southwest Washington (Fig. 1). Coastal tailed frogs (*Ascaphus truei*) occurred in all streams. In contrast, *Dicamptodon* and *Rhyacotriton* were represented, respectively, by two and three species. The two *Dicamptodon* species, Cope's giant salamanders (*D. copei*) and coastal giant salamanders (*D. tenebrosus*), co-occurred in all streams in northwest Oregon and southwest Washington. Cope's giant salamanders occur on the Olympic Peninsula (Adams and Bury 2002), but its range on the Peninsula was just outside our study blocks (M. Hayes, J. Tyson, unpubl. data). In the analyses, the two species of giant salamanders were treated collectively because they cannot be unambiguously identified morphologically. Columbia torrent salamanders (*Rhyacotriton kezeri*) occurred in the Coast Range of northwest Oregon and southwest Washington, Cascade torrent salamanders (*R. cascadae*) in the south Cascade Range, and Olympic torrent salamanders (*R. olympicus*) in the Olympic Range (Fig. 1).

Treatments: We used a replicated before-after control-impact (BACI) paired design (Underwood 1994, Smith 2002), with two years each of pre- and post-treatment data collection. Each stream was divided into a 50-m treatment (downstream) and a 50-m reference (upstream) reach separated by 50-94 m (Fig. 2). With paired treatment and reference reaches we were better able to control for possible confounding factors such as substrate composition and competency, gradient, aspect, and elevation (Hawkins et al. 1983), all of which are thought to influence SAA abundance. We spaced treatment and reference reaches at least 50-m apart to maintain relative independence between reaches in terms of SAA movement patterns as a consequence of the ≤50-m movement scale of the SAA life stages studied (Nussbaum and Tait 1977, Wahbe and Bunnell 2001, Ferguson 2000). Thus, it was unlikely that individuals inhabiting one reach would move to another reach during the course of this study. Variability in length of the intervening (non-sampled) reach reflected limitations of local topography (e.g., areas too steep for access) and other stream characteristics in order to match treatment and reference reaches as closely as possible. Our choice of study reach length represented a compromise among a desire to minimize reach variation in aspect, gradient, and substrate; feasibility of treatment application; and enough length to ensure a treatment effect.

One of three shade retention treatments (≈ 0%, 30%, and 70% canopy cover; hereafter no-, low-, and intermediate-shade; respectively) was randomly assigned to treatment reaches in each block. We reduced shade to specified treatment levels by removing the appropriate vegetation based on readings of the middle two rows of a concave spherical densiometer. Multiple densiometer readings were taken from the mid-channel position at the bottom, middle, and top of each treatment reach. Shade reductions were achieved by iteratively removing shrubs

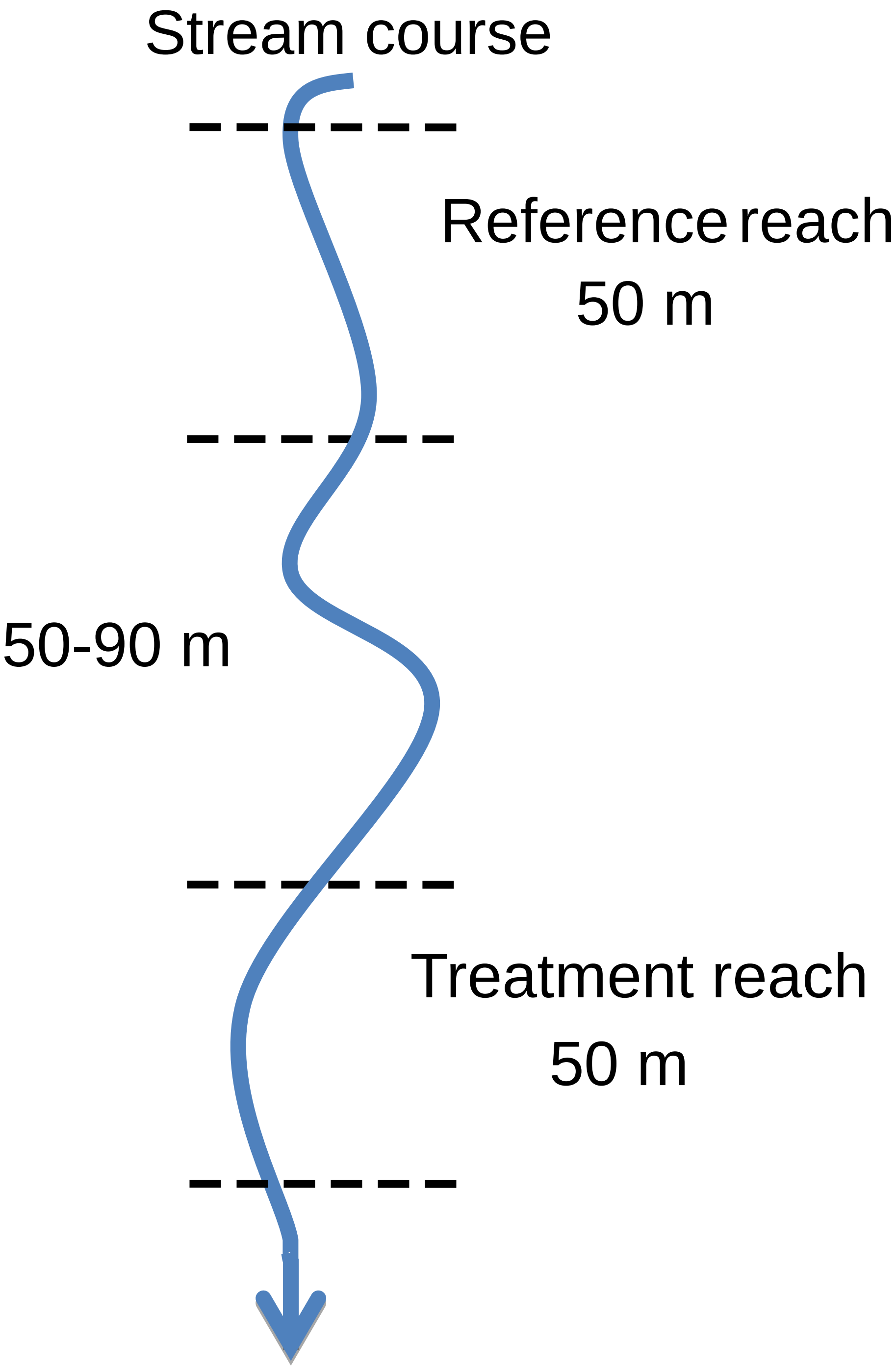


Fig. 2. Schematic of typical study reaches configuration for a stream.

and trees that provided shade directly over the channel and then, as needed, by removing vegetation further into the riparian area based on the two middle rows of the densiometer (about 10-20 m). We considered only the two middle rows of the densiometer (12 squares) to reduce the angle of view of the densiometer, and avoid removing vegetation far from the stream channel that did not shade the stream or provided shade only at very low sun angles. We also implemented vegetation removal in a manner that resulted in cover that was approximately evenly distributed along treatment reaches. Thus, full densiometer readings exceeded those of the treatment targets, i.e., mean canopy cover based on full densiometer readings were 40%, 61%, and 77% for the no-, low-, and intermediate-shade treatments, respectively. In each post-treatment sample year, we also took periodic densiometer readings (center two rows only) to determine whether vegetation regrowth required touch-up removals to maintain assigned shade levels. To ensure that we did not increase sediment input to treatment reaches we reduced vegetation cover by directional falling of trees with chainsaws and clearing of brush with chainsaws or pruning loppers. Material that fell into the stream was immediately removed.

Study chronology and treatment application was staggered. Study reaches in each block in the northwest Oregon and southwest Washington were sampled during summers 2004 and 2005 (pre-treatment), and 2006 and 2007 (post-treatment). Treatment application in those blocks occurred during fall-spring 2005-2006. Streams in the Olympic block were originally added in 2005. However, six streams on U.S. Forest Service lands (comprising two of the three blocks) were lost because approval for implementation of the no- and low-shade treatments was denied. Replacements for four of the streams were found on DNR lands early in 2006, resulting in two complete blocks and an extra intermediate-shade treatment. Pre-treatment sampling on all seven streams occurred in 2006 and 2007, treatment application took place in fall-spring 2007-2008, and post-treatment sampling occurred in 2008 and 2009.

Response Variables

<u>Cover and light</u>: Vegetation cover and light (PAR) reaching the streams were estimated for each reach every 2-4 weeks. Percent canopy cover or density (Jennings et al. 1999) and PAR estimates (μmols/m^2/sec) were taken at 10-m intervals along each reach starting at the downstream end (a total of six per reach). Cover estimates were made using the entire grid of a convex spherical densiometer held at the stream surface facing the four major compass directions; and dominant canopy species were identified. PAR estimates were taken at the stream surface with an LI-190SA quantum sensor and LI-250A light meter (LI-COR PO Box 4425, Lincoln, NE 68504). The light meter averages PAR readings over a 15-second interval and we took three averaged readings at each point. PAR readings were averaged over each stream reach for each year.

<u>Water temperature</u>: We monitored water temperature in each reach from June-September each year using Onset Stowaway™ or Tidbit™ data loggers (Onset Computer Corporation, Bourne, MA 02532) programmed to record water temperature every 30 min. Data loggers, housed in PVC pipe with numerous 12 mm holes, were placed at the bottom of each treatment and reference reach. Whenever a stream was visited, the data loggers were checked and adjusted to maintain a completely submerged position. Data loggers were calibrated following Schuett-Hames et al. (1999) or the manufacturer's instructions.

We examined the data to identify the maximum water temperature during the entire time series for each reach each year (seasonal maximum). We also calculated the seven-day moving average of the maximum daily water temperature for each reach each year. The data logger manufacturer indicated a ± 0.2^{o} C error rate, so we rounded estimates to the nearest 0.5^{o} C.

Stream productivity: We estimated productivity by placing five 15 x 15-cm unglazed quarry or clay tiles in all reaches in May-June at 10-m intervals. Tiles were collected approximately four months later in late September-early October, placed in plastic storage bags, and frozen until processed in the lab. Standardization for the precise time interval tiles were in the stream was done post-processing. In the lab, we scraped the tiles of algae and other organisms after removal of macroinvertebrates and coarse debris. We then filtered, oven-dried, and weighed the scraped material. Subsequently, the scraped material was ashed in a muffle furnace at 500^{o} C for 15 min, and reweighed (Hauer and Lamberti 1996). We estimated periphyton accumulation on the tiles as g/cm^{2} ash-free dry mass (AFDM)/reach/year.

Stream drift: To index stream productivity, potential macroinvertebrate prey for salamanders, assess treatment effects on litter inputs, and assist in interpretation of our results, we collected drift samples from each reach in the spring, summer, and fall each year (Wipfli and Gregovich 2002, Wipfli 2005). For each sampling period, a sandbag weir was established across the bottom of each reach with a 10-cm plastic pipe set flush with the stream bottom for outflow. The pipe extended about four-cm upstream of the weir and another 50-cm below the weir and was positioned to capture most of the surface flow of the reach. A fine mesh (250 µm) nylon sock was attached to the downstream end of the pipe to capture the material that flowed through the pipe. To ensure that contributions of drift originated exclusively from the length of study reaches, the same weir and pipe system was established at the top of each reach. These apparatuses were left over night and retrieved the next day (18-30 hours later, Danehy et al. 2011) capturing both an evening and morning pulse of drifting macroinvertebrates. The contents of the nylon socks were transferred to large plastic storage bags in the field, and filled with enough 70% ethanol to cover the contents. The plastic bags were then placed in a freezer until processing.

Stream discharge (ml/sec) was measured for each reach either immediately prior to attaching the nylon bag to the pipe or the next day, when the bag was removed by recording the time needed to fill a 1000-ml beaker with water coming through the pipe three times. The three measurements were averaged to estimate discharge for that sampling period for each reach. Following each sampling period, the weir and pipe assemblies were dismantled. Discharge was measured to standardize drift by stream flow; we did not expect shade reductions over 50 m of stream length to affect stream discharge.

In the lab, the contents of each bag were rinsed through a series of stacked sieves (5-mm, 2-mm, and 250-µm mesh) and the contents of the two larger mesh sieves separated by hand with the aid of a 10× dissecting microscope into the following components: deciduous leaves, conifer needles, wood, other vegetation, insects, inorganic material, and miscellaneous other material. Organic matter, excluding insects, collected from these sieves was oven-dried for 24-48 h at 60^{o} C, depending on the amount of material, and weighed to the nearest 0.0001 g. For analyses, these samples were combined and labeled as coarse particulate organic matter (CPOM).

The contents of the 250-µm mesh sieve were separated into the same components, except for organic matter that could not be identified – primarily small pieces of vegetation. The remaining material was removed from the sieve, oven-dried at 60^{o} C for 24-48 h, weighed to the nearest 0.0001 g, baked in a muffle furnace at 500^{o} C until all the organic material was ashed, and then reweighed. The difference between the two weights was determined and labeled fine particulate organic matter (FPOM).

Aquatic macroinvertebrates were identified to the lowest taxonomic level necessary to assign them to a functional feeding group (filterers, gatherers, scrapers, shredders, and predators) and the number of individuals of each taxon recorded. Aquatic macroinvertebrates were then composited by functional group, dried to a constant weight in an oven at 60^{o} C, then weighed to the nearest 0.0001 g.

The analyses of the drift samples followed the procedures of Wipfli and Gregovich (2002) and Wipfli (2005). All drift components (CPOM, FPOM, macroinvertebrate functional groups) were quantified as g/m^3 of stream flow and g/day (24 hr). In addition, individual macroinvertebrates captured were also quantified as number/m^3 of flow and number/day.

Amphibian abundance: We estimated amphibian abundance in each reach during low flow (late July-early October) each year. Five 2-m long plots with a width equivalent to the wetted channel were sampled in each reach by randomly assigning the first plot within the first 10-m segment then locating the other four plots at successive 10-m intervals. We sampled each plot by blocking its lower margin with a fine-mesh screen and removing all wood and cobble, then raking the gravel and fines while holding a dip net below the area searched. The blocking screen was checked for amphibians as the plot was searched and when the plot search was finished. We identified each amphibian captured to species (except individuals of *Dicamptodon*), life stage (larvae, metamorph, juvenile or adult) and sex, whenever possible. We also weighed (to the nearest 0.1 g) and measured (total and snout-vent/urostyle length to the nearest 0.1 mm) either all individuals or a maximum of 10 individuals of each species/plot to estimate body condition. For plots with more than 10 individuals of each species, animals were held in a plastic bag or bucket until the plot search was completed and then 10 were selected without bias for measuring.

We estimated the probability of detecting amphibians (p) in the plots by a repeat sample of a randomly selected plot in each reach each year. After the initial search of the plot, a block screen was established along the upper edge of the plot. Amphibians captured during the initial search were held temporarily in plastic bags. Block screens remained in place until the plot was re-visited 2-24 hours later. All material removed from the stream was replaced after plot searches. Detection probabilities were estimated as: $p = C_i/C_t$ where C_i is the number of initial captures and C_t is all captures from the two searches. This approach is similar to a mark-recapture procedure in estimating individual p as individuals held in plastic bags are analogous to a marked sample and the block nets and relatively short time period meet the closure assumption. Amphibian counts for each species/age/stage were summed over all plots/reach/year and adjusted by p estimates.

Amphibian body condition: We estimated the body condition (energy stores) of individual amphibians captured during abundance surveys using the scaled mass index (SMI) of Peig and Green (2009, 2010). We used total length as the body structure measure for larval tailed frogs and the salamanders and snout-urostyle length for tailed frog metamorphs and post-metamorphs. An ordinary least squares regression was used to estimate the coefficient of the SMI power function. MacCracken and Stebbings (2012) tested this procedure with American bullfrog (*Lithobates catesbeiana*) larvae and post-metamorphic juveniles and rough-skinned newts (*Taricha granulosa*) and found a high correlation ($r \geq 0.8$) among energy stores and the SMI. The SMI for each individual for each species and stage (*A. truei* only) was averaged by stream reach and year.

Amphibian growth rates: Growth rates (g/week) were estimated by stocking species-specific, in-stream enclosures with four giant salamander or six individuals of the other species (all larvae) in both treatment and reference reaches of each stream. These stocking levels were based on both sample size considerations and densities of these species reported in the literature. Animals for introduction to the enclosures were taken from each stream either below the treatment reach, $\geq$ 50 m above the reference reach, or from the nearest stream not used in the study. All reaches had one enclosure with *A. truei*, and one with the local species of *Rhyacotriton*. All reaches except those on the Olympic Peninsula also had enclosures with *Dicamptodon* spp.

Enclosures were transparent plastic boxes (0.17-0.26 m^2 bottom surface area, 13-16 cm tall) placed in the streams in May. We placed enclosures at 12-m intervals, starting at the 12-m mark from the downstream end of each reach. We maintained water flow and some drift into enclosures by cutting three eight-cm holes in the upstream and downstream ends of the enclosures that were covered with three-mm mesh screen. We modified the enclosure in two ways to ensure adequate flow: 1) we drilled numerous one-mm diameter holes in the bottom and sides of each enclosure; and 2) we inserted two lengths of 2.5-cm diameter PVC pipe through the top of the upstream side of the enclosure and placed the opposite ends of these pipes in the stream. Six-mm mesh screens covered the pipe ends, which prevented amphibians and crayfish from entering the enclosure but allowed the passage of most macroinvertebrates as well as fine detritus. We also cut out the center of the lid for each enclosure so that a six to eight-cm lip remained when attached to minimize shading and enable litterfall and volant invertebrates to drop into enclosures as well as to keep amphibians from escaping.

We filled each enclosure with about six cm of sand to cobble-sized rock from the adjacent stream location. The enclosures were established two to four weeks prior to placing amphibians in them. Amphibians were weighed and measured when introduced to an enclosure and each was individually marked with colored fluorescent elastomer injected under the skin.

We visited enclosures every seven to 14 days. On each visit, screens were cleaned and enclosures were adjusted as necessary to maintain water flow. On every other visit, we weighed amphibians, noted the development stage for *A. truei*, and recorded the location of each amphibian within the enclosure. If individuals were missing, they were occasionally found close by and returned, or new ones were captured and added at that time or within a week to maintain a minimum of four animals in the enclosures. Growth rates of marked individuals were calculated as the change in mass between their initial introduction to an enclosure and each subsequent weighing. These estimates were then averaged and standardized by the number of weeks in the enclosure. To be used in the analysis, individuals had to be in the enclosures for a minimum of four weeks, but no longer than 16 weeks. We truncated the interval used at 16 weeks because the sample size of individuals extending beyond that time interval was too small.

We also established a separate enclosure in each reach to estimate a possible enclosure effect (Mallory and Richardson 2005) by assessing periphyton accrual and water temperature. These enclosures were identical to the others, except that they lacked amphibians, had minimal stream substrate, and three clay tiles. In addition, a water temperature data logger was added to an enclosure in either the reference or treatment reach of each stream, based on a random draw. This allowed us to determine whether enclosures differed from the stream in water temperature and periphyton accumulation.

Data Quality Control: We took several steps to ensure data quality. In the field, data were recorded with hand-held computers (Dell Axim PDAs) directly into Excel spreadsheets. This insured that all observers consistently collected the complete set of data at each site for each sample, assisted in the recognition of information that was entered incorrectly, and eliminated the transfer of data from data sheets to a spreadsheet program which can also introduce transcription errors. Data were also checked daily for errors and consistency. In addition, backups were created by printing copies of spreadsheets or by creating backup files on a desktop computer in the office. Each spreadsheet contained a column for observers to enter notes on unusual conditions that might have affected estimates, minor adjustments to sampling protocols, etc.

We also captured and corrected errors as data were being summarized and formatted for analyses. The pivot table feature of Excel was often used to average subsamples (see below) of the various metrics measured, which was useful in quickly identifying data that contained outliers, inconsistent sample sizes, mislabeled sample units, and other miscellaneous problems. In addition, the results of data analyses routines (see below) contained diagnostic graphs (e.g., plots of residuals), degrees of freedom, etc. that could also signal data errors. Finally, if the results of data analyses were inconsistent with expectations and unusual, that would also trigger an examination of data matrices for errors. In this study, this process revealed two major errors that were the inadvertent consequence of data handling: (1) the SUM and AVERAGE functions in an Excel program were excluding some cells in the calculations, and (2) errors also occurred when importing Excel files into SYSTAT, e.g., some cells were left blank and incorrect numbers appeared in others.

Data Analyses: The study design contrasted a reduced shade level reach (treatment) with a paired reference reach on each stream. Thus, the basic metric for analysis of each response variable was the difference between the treatment and reference reaches for each stream, i.e., the raw effect size (ES). This approach has the advantages of normalizing data, and reducing both variance and heteroskedasticity. The base data matrix for the analysis of each response variable consisted of the ES estimate for each shade level in each block each year (years were further assigned to pre- and post-treatment periods; differentially across ecoregions because of sampling stagger). We also assigned each block to an ecoregion (Coast Range, Cascade Mountains, and Olympic Peninsula). To make direct contrasts between shade treatments and reference conditions, we included a reference dummy variable in the data matrix as a separate treatment. This was necessary because reference reaches were not independent of treatment reaches with respect to individual streams, and instream comparisons involved treatment-reference reach contrasts.

We analyzed the data with linear mixed effects models (McDonald et al. 2000, Zurr et al. 2009) with period (pre- and post-treatment), shade (no-, low-, intermediate-, reference), and the period × shade treatment interaction as fixed effects. Year, block, and ecoregion (where applicable*)* were modeled as random effects. Block was nested within ecoregion for giant salamanders and tailed frogs. We assessed model fit by examination of residual plots. For models producing strong patterns in the residuals (see Zurr et al. 2009); we rank-transformed the data (Iman and Conover 1979, Conover and Iman 1981). Response variables that were rank transformed are noted in the text, tables, and figures.

Emphasis is placed on the period × treatment interaction term (hereafter interaction) in a BACI design (Underwood 1994, McDonald et al. 2000). However, contrasts between each combination of period and shade level can help to explain the interactions and were also of interest. We were most concerned about guarding against a Type II statistical error (i.e., declaring no treatment effect when one exists) in this study, an approach used in ecological studies with relatively few replicates (Toft and Shea 1983, Toft 1991, Schrader-Frechette and

McCoy 1993). To that end, we made pair-wise contrasts with the more liberal (i.e., lower *P*-value estimates) Fisher's Least Significant Difference test, and focused on interaction terms and individual contrasts that produced *P*-values $\leq$ 0.1, and examined raw effect sizes. These analyses were performed with SYSTAT v.12 or 13.

We used the same mixed model approach to examine variation in detection probabilities (*p*) for each amphibian species that may be attributable to the same fixed and random effects as for the primary response variables. We also used Spearman correlations to examine the relationships between estimates of *p* and amphibian abundance as well as the elapsed time (hours) between the initial search of a plot and the resampling of the same plot.

RESULTS

The following comparisons were made for each response variable for both the raw data and effect size estimates. We first compare the percent difference among stream reaches (shade level) for the pre-treatment period, then percent differences among stream reaches post-treatment, then percent differences for each reach pre- to post-treatment. For ES estimates, *P*-values from the mixed models are presented for those comparisons as well as for the interaction term.

Canopy Cover: Pre-treatment variation in canopy cover among treatment and reference stream reaches was low (0-5%) with cover estimates, based on the entire densiometer grid, ranging from 92 to 97% (Table 1). Substantial effort ($\geq$ 8 person-days/reach) was required to reach the assigned shade reduction levels based on readings of the middle rows of a densiometer (over the channel and the adjacent riparian area). Reducing vegetation that appeared beyond the middle rows of the densiometer was a secondary objective, resulting in greater cover estimates and greater variation in those estimates because they were based on the entire densiometer view compared to pre-treatment estimates (Table 1). Mean ES estimates for canopy cover were small and relatively consistent pre-treatment, and increased by more than an order of magnitude and were all negative post-treatment (Table 1).

Photosynthetically Active Radiation: Mean PAR estimates varied $\leq$74% (20 μmols/m^2/sec) among reaches pre-treatment (Table 1). Treatments resulted in monotonically increasing amounts of PAR reaching the streams as a function of declining canopy cover, meeting the primary study objective of creating a nearly complete gradient in light levels. Post-treatment mean PAR estimates for the treatment reaches were an order of magnitude greater than pre-treatment estimates. Post-treatment estimates for the no-shade reaches were 34% greater than the low-shade reaches, 155% greater than the intermediate-shade reaches, and 10-fold greater than reference reaches. The low shade treatment had mean PAR estimates 91% greater than the intermediate-shade treatment, and 649% greater than reference reaches. The intermediate-shade treatment had mean estimates 293% greater than the reference reaches. In addition, PAR estimates for reference reaches increased by 43% between pre- and post-treatment periods due to storm blowdown, flooding, and channel meander that effected canopy cover. Nevertheless, this increase in PAR was less than one sixth the magnitude of the smallest post-treatment difference (the intermediate-shade level) between any treatment and the reference.

Pre-treatment mean ES estimates ranged from –10 to 0 (Fig. 3) and contrasts among reaches were not significant (*P* = 0.8-1.0). Post-treatment ES estimates were over two orders

Table 1. Mean(SE) percent canopy cover and photosynthetically active radiation (PAR, μmols/m^2/sec) at stream surfaces along 50-m stream segments for pre- and post-treatment periods (2 years each) and four experimental shade levels for headwater streams in northwest Oregon, southwest Washington, and the Olympic Peninsula, Washington. Sampling occurred during May-October, 2004-2009.

Period and shade level	Canopy cover[a]	ES[b]	PAR
Pre-treatment			
No	97 (1)	2	41 (16)
Low	97 (2)	-1	27 (4)
Intermediate	96 (<1)	-2	47 (14)
Reference	92 (5)		39 (4)
Post-treatment			
No	40 (4)	-53	682 (75)
Low	61 (3)	-33	509 (52)
Intermediate	77 (3)	-18	267 (35)
Reference	97 (2)		68 (9)

[a] estimated with a concave spherical densitometer and includes full view of the densitometer.

[b] treatment minus reference estimates.

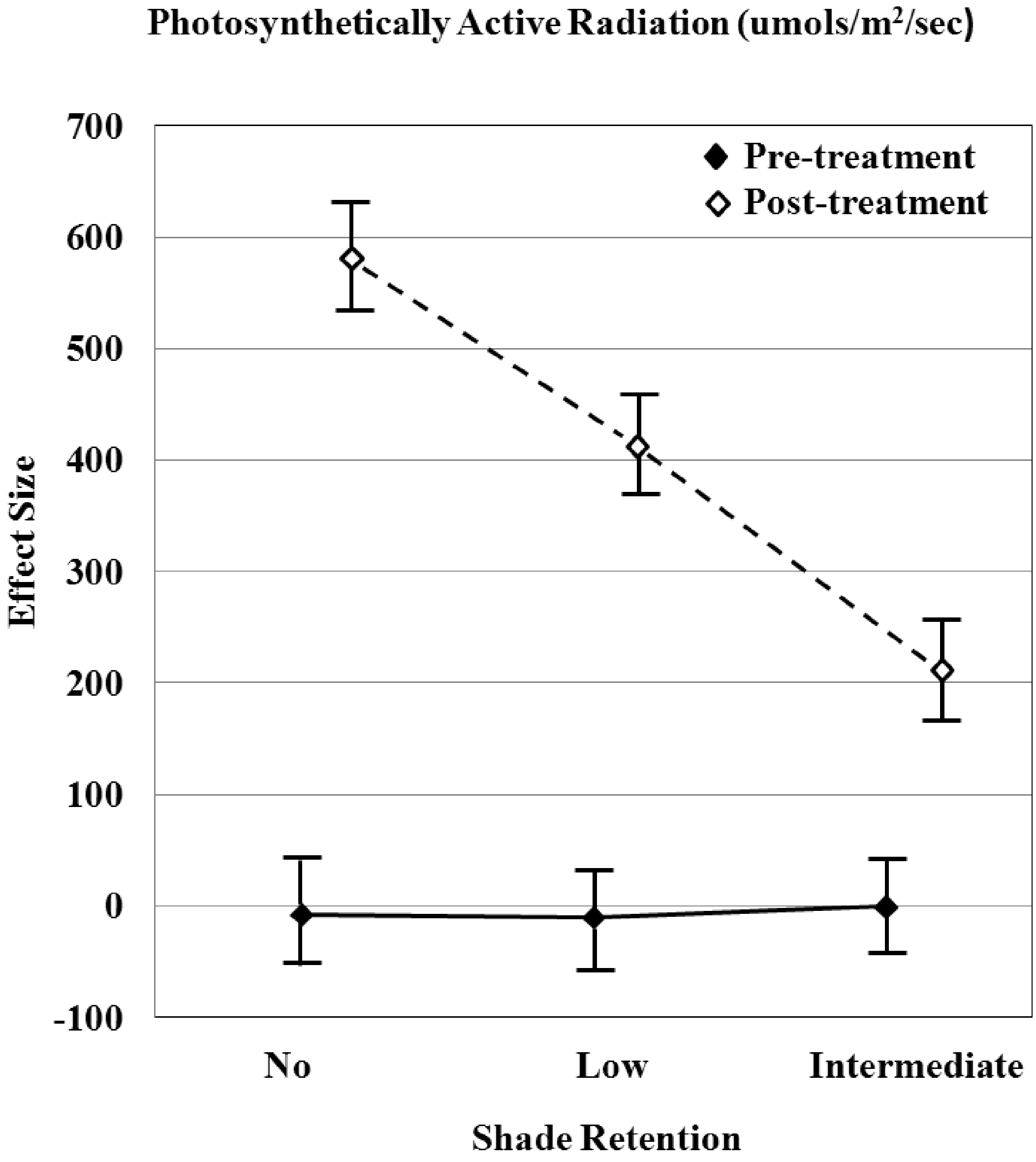


Fig. 3 Mean (SE) effect size (treatment-reference) for estimates of photosynthetically active radiation (umols/m^2/sec) along stream reaches randomly assigned three levels of shade retention for both pre- and post-treatment periods (two years each) for 25 streams in northwest Oregon and western Washington. Sampling occurred from 2004-2009.

of magnitude greater than pre-treatment estimates and all were positive resulting in a significant (*P* = 0.0001) interaction term. Trends in mean ES among reaches post-treatment were similar to those for the raw data and all contrasts were significant (*P* = 0.0001-0.001).

Water temperatures: Prior to treatment implementation, mean maximum daily water temperature and seven-day moving average differed from 0 to 7% across stream reaches and 0 to 15% among enclosures in treatment and reference reaches (Table 2). In stream reaches, we recorded progressive increases in mean maximum (0-24%) and the maximum seven-day moving average (4-22%) pre- to post-treatment with decreasing shade levels (Table 2). In particular, the intermediate-shade level showed the smallest change (<1° C), the low level showed a greater change (2.0-2.5° C), and the no-shade level had the greatest change (3.0-3.5° C). In contrast, in reference reaches, both metrics showed almost no change (≤0.5° C) pre-to-post-treatment in the stream, whereas both decreased 1.0 to 1.5° C in enclosures.

All enclosures in treatment reaches had increases in temperature pre- to post-treatment for both metrics (Table 2). In particular, the no-shade level showed the smallest change (1.5-2.5° C), the low-shade level a larger change (2.0-2.5° C), and the intermediate-shade level had the greatest change (2.5-4.0° C). However, in context of absolute temperature levels, enclosures in the low-shade treatment reaches had water temperatures for both metrics being greater than all other stream treatment reaches in both pre- (1.5-2.0° C) and post-treatment (1.5-2.0° C) years. The low-shade treatment was also higher than reference enclosures for both metrics (<1.0-4.0° C) except for the pre-treatment seasonal maximum where it was identical to the reference.

Mean ES estimates for seasonal maxima ranged from 0.5-0.8 among stream reaches pre-treatment (*P* = 0.60-0.93) and from 0.9-3.6 post-treatment (*P* = 0.0001-0.04). The greatest

Table 2. Mean(SE) maximum water temperature (° C) recorded (MAX) and seven-day moving average maximum daily water temperature (7-DAY) and for streams and enclosures for pre- and post-treatment periods (two years each) at four shade levels for headwater streams in northwest Oregon, southwest Washington, and the Olympic Peninsula, Washington. Temperatures were sampled during June-October, 2004-2009 at one-half hour intervals.

Shade level,	Pre-treatment		Post-treatment	
stream or enclosure	MAX	7-DAY	MAX	7-DAY
No				
Stream	14.5 (0.5)	13.5 (0.5)	18.0 (0.9)	16.5 (0.8)
Enclosure	14.5 (0.4)	13.5 (0.6)	17.0 (1.2)	15.0 (0.8)
Low				
Stream	15.0 (0.7)	14.0 (0.6)	17.0 (0.5)	16.0 (0.4)
Enclosure	16.0 (1.7)	15.0 (1.3)	18.0 (0.8)	17.0 (0.7)
Intermediate				
Stream	15.0 (0.8)	13.5 (0.6)	15.0 (0.6)	14.0 (0.6)
Enclosure	14.0 (0.7)	13.0 (0.5)	18.0 (1.7)	15.0 (0.9)
Reference				
Stream	14.0 (0.3)	13.0 (0.3)	14.0 (0.3)	13.5 (0.3)
Enclosure	16.0 (0.7)	14.0 (0.6)	14.5 (0.5)	13.0 (0.5)

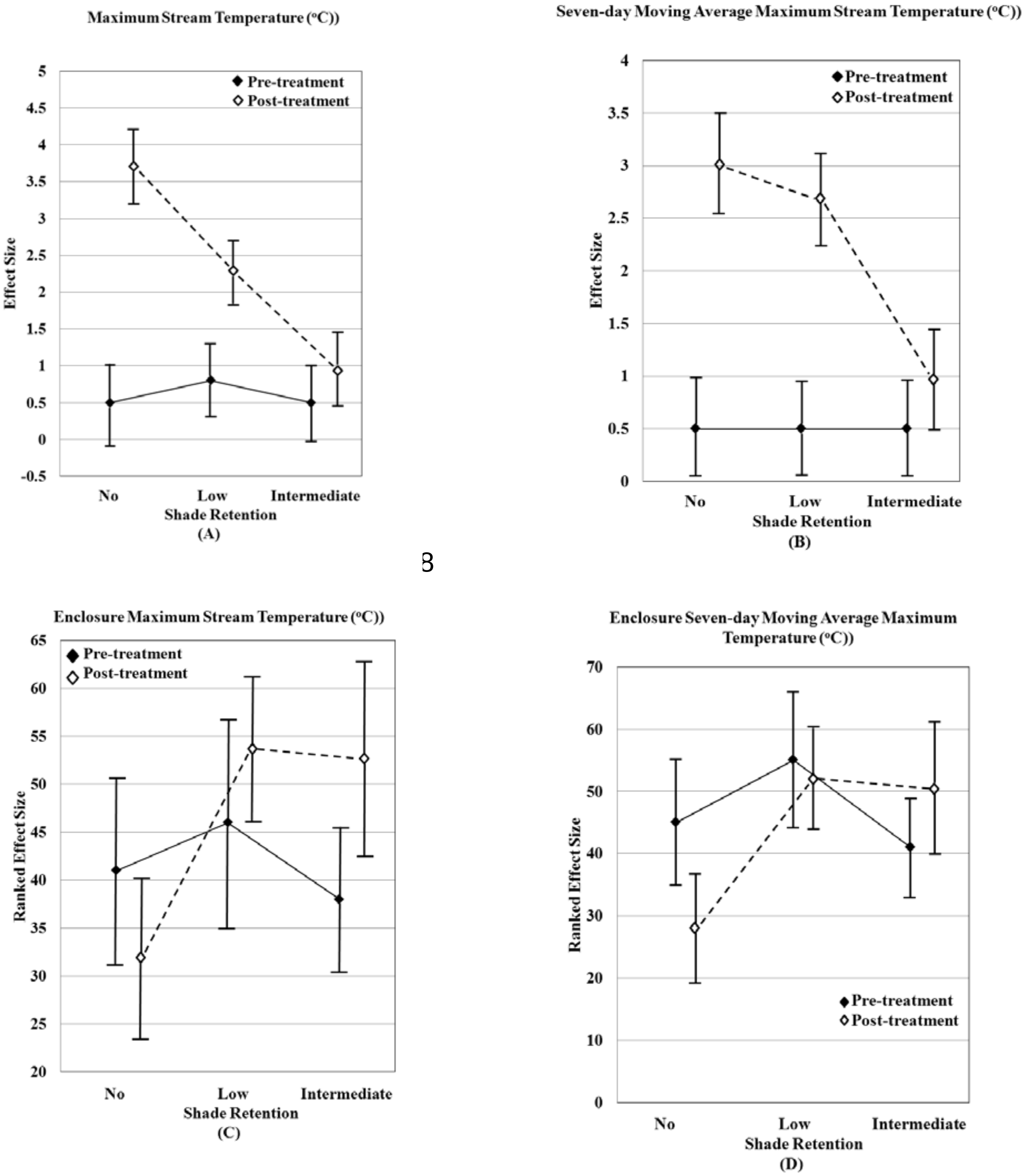


Fig. 4. Mean (SE) raw effect size (treatment-reference) for seasonal maximum water temperature (^{o}C) for stream reaches (A and B, respectively) or enclosures (ranked) in streams (C and D, respectively) randomly assigned to one of three levels of shade retention for both pre- and

post-treatment periods (two years each) for 25 streams in northwest Oregon and western Washington. Sampling occurred from 2004-2009. increases from pre- to post-treatment were in the no- (*P* = 0.0001) and low-shade (*p* = 0.03) reaches (Fig. 4a), which resulted in a significant (*P* = 0.001) interaction term. Trends in ES estimates for the maximum seven-day moving average were very similar to trends in seasonal maximum ES estimates (Fig. 4b), also resulting in a significant (*P* = 0.0001) interaction term.

For enclosures, ES estimates for both measures of water temperature resulted in a funnel-shaped pattern for model residuals. Rank-transformations resulted in better dispersion of the residuals for both metrics. Ranked ES for seasonal maxima differed by 5 to 18% (*P* = 0.56-78) among reaches pre-treatment (Fig. 4c). Post-treatment ranked ES differed by 2 to 69% among treatments with the no-shade reaches mean smaller than thel ow- and intermediate- treatments (*P* = 0.05). Ranked ES estimates declined 28% pre- to post-treatment in the no-shade reaches (*P* = 0.24) but increased 18-39% pre- to post-treatment for the low-and intermediate-shade reaches (*P* = 0.54 and 0.22), respectively, resulting in a significant (*P* = 0.03) interaction term.

Mean ranked ES estimates of the maximum seven-day moving average for the enclosures differed by 10 to 34% pre-treatment (*P* = 0.31-0.80) (Fig. 4d). Post-treatment ranked ES estimates differed by four to 86% (*P* = 0.02-0.88), with the no-shade reaches lower than both the low-and intermediate- reaches (*P* = 0.02, 0.07, respectively). These trends resulted in an interaction term with a *P*-value of 0.11.

In summary, maximum stream temperatures responded to different levels of shade retention in an approximately negative linear fashion. Overall, temperatures increased 0.0 to 4.0 °C in the enclosures and slightly less (0.0-3.5°C) outside of enclosures. In stream reaches, maximum seven-day moving average temperatures exceeded 16.0° C in the no- and low-shade treatments. Maximum water temperature changes in the enclosures were more variable and greater than reach temperatures, non-parallel during both periods, and did not track any pattern relative to shade levels, generally being greatest in both low-and intermediate-shaded reaches, post-treatment.

Periphyton accrual: Pre-treatment mean estimates of periphyton accrual (g AFDM/m^2) among the different shade levels differed by 3 to 21%; treatment implementation increased variability as differences among reaches were 18 to 105% (Table 3). Periphyton accrual increased in all treatment reaches by 2 to 105% (greatest in no-shade reaches, least in low-reaches) pre- to post-treatment, but declined by 13% in references reaches. Post-treatment estimates differed by only four percent between the low-and intermediate-shade retention reaches. Mean periphyton accrual in the enclosures varied by 2 to 35% pre-treatment and 1 to 84% post-treatment, increasing in all reaches, most notably at the no- and intermediate-shade levels (Table 3).

Raw ES estimates produced a strong funnel-shaped pattern in model residuals (heteroskedasticity) for both stream and enclosure estimates, which improved following rank-order transformation. Mean ranked ES for streams differed by 2 to 30% pre-treatment and mean ranked ES for the no-shade reaches was greater ($P = 0.05$) than that for the references (Fig. 5). Differences in ranked ES among stream reaches post-treatment ranged from 1 to 23% ($P =$ 0.0001-0.96) with the largest differences between the no-shade and low-and intermediate- levels; however, the interaction term was not significant ($P = 0.23$). Ranked ES exhibited similar increases in the enclosures in all reaches from pre- to post-treatment periods, except for the intermediate- reaches where ranked ES declined by 5% (Fig. 5a).

Patterns of periphyton accrual on tiles in the enclosures followed the same general trends as those in the streams, pre-treatment (Table 3). However, post-treatment, tiles in the enclosures tended to have a larger amount of periphyton (24-123%) than tiles in the stream (Table 3).

Table 3. Mean(SE) periphyton accumulation (g ash-free dry mass/m^2) and on unglazed quarry tiles along 50-m stream segments and amphibian enclosures for pre- and post-treatment periods (2 years each) and four experimental shade levels for headwater streams in northwest Oregon, southwest Washington, and the Olympic Peninsula, Washington. Streams were sampled during May-October, 2004-2009.

Period and shade level	Stream	Enclosure
Pre-treatment		
No	0.39 (0.15)	0.46 (0.18)
Low	0.47 (0.14)	0.54 (0.21)
Intermediate	0.40 (0.15)	0.40 (0.15)
Reference	0.44 (0.13)	0.45 (0.11)
Post-treatment		
No	0.80 (0.32)	1.03 (0.44)
Low	0.48 (0.17)	0.68 (0.16)
Intermediate	0.46 (0.14)	0.67 (0.22)
Reference	0.39 (0.12)	0.56 (0.13)

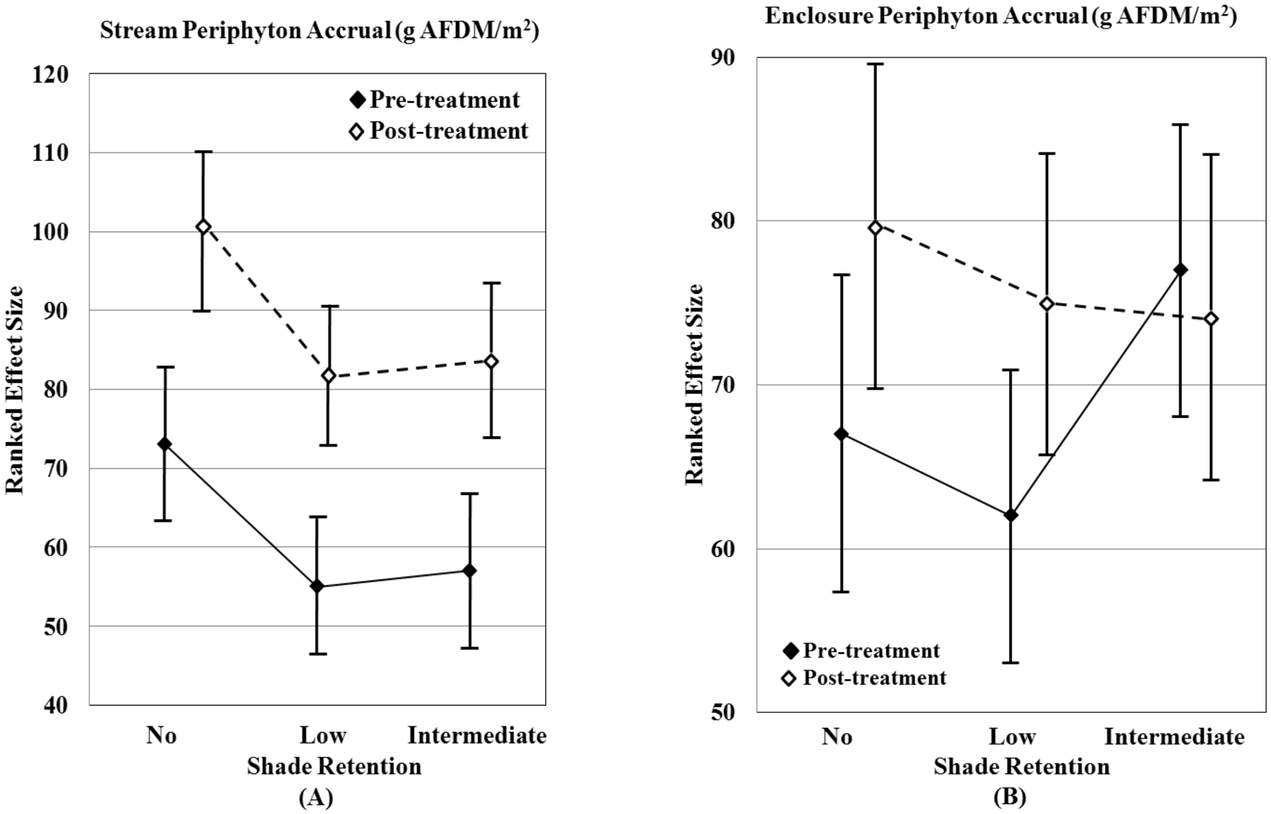


Fig. 5. Mean (SE) ranked effect size (treatment-reference) for estimates of periphyton accrual (g ash-free dry mass/m^2) on tiles placed in stream reaches (A) or enclosures in streams (B) randomly assigned to one of three levels of shade retention for both pre- and post-treatment periods (two years each) for 25 streams in northwest Oregon and western Washington. Sampling occurred from 2004-2009.

Ranked ES estimates of periphyton on the tiles in the enclosures differed (*P* = 0.70-0.26) by 8 to 24% pre-treatment, but only 1 to 8% post-treatment (*P* = 0.97-0.66) (Fig. 5b). Pre- to post-treatment, ranked ES increased 18% and 19% in the no- (*P* = 0.38) and low- (*P* = 0.37) shade reaches, respectively, but declined by 5% (*P* = 0.79) in the intermediate- reaches (Fig. 5b). The interaction term was not significant (*P* = 0.78).

Stream drift: The mass of the various components of stream drift (CPOM, FPOM, aquatic macroinvertebrates) and associated ES estimates were highly variable. The data contained outliers resulting in heteroskedasticity in model residuals. Raw effect sizes were rank-transformed for analysis, which improved the dispersion of model residuals.

CPOM: In general, mean CPOM drift (kg/m^3) differed among reaches by 5 to 179% pre-treatment which increased to 179 to 564% post-treatment (Table 4). In contrast, mean mass of CPOM/day varied by 0 to 17% among reaches pre-treatment, whereas post-treatment differences ranged from 50 to 917%. CPOM declined 329 to 400% in the no- shade reaches for both metrics, pre- to post- treatment, but increased 79% in the low-and 19,690% in the reference reaches when quantified by m^3 of flow. In contrast, when quantified as g/day, CPOM also declined (100-200%) in the low-and intermediate- reaches, but increased by 13,014% in the reference reaches.

The interaction term for mean ranked ES of kg CPOM/m^3 was insignificant (*P* = 0.19). Mean ES estimates varied 0 to 9% (*P* = 0.38-0.98) pre-treatment. Drift of CPOM was 2 to 22% lower (*P* = 0.16-0.12) in the no-shade reaches than the low-and intermediate- reaches post-treatment, respectively, and declined 4 to 38% pre- to post-treatment with the largest decline (*P* = 0.008) in

Table 4. Mean(SE) mass or counts of stream drift components (detritus and macroinvertebrate functional class) per m^3 of stream flow and per day (24 h) for pre- and post-treatment periods (2 years each) at four shade levels for headwater streams in northwest Oregon, southwest Washington, and the Olympic Peninsula, Washington. Streams were sampled during May-September 2004-2009.

	Pre-treatment Shade level				Post-treatment Shade level			
Drift Component	No	Low	Intermediate	Reference	No	Low	Intermediate	Reference
Detritus								
$CPOM^b/m^3$ (kg)	31 (19)	19 (7)	53 (41)	20 (7)	7 (2)	34 (10)	19 (2)	3958 (3935)
$CPOM^b$/ day (kg)	6 (3)	6 (3)	6 (3)	7 (4)	1 (<1)	3 (<1)	2 (1)	918 (915)
$FPOM^c/m^3$ (kg)	40 (34)	9 (3)	147 (138)	20 (15)	7 (3)	16 (9)	14 (8)	10 (3)
FPOM/day (g)	3 (2)	2 (1)	8 (7)	13 (12)	1 (<1)	1 (<1)	1 (1)	1 (<1)
Macroinvertebrate Functional Class								
Scrapers/m^3 (g)	39 (30)	26 (8)	43 (24)	46 (23)	11 (4)	54 (19)	37 (18)	22 (6)
Scrapers/day (mg)	35 (13)	83 (32)	77 (44)	125 (62)	23 (9)	63 (26)	70 (44)	44 (6)
Shredders/m^3 (g)	24 (8)	50 (36)	58 (43)	52 (19)	6 (3)	28 (9)	43 (12)	18 (4)
Shredders/day (mg)	45 (9)	34 (14)	33 (9)	66 (26)	13 (5)	46 (21)	25 (6)	20 (4)
Filterers/m^3 (g)	7 (4)	7 (2)	10 (7)	6 (2)	6 (2)	32 (15)	3 (1)	6 (1)
Filterers/day (mg)	20 (13)	17 (6)	9 (4)	13 (5)	13 (4)	49 (18)	5 (2)	12 (5)

Table 4. Continued.

Gatherers/m^3 (g)	23 (8)	5 (1)	11 (3)	10 (1)	23 (6)	47 (30)	38 (20)	20 (10)
Gatherers/day (mg)	53 (17)	13 (5)	17 (8)	23 (6)	33 (9)	129 (111)	46 (26)	15 (2)
Predators/m^3 (g)	233 (155)	105 (50)	62 (26)	46 (23)	16 (6)	36 (8)	26 (11)	30 (8)
Predators/day (mg)	212 (<1)	197 (<1)	165 (<1)	131 (<1)	22 (8)	26 (5)	23 (7)	33 (10)
Total/m^3 (g)	346 (204)	201 (71)	198 (51)	173 (50)	98 (33)	208 (57)	154 (38)	108 (11)
Total/day (mg)	390 (165)	359 (188)	17 (152)	93 (102)	175 (69)	25 (170)	73 (30)	58 (28)
Total Count/m^{3}x10^3	46 (22)	47 (26)	25 (12)	63 (34)	287 (148)	269 (111)	123 (18)	183 (40)
Total Count/day	10 (2)	7 (2)	5 (2)	8 (2)	117 (54)	105 (62)	102 (60)	88 (46)

[b] coarse particulate organic matter; leaves, needles, twigs, wood, stems, etc. between >2mm.

[c] fine particulate organic matter, <2mm and > 250

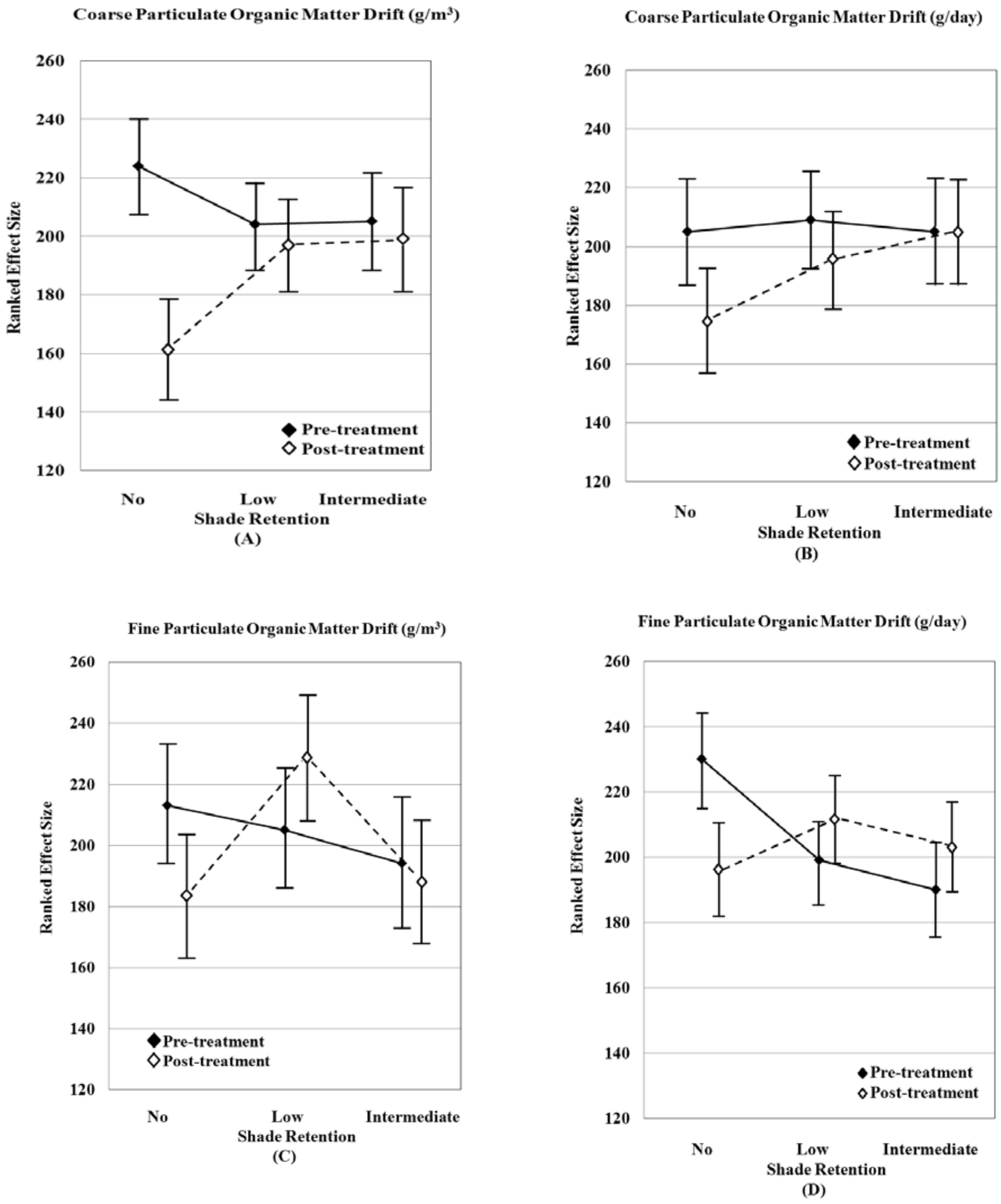
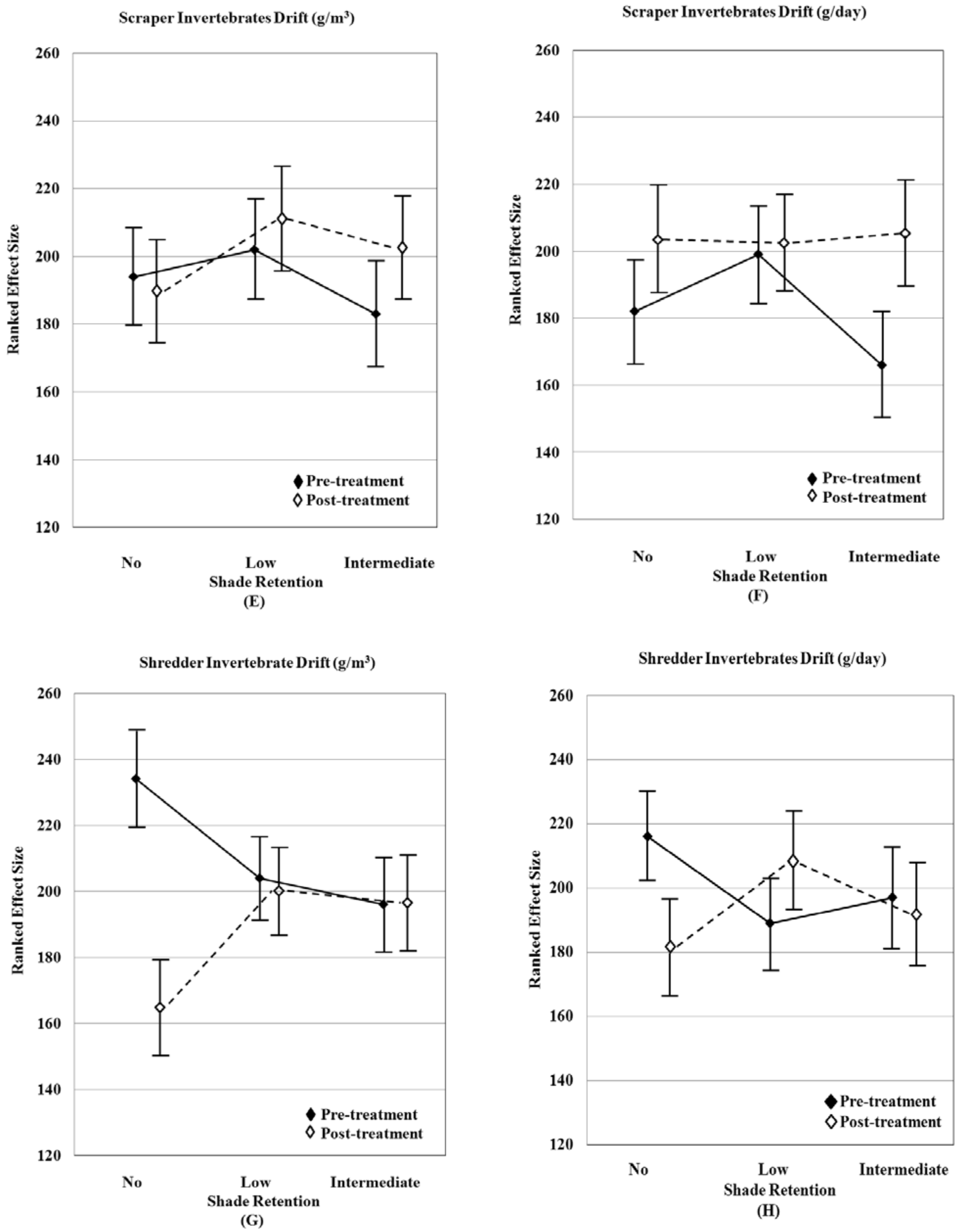


Fig. 6. Mean (SE) ranked effect size (treatment-reference) for drift components (coarse particulate organic matter [A, B], fine particulate organic matter [C, D] and aquatic macroinvertebrate functional classes [E-R]) quantified as g/m^3 of flow, g/day, and counts for stream reaches randomly assigned to one of three levels of shade retention for both pre- and post-treatment periods (two years each) for 25 streams in northwest Oregon and western Washington. Sampling occurred from 2004-2009.



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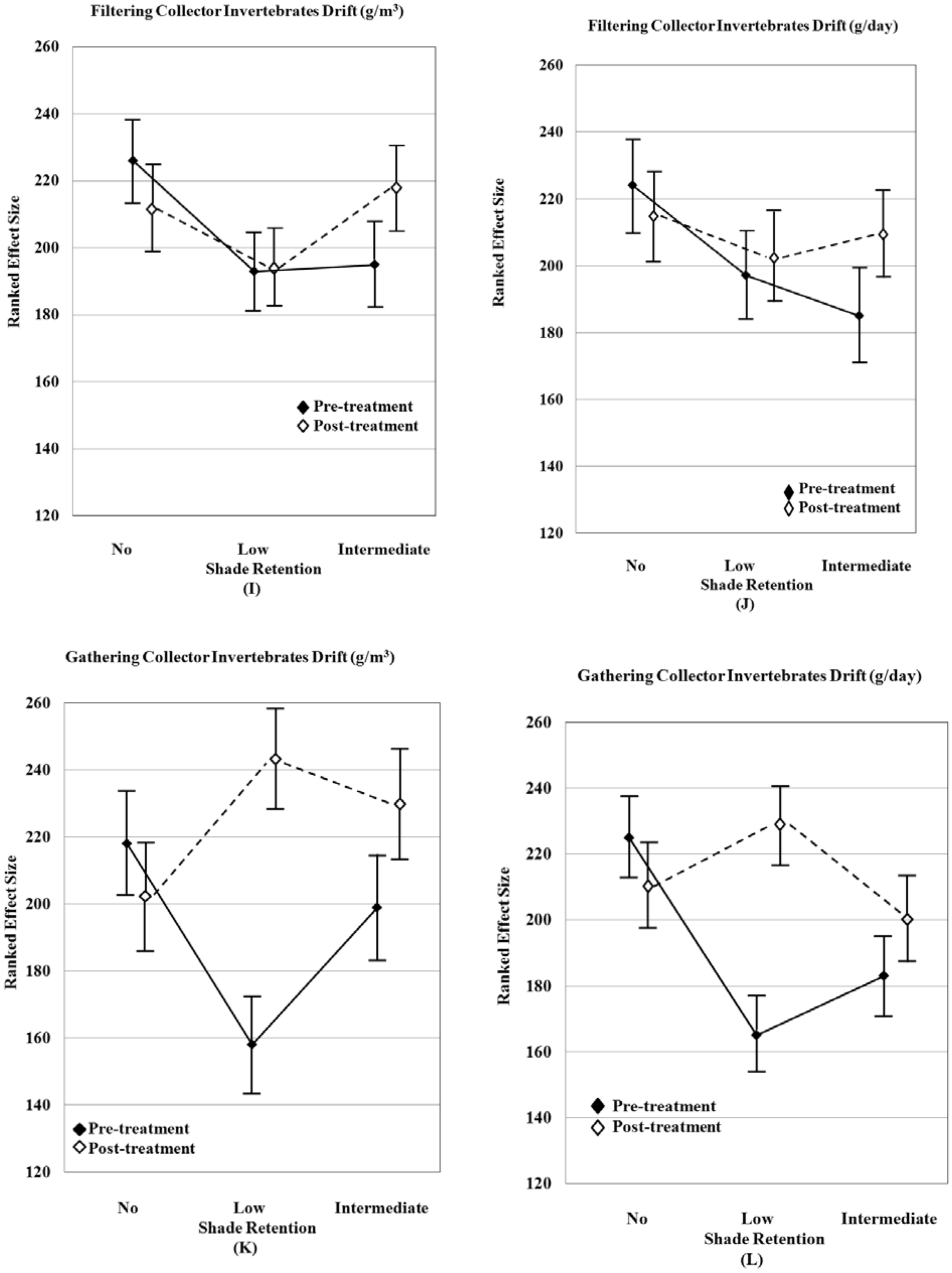

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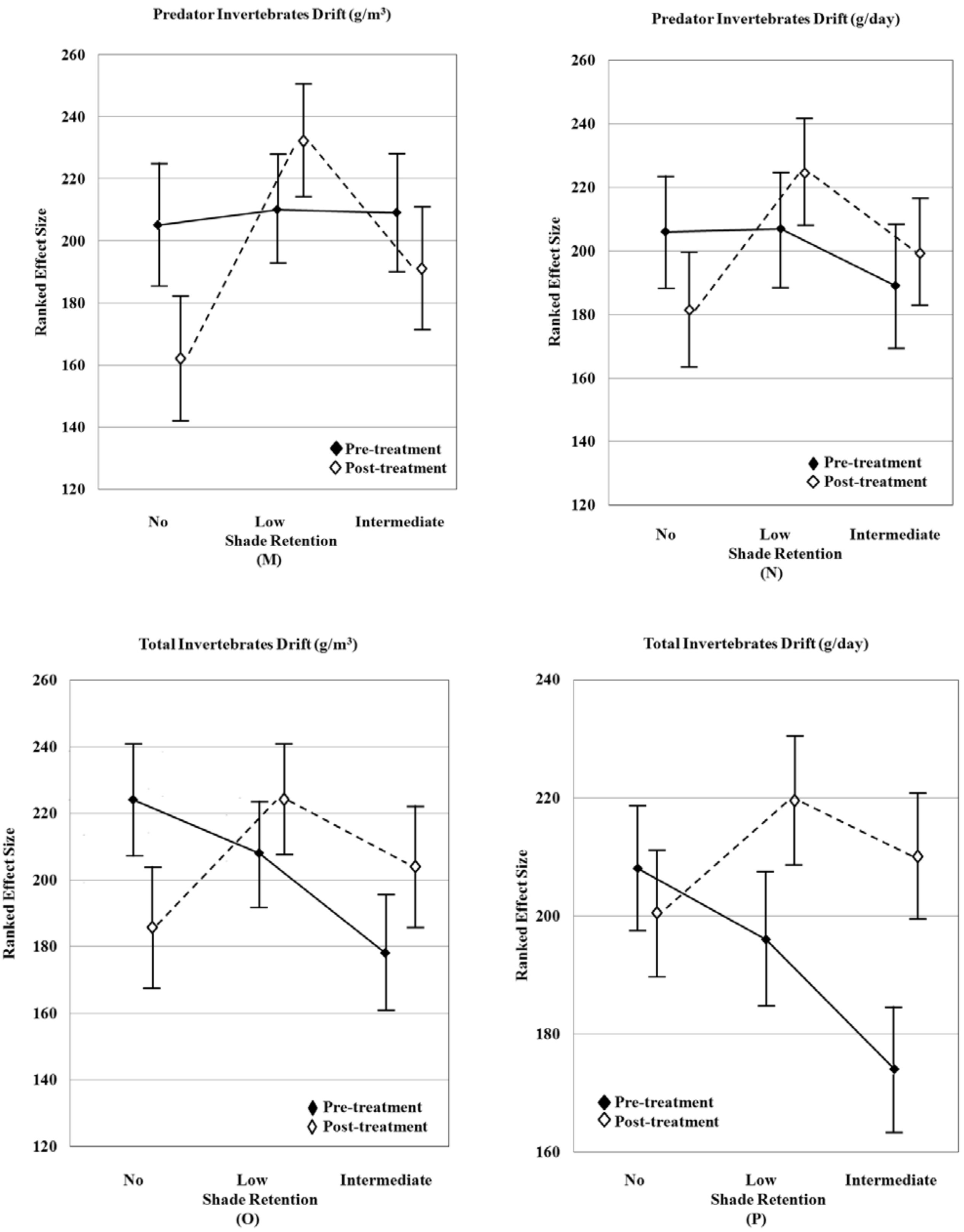

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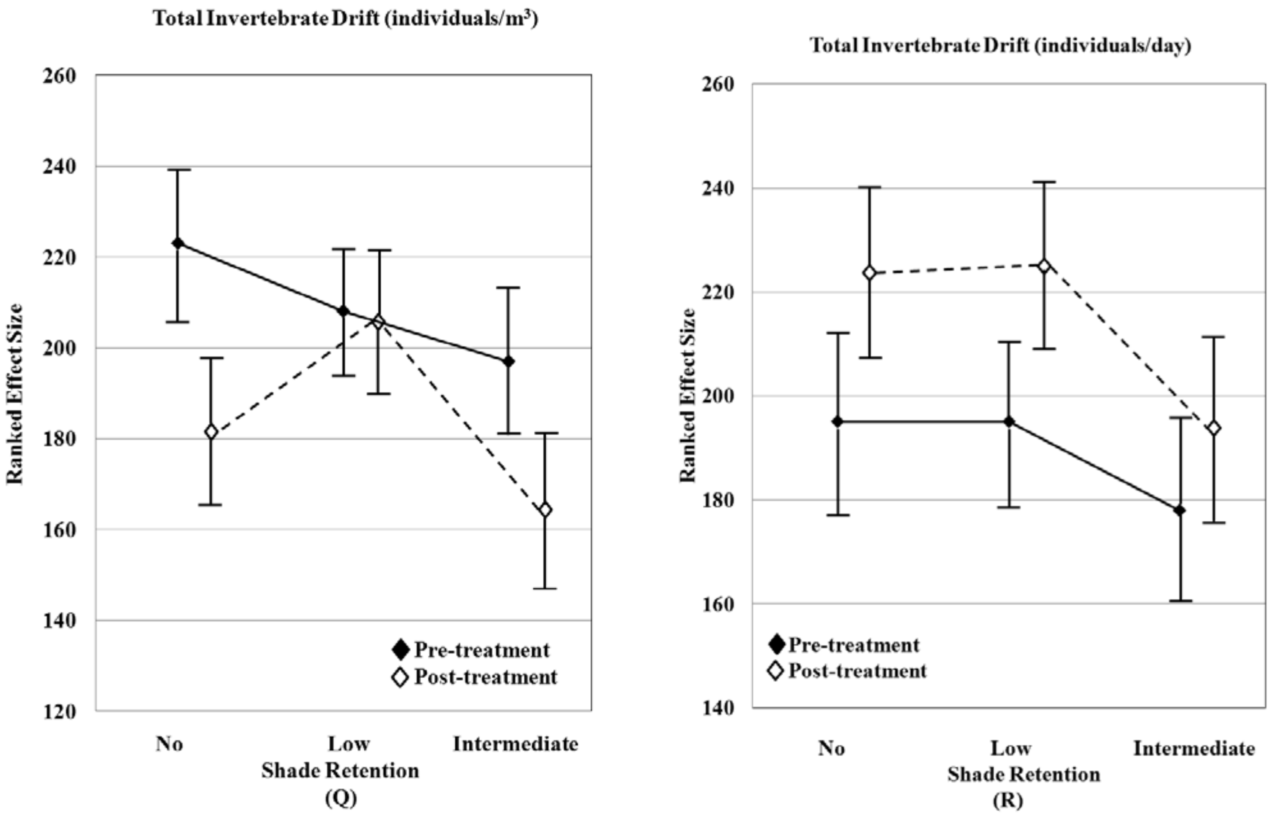

Fig. 6. Continued.

the no-shade reaches followed by the low- (*P* = 0.65) and intermediate- (*P* = 0.78) reaches (Fig. 6a). Mean ES of g CPOM/day followed the same patterns as kg CPOM/m^3, but the differences were not as large and the interaction term was not significant (*P* = 0.75).

<u>FPOM</u>: Trends in drift of FPOM (kg/m^3 or g/day) differed among reaches pre-treatment 50 to 1533%, but only 0 to 129%, post-treatment (Table 4). Pre- to post-treatment declines in FPOM (kg/m^3) occurred in the no-shade (471%), intermediate- (950%), and reference (100%); but increased 78% in the low-shade reaches. FPOM (g/day) declined 100 to 1200% in all reaches pre- to post treatment, with the greatest declines in the reference and intermediate-shade reaches, respectively.

Mean ranked ES for kg/m^3 varied 4 to 10% (*P* = 0.42-0.72) among reaches pre-treatment and 2 to 24% (*P* = 0.05-0.86) post-treatment with trends mirroring those of raw kg/m^3 estimates (Fig. 6b). The interaction term for this metric was not significant (*P* = 0.43). However, mean ES for g/day of FPOM increased in the low-and intermediate- reaches by 7% and 8%, respectively from pre- to post-treatment periods (*P* = 0.53 and 0.50, respectively)and declined in the no-shade reach by 17% (*P* = 0.16).

In summary, drift levels were highly variable, with estimates based on mass/m^3 of flow more variable than estimates based on g/day, particularly post-treatment. Inputs of allochtonous materials to streams as measured by drift appeared to decline in the no-shade reaches following shade reductions, but the non-significant interactions make this pattern ambiguous. Drift quantification based on flow and g/day did not always agree in direction (+, –) of change.

Macroinvertebrate drift: Macroinvertebrate drift among periods, treatments, and metrics was also highly variable even when taxa were combined by functional class (Table 4, Fig. 6e-r).

***Scrapers*:** Drift (g/m^3) of scrapers differed 7 to 77% pre-treatment and 46 to 391% post-treatment, declining in all reaches pre- to post-treatment (16-255%), except the low-shade reaches (108% increase, Table 4). Quantified as mg/day, mean drift of scrapers differed by 8 to 257% pre-treatment and 11 to 204% post-treatment across reaches and declined (10-184%) in all reaches pre- to post-treatment.

Mean ranked ES of scrapers (g/m^3) differed 4 to 10% among all reaches pre-treatment ($P = 0.42$-0.73) and 4 to 9% ($P = 0.43$-0.72) post-treatment (Fig. 6e). Mean ES based on g/m^3 increased 4% ($P = 0.69$) in the low-shade reaches and 11% ($P = 0.42$) in the intermediate reaches pre- to post-treatment, but declined <1% in the no-shade reaches ($P = 0.96$), resulting- in a non-significant ($P = 0.91$) interaction term. In contrast, when quantified as mg/day, (Fig. 6f) ES increased 2 to 24% for all reaches and was greatest in intermediate- reaches ($P = 0.09$) and smallest in the low-shade reaches ($p = 0.85$) also resulting in a non-significant interaction term ($P = 0.56$).

Overall, raw estimates of the mass of scrapers declined in all treatments except for the low-shade level (g/m^3), and declines were greatest in the no-shade treatment, but the non-significant interaction terms indicate that these changes are not driven by the treatments alone. Scrapers also declined in the references at levels greater than or equal to the no-shade treatment. After accounting for the post-treatment decline in reference reaches, ES estimates increased in all treatments except at the no-shade level (g/m^3). Again, the non-significant interaction term reveals little linkage to treatments.

***<u>Shredders</u>*:** Drift (g/m^3) of shredders differed among reaches by 4-142% pre-treatment, and was greatest in the intermediate-shade and reference reaches. Drift of shredders post-treatment differed among reaches by 56-616% and was also greatest in the intermediate- reaches. Shredders (g/m^3) declined by 35-300% pre- to post-treatment, the decline being greatest in the no-shade and reference reaches (Table 4). Shredder drift (mg/day) differed by 3-100% among reaches and was greatest in the reference and no-shade reaches, pre-treatment. Post-treatment estimates differed by 25-254% among reaches and were greatest in the intermediate- and low-shade reaches. Shredder drift as mg/day varied by 32-230% from pre- to post-treatment periods, and with the greatest declines in the no-shade and reference reaches (Table 4).

Mean ranked ES (g/m^3) of shredder drift differed by 4-19% (P = 0.10-0.72) among reaches pre-treatment and 2-21% (P = 0.12-0.89) post-treatment (Fig. 6g). Shredder drift (g/m^3) declined pre- to post-treatment about 42% (P = 0.003) in the no-shade reaches, but changed little at the other shade levels (-2 to <1%, P = 0.87-0.96), resulting in a significant interaction term (P = 0.09). Mean ES based on g/day (Fig. 6h) of shredders followed similar patterns when contrasting reaches (pre- and post- values ranged from 4-14% differences, P = 0.25-0.70). Pre- to post-treatment ES estimates declined 18% and 2% in the no- (P = 0.16) and intermediate- (P = 0.85) shade reaches, respectively, and increased 10% in the low-shade reaches (P = 0.41). In contrast to the g/m^3 metric, the interaction term was not significant (P = 0.46).

In summary, drift of shredders differed more among reaches post- than pre-treatment for both metrics and declined from pre- to post-treatment periods at the lowest levels of shade retention. Ranked ES estimates were less variable among reaches during both pre- and post-treatment periods for both metrics and declined the most in the no-shade reaches.

Filtering collectors: Average g/m^3 of drift of filtering collectors (filterers) differed by 0 to 67% among reaches pre-treatment, and 0 to 967% post-treatment (Table 4). Mean g/m^3 of filterers did not change in the reference reaches and declined by 17% in the no-shade reaches, but increased by 357% in the low- reaches and declined by 233% in the intermediate- reaches pre- to post-treatment.

Mean mg/day of filterers differed 18 to 54% among reaches pre-treatment, and 8 to 880% post-treatment, and followed similar patterns as g/m^3 in terms of relative magnitude and direction of change between periods. In general, mass of filterers for both metrics declined pre- to post-treatment, except in the low-shade reaches where increases occurred.

Mean ranked ES for g/m^3 of filterers differed 1 to 18% pre-treatment (P = 0.10-0.90) with the no-shade reaches smaller than both the low- and intermediate- reaches (Fig. 6i). Mean ES varied 3 to 13% across reaches post-treatment (P = 0.27-0.76) (Table 4). Mean ES of g/m^3 declined 2-9% pre- to post-treatment (P = 0.90-0.46) in the low- and no-shade reaches, respectively, but increased (P = 0.40) 10% in the intermediate- reaches. The interaction term was not significant (P = 0.72).

The interaction term was also not significant (P = 0.66) for the ES analysis based on mg/day of filterers. Mean ES differed (P = 0.10-0.88) 6 to 21% among reaches pre-treatment with the greatest difference between the no-shade and intermediate- reaches (Fig. 6h). In contrast, ES estimates differed by only 1 to 6% post-treatment (P = 0.20-0.92), but increased pre- to post-treatment by 2% (P = 0.86) and 16% (P = 0.23) in the low- and intermediate-shade reaches, respectively, but declined 6% (P = 0.60) in the no-shade reaches.

In summary, relatively large differences existed in the drift of filterers among some reaches pre-treatment. Changes in filterer abundance due to shade reductions were relatively small and inconsistent among shade levels, metrics (g/m^3 or mg/day), and data (raw or ES).

__Gathering collectors__**:** Drift (g/m^3) of gathering collectors (gatherers) differed 10 to 360% among reaches, pre-treatment and 15 to 135%, post-treatment; increased pre- to post-treatment in the low- (840%), intermediate- (245%), and reference reaches (100%), but did not change in the no-shade reaches (Table 4). Gatherer estimates, quantified as mg/day, differed 31 to 308% among reaches pre-treatment and 39 to 760% post-treatment. Pre- and post-treatment comparisons mirrored trends in g/m^3, with increases of 892% in the low- reaches and 171% in the intermediate- reaches, but declines of 61% and 53% in the no-shade and reference reaches, respectively.

Mean ranked ES (g/m^3) of gatherers differed 11 to 36% pre-treatment ($P = 0.008$-0.41) with the largest difference between the no-and low-shade reaches. Post-treatment variation was relatively less (6-19%, $P = 0.09$-0.56), and mean ES increased ($P = 0.0001$-0.19) by 54% and 16% in the low- and intermediate-shaded reaches, respectively, pre- to post-treatment, and declined by 7% in the no-shade reaches ($P = 0.54$) (Fig. 6k), resulting in a significant interaction term ($P = 0.008$). The same pattern (Fig. 6l) was observed for mass of gatherers/day (interaction term, $P = 0.06$).

In summary, gatherer abundance differed among reaches pre-treatment and displayed large increases following shade reductions at the low- and intermediate-shade levels. Both metrics and data types resulted in similar patterns.

__Predators__**:** Drift of predators expressed as g/m^3 of flow differed 35 to 456% pre-treatment and 15 to 125% post-treatment and declined pre- to post-treatment in all reaches 53 to

1,356%; most notably at the no-and low-shade levels (Table 4). Drift of predators in mg/day was relatively more uniform among the reaches for both pre-and post-treatment periods, and declined by approximately an order of magnitude in all reaches.

Mean ranked ES based on g/m^3 of flow differed by <1-2% among reaches pre-treatment (P = 0.81-0.95) and 18 to 43% (P = 0.002-0.18) post-treatment with the mean ES estimate greatest for the low- reaches (Fig. 6m). ES based on g/m^3 declined pre- to post-treatment 8 to 26% (P = 0.53, 0.08) in the intermediate- and no-shade reaches, respectively, but increased 11% (P = 0.32) in the low-shade reaches. These trends resulted in a non-significant (P = 0.22) interaction term. Ranked ES based on mg/day followed a similar pattern (Fig. 6n), but also increased pre- to post-treatment for intermediate-shade reaches (5%, P = 0.70). The interaction term for mg/day was also not significant (P = 0.59).

Overall, shade reductions reduced predator abundance with the largest declines occurring in the no-shade reaches, but the non-significant interaction indicates little effect of the treatments. Mean ranked ES estimates increased slightly at moderate light levels for all metrics except for g/m^3 at the intermediate-shade level, but the basis of this pattern is unclear.

***Total macroinvertebrates*:** Mean drift (g/m^3) of all macroinvertebrates combined differed 2 to 100% among reaches pre-treatment being greatest in the no-shade reaches and differed 10 to 112%, post-treatment with the greatest estimates in the low- and intermediate- reaches (Table 4). Total drift (g/m^3) declined 29 to 253% from pre- to post-treatment periods in all reaches but the low-shade reaches where it increased 3%. Pre-treatment total mg/day of macroinvertebrate drift differed by 8 to 33% with progressively smaller estimates from the no-shade to reference reaches. In contrast, differences among reaches ranged from 1 to 106% post-treatment with the largest estimates in the no-shade, followed in declining order by intermediate, reference, and low-shade reaches. Pre- to post-treatment declines of 10 to 123% occurred across all reaches with the largest declines seen in the low-shade treatments.

Mean ranked ES for total drift (g/m^3) differed 8 to 26% pre-treatment ($P = 0.05$-0.48), with the no-shade reaches greater than the other reaches (Fig. 6o). Post-treatment ES based on g/m^3 differed 8 to 21% among reaches ($P = 0.09$-0.45) with the low-shade reaches greater than other reaches. A pre- to post-treatment decline of 21% occurred in the no-shade reaches ($P = 0.12$), but increases of 8 to 16% occurred in the other reaches ($P = 0.24$-0.50), resulting in a non-significant interaction term ($P = 0.20$). Trends in ES for mg/day of total macroinvertebrate drift differed 6 to 20% pre-treatment ($P = 0.16$-0.60), declining progressively from the no-shade treatment (Fig. 6p). Post-treatment ES varied 4 to 8% across all shade levels ($P = 0.38$-0.73), being greatest in the low- and intermediate- reaches. Pre- to post-treatment ES declined in the no-shade reaches (3%, $P = 0.78$), but increased 11 to 21% ($P = 0.14$-0.34) in the other reaches, resulting in a non-significant interaction term ($P = 0.55$, Table 4).

Counts of individual macroinvertebrates/m^3 of flow varied from 25,000 to 63,000 (2-152%) among reaches, pre-treatment and was largest in the reference reaches followed by the low, no-and intermediate-shade reaches (Table 4). Post-treatment, counts differed 7 to 133% among reaches and were greatest in the no-shade reaches followed by the low, reference, and then the intermediate- reaches. Counts increased inversely with the amount of shade reduced from pre- to post-treatment periods from 190 to 524%. Counts of individual macroinvertebrates captured/day varied 14 to 100% among reaches, pre-treatment, and were greatest for the no-shade reaches (Table 4). Post-treatment totals varied 3 to 33% with the no-shade reaches maintaining the greatest counts. Pre- to post-treatment differences ranged from 1000 to 1940%, with all reaches including the reference having large increases.

Mean ranked ES for total number of macroinvertebrates/m^3 of flow differed 6 to 13% among reaches pre-treatment (*P* = 0.26-0.63) and 10 to 24% post-treatment (*P* = 0.07-0.46) with the ES estimate for low-shade reaches greater than the intermediate- reaches (Fig. 6q). Pre-to post-treatment estimates decreased from 1 to 23% with the largest decline in the no-shade reaches (*P* = 0.08) followed by the intermediate- reaches (*P* = 0.17), resulting in a non-significant (*P* = 0.47) interaction term. Trends in mean ranked ES for numbers of individuals/day (Fig. 6r) followed similar patterns except that pre- to post-treatment estimates increased 9 to 16% for all reaches with the greatest increase (*P* = 0.16) in the low- reaches followed by the no-shade reaches (*P* = 0.22). The interaction term was also not significant (*P* = 0.82).

In summary, macroinvertebrate abundance by functional class or totals was highly variable pre- and post-treatment. In general, estimates based on stream flow were more variable than estimates of amount/day. Overall, macroinvertebrate response to the treatments was limited and inconsistent in direction. However, gatherers increased with reduced shade, particularly at low-shade retention, but shredders decreased with reduced shade, particularly at the no-shade level. Significant interaction terms for gatherers and shredders indicate that those changes are attributable to treatments; interaction terms for overall macroinvertebrates and all other groups were not significant. In general, the largest responses to treatments occurred in the no-and low-shade retention levels, but was negative and positive, respectively. Mean ES estimates did not follow the same trend as the raw data, largely due to simultaneous changes in reference reaches.

Amphibian detection probability and counts: Detection probabilities (*p*) ranged from 0.65 to 1.00 (Table 5). There was no-significant interaction among *p* estimates for any species.

Table 5. Mean(SE) probability of detecting stream associated amphibians sampled in 2-m long in-stream plots for pre- and post-treatment periods (2 years each) and four experimental shade levels for headwater streams in northwest Oregon, southwest Washington, and the Olympic Peninsula, Washington. Streams were sampled during July-September 2004-2009.

	Pre-treatment				Post-treatment				
	Shade level				Shade level				
Species	No	Low	Intermediate	Reference	No	Low	Intermediate	Reference	Mean[a]
Ascaphus truei	0.82(0.14)	0.65(0.11)$^{\psi,\pi,\varphi,\tau,\omega}$	0.87(0.13)$^{\psi}$	0.83(0.11)$^{\pi}$	0.87(0.11)$^{\varphi}$	0.92(0.11)$^{\tau}$	0.82(0.12)	0.93(0.09)$^{\omega}$	0.87(0.02)
Dicamptodon spp.	0.94(0.09)$^{\psi}$	0.95(0.10)	0.72(0.10)$^{\psi,\pi,\varphi}$	0.92(0.07)$^{\varsigma}$	0.92(0.11)$^{\varphi,\tau}$	0.76(0.08) $^{\pi,\varsigma,\tau,\omega}$	0.85(0.08)	0.88(0.06)$^{\omega}$	0.91(0.01)
Rhyacotriton cascadae	1.00(0.00)	1.00(0.14)	no data	0.78(0.05)	1.00(0.07)$^{\psi}$	1.00(0.10)	0.79(0.08)$^{\psi,\pi}$	0.96(0.05)$^{\pi}$	0.99(0.01)
R. kezeri	no data	no data	0.83(0.2)	1.00(0.19)	1.00(0.08)	1.00(0.10)	1.00(0.10)	0.83(0.07)	0.97(0.03)
R. olympicus	1.00(0.21)	0.90(0.13)	1.00(0.17)	0.77(0.12)	no data	no data	0.98(0.28)	0.88(0.23)	0.92(0.04)

[a] Average of estimates that did not differ from each other.

Estimates followed by the same symbol were significantly different ($P \leq 0.1$).

However, there were some large differences in estimates for tailed frogs, giant salamanders, and Cascade torrent salamanders in both pre- and post-treatment periods. For tailed frogs, the estimate for the low-shade reaches pre-treatment was 28 to 43% smaller (*P* = 0.004-0.07) than the intermediate- and reference reaches pre-treatment, respectively, and the no-shade, low, and references reaches post-treatment. Differences for giant salamanders between reaches (*P* = 0.05-0.09) were due to the lower estimates for the intermediate- reaches pre-treatment and the low-reaches, post-treatment. In contrast, the *p* estimate for Cascade torrent salamanders was lower (*P* = 0.07- 0.09) for the intermediate- reaches compared to the no-shade and references reaches post-treatment. No differences in *p* were found for the other taxa.

Given the differences in *p* described above, we adjusted counts for tailed frogs in thel ow-shade reaches pre-treatment by 0.65, giant salamanders by 0.72 for the intermediate- reaches pre-treatment and 0.76 for the low- reaches post-treatment, and Cascade torrent salamanders by 0.79 for the intermediate- reaches post-treatment. For all other reaches, counts were adjusted by the overall mean (0.87-0.99) for each species (Table 5), prior to analyses. Raw effect sizes for counts of each species were approximately normally distributed and did not result in outliers or heteroskedasticity in model residuals.

<u>Tailed frogs</u>**:** Mean tailed frog counts (all development stages) varied 43 to 333% among reaches, pre-treatment, and were greatest in the low-shade reaches, followed in order by the no-shade, reference, and intermediate reaches (Table 6). Post-treatment differences in counts ranged from 8 to 33% with the smallest difference between the intermediate-shade reaches and both the reference and no-shade reaches with the greatest between the low- and reference reaches. A 40 to 333% increase was found in tailed frog numbers in all reaches, pre- to post-

Table 6. Mean(SE) number (corrected for detection probability) of stream associated amphibians in 50-m stream reaches for pre- and post-treatment periods (2 years each) and four experimental shade levels for headwater streams in northwest Oregon, southwest Washington, and the Olympic Peninsula, Washington. Streams were sampled during July-September 2004-2009.

	Pre-treatment shade level				Post-treatment shade level			
Species	No	Low	Intermediate	Reference	No	Low	Intermediate	Reference
Ascaphus truei	10 (3)	13 (5)	3 (1)	7 (1)	14 (4)	16 (6)	13 (4)	12 (2)
Dicamptodon spp.	19 (3)	19 (3)	16 (4)	15 (2)	26 (5)	31 (5)	25 (5)	23 (2)
Rhyacotriton cascadae	9 (6)	5 (3)	2 (1)	9 (3)	10 (4)	13 (6)	11 (6)	11 (3)
R. kezeri	1 (1)	1 (<1)	2 (1)	2 (1)	5 (3)	5 (1)	5 (3)	6 (2)
R. olympicus	4 (1)	3 (2)	1 (<1)	2 (1)	<1 (<1)	1 (1)	3 (2)	2 (1)

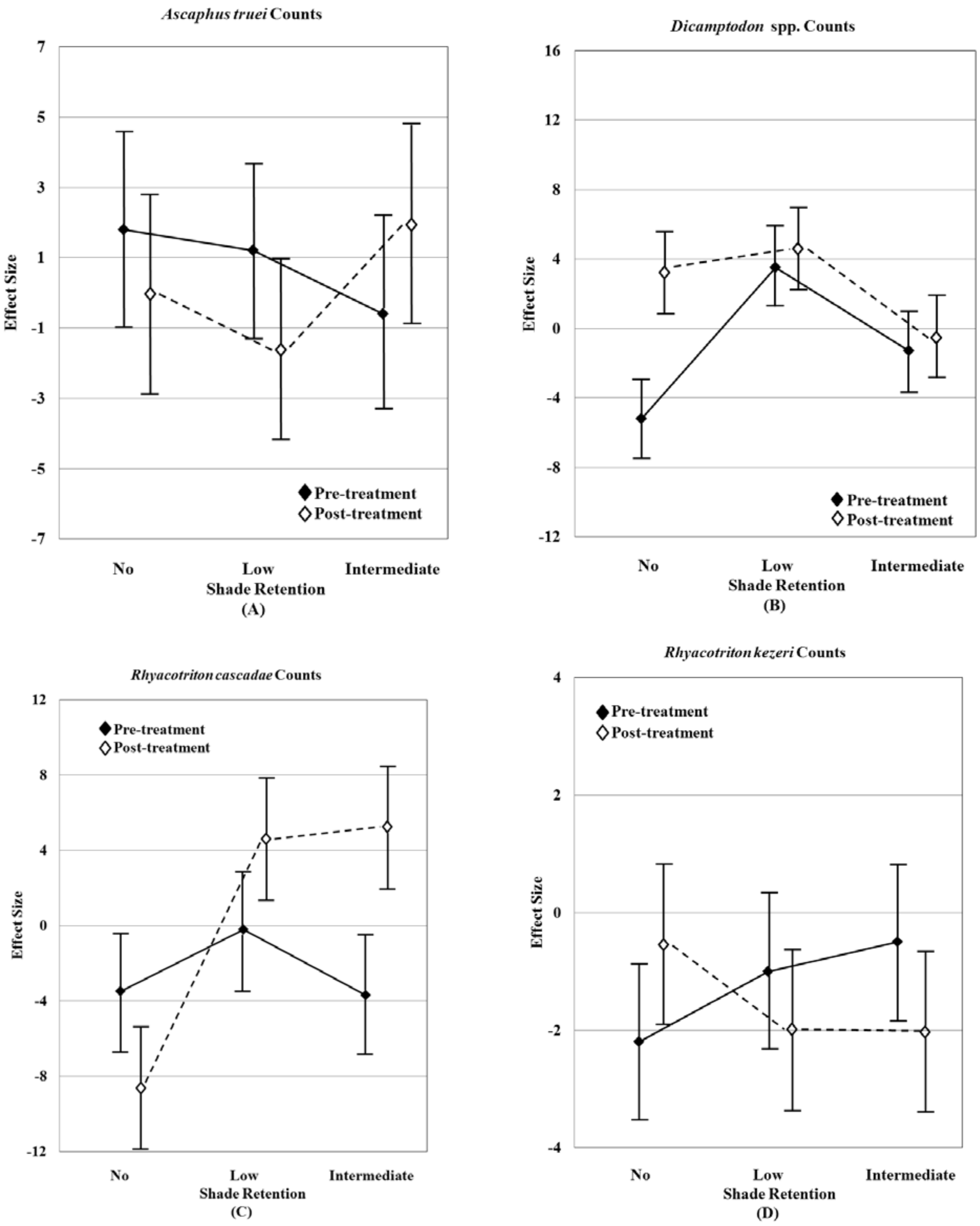

Fig. 7. Mean (SE) effect size (treatment-reference) of counts of tailed frogs (*Ascaphus truei*; A) giant salamanders (*Dicamptodon* spp.; B), and torrent salamanders (*Rhyacotriton* spp.; C-E), corrected for detection probabilities, for pre- and post-treatment periods (two years each) in 25 stream reaches in northwest Oregon and western Washington randomly assigned to three shade retention levels. Sampling occurred in 2004-2009.

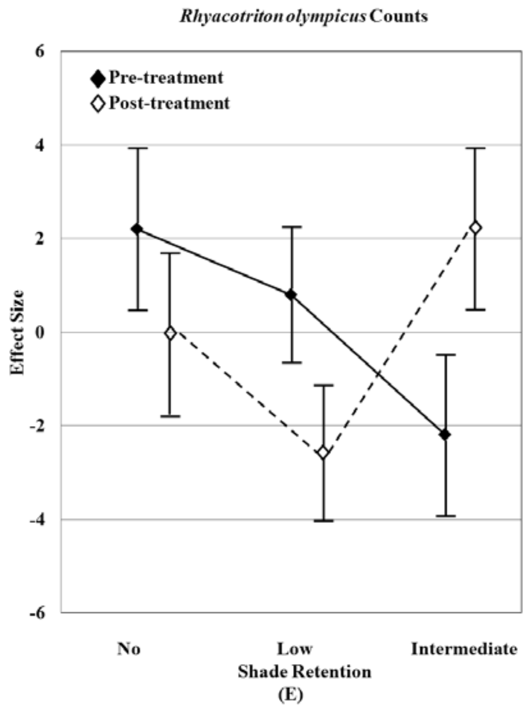

Fig. 7. Continued.

treatment, with the smallest increase in the low-shade reaches and greatest in the intermediate reaches.

Mean ES for tailed frog counts differed 100 to 200% pre-treatment (*P* = 0.37-0.67), being greatest for the no-shade reaches, and differed by 0 to 200% post-treatment (*P* = 0.56-0.93), being greatest for the intermediate-shade level (Fig. 7a). Mean ES declined (*P* = 0.37-0.98) pre- to post-treatment in the no-shade reaches (200%), did not change for the low- reaches, but increased 300% in the intermediate- reaches (*P* = 0.37), resulting in a non-significant (*P* = 0.74) interaction term.

<u>Giant salamanders</u>**:** Counts of giant salamanders differed by 7 to 73% among reaches pre-treatment with the largest difference between the no-and low-shade reaches (Table 6). Post-treatment variation was similar (4-35%) with the greatest difference between the low-shade and reference reaches. Counts increased in all reaches by 53 to 136% pre- to post-treatment, with the greatest increase in the no-shade reaches, followed by the low- and intermediate reaches, then the references (Table 6).

Mean ES estimates differed 340 to 800% (*P* = 0.001-0.27) pre-treatment with the largest difference between the no-and low-shade reaches (Fig. 7b). ES estimates differed 50 to 512 % (*P* = 0.002-0.29) post-treatment. Mean ES estimates increased 220% in the no-shade reaches (*P* = 0.002), 29% in the low- reaches (*p* = 0.42), and declined by 100% in the intermediate reaches (*P* = 0.88), resulting in a significant interaction term (*P* = 0.08).

<u>Cascade torrent salamanders</u>**:** Cascade torrent salamander counts differed from 0 to 350% across stream reaches, pre-treatment and were greatest in the no-shade and reference reaches followed by the low- and intermediate- reaches, respectively (Table 6). Post-treatment torrent salamander counts differed by 0-30%, and were greatest in the low-, intermediate-, reference, and no-shade reaches, respectively. Mean counts also increased (11-450%) pre- to post-treatment in all streams, with the greatest increase in both the intermediate and low-shade reaches.

Mean ES estimates differed from 100 to 300% among reaches pre-treatment (P = 0.24-0.56) and 50 to 313% post-treatment (P = 0.0001-0.65). Pre-treatment, the largest differences were between the no-shade reaches and the intermediate and low- reaches, whereas post-treatment; both the low- and intermediate- reaches were different from the no-shade reaches (Fig. 7c). Mean ES estimates declined by 50% pre- to post-treatment in the no-shade reaches (P = 0.50), but increased by 300% in the low- reaches and 250% in the intermediate reaches (P = 0.12, 0.01, respectively), resulting in a significant (P = 0.10) interaction term (Table 6).

<u>Columbia torrent salamanders</u>**:** Mean counts of Columbia torrent salamanders were relatively low (ranging from 1 to 2) and differed from 0 to 100% among reaches pre-treatment, with the largest difference between both the no-and low-shade reaches compared to the intermediate and reference reaches (Table 6). Differences among reaches post-treatment (mean counts of 5 and 6) were not as great ranging from 0 to 20%, but were greatest between all the treatment reaches and the references. Counts increased 150 to 400% pre- to post-treatment, with the largest increase in the no-and low-shade reaches followed by the reference (Table 6).

Mean ES estimates for Columbia torrent salamanders differed from 0 to 200% pre-treatment (P = 0.29-1.00), with the smallest estimate for the no-and low-shade reaches and the largest for the intermediate reaches (Fig. 7d). Post-treatment ES estimates differed from 0 to

100% (*P* = 0.51-0.80) with the smallest estimate for both the low- and intermediate- shade reaches. Mean ES declined 100% in the low-shade reaches (*P* = 0.89) and 300% (*P* = 0.21) in the intermediate reaches, but did not change in the no-shade reaches pre- to post-treatment, resulting in a non-significant (*P* = 0.61) interaction term (Table 6).

Olympic torrent salamanders: Similar to Columbia torrent salamanders, mean counts of Olympic torrent salamanders were relatively low and varied from 33 to 300% among reaches pre-treatment and 100 to 200% post-treatment. In contrast to the other SAAs studied, Olympic torrent salamander counts declined 200 to 400%, pre- to post-treatment, except in the intermediate-shade reaches where they increased by 200%; there was no change in the reference reaches (Table 6). Declines were greatest in the no- shade followed by the low-shade reaches.

Mean ES differed from 100 to 400% among reaches pre-treatment (*P* = 0.03-0.35) and were greatest for the no- and intermediate-shade reaches (Fig. 7e). Estimates differed by 200-250% post-treatment (*P* = 0.05-0.37) with the largest difference between the intermediate-shade reaches and the low- reaches. Mean ES declined pre- to post-treatment by 400% in the no-shade (*P* = 0.21), 200% in the low- reaches (*P* = 0.14), but increased 100% in the intermediate reaches (*P* = 0.05), resulting in a significant (*P* = 0.06) interaction term.

In summary, corrected raw counts, except those of Olympic torrent salamanders, increased from pre-to post-treatment periods in all reaches, including references. Trends based on ES estimates were non-parallel among the five species. The greatest effects ($P \leq 0.1$) of shade reductions on giant salamanders occurred at the lowest level of shading, but for Cascade torrent salamanders and Olympic torrent salamanders at intermediate levels. Though not large,

Table 7. Mean(SE) scaled mass (g) index (SMI) of body condition for five taxa of stream associated amphibians free-ranging in stream segments and for pre- and post-treatment periods (2 years each) at four shade levels for headwater streams in northwest Oregon, southwest Washington, and the Olympic Peninsula, Washington. Streams were sampled during July-September 2004-2009.

Species and	Pre-treatment shade level				Post-treatment shade level			
development stage	No	Low	Intermediate	Reference	No	Low	Intermediate	Reference
Ascaphus truei								
Larvae	1.0(0.05)	0.9(0.03)	0.9(0.02)	1.0(0.04)	0.9(0.01)	0.9(0.01)	0.9(0.01)	0.8(0.03)
Metamorphs	1.1(0.06)	1.0(0.09)	1.3(0.25)	1.0(0.05)	1.1(0.06)	1.2(0.05)	1.3(0.03)	1.0(0.03)
Adults	5.4(0.42)	4.7(0.29)	4.0(0.63)	4.3(0.16)	3.8(0.28)	4.2(0.18)	4.4(0.16)	4.2(0.19)
Dicamptodon spp.	3.4(0.06)	3.4(0.06)	3.4(0.05)	3.5(0.12)	3.3(0.04)	3.5(0.04)	3.3(0.04)	3.4(0.04)
Rhyacotriton cascadae	1.1(0.02)	1.4(0.04)	1.2(0.05)	1.2(0.02)	1.1(0.02)	1.2(0.02)	1.2(0.04)	1.2(0.02)
R. kezeri	0.8(0.04)	0.7(0.12)	0.7(0.03)	0.8(0.05)	0.7(0.04)	0.7(0.01)	0.7(0.02)	0.7(0.01)
R. olympicus	1.6(0.06)	1.7[a]	2.0(0.34)	1.6(0.04)	NA[b]	1.8[a]	1.9[a]	2.2(0.34)

[a] only 1 individual captured in this category.

[b] not available, no captures in this category.

ES changes pre- to post-treatment ($P \geq 0.1$) were inconsistent for other species and not solely attributable to shade reductions.

Amphibian body condition: Body condition ES calculated from SMI estimates produced strong patterns in the model residuals for each species and all life stages for tailed frogs, so were rank-transformed; this improved the dispersion of residuals in each case. Separate analyses were conducted for tailed frog larvae, metamorphs, and adults. Too few juvenile tailed frogs were captured for analysis. In addition, the sample of tailed frog metamorphs and adults was incomplete (not all cells in the data matrix had entries), but enough existed so that estimates were available for all period and treatment combinations. In contrast, for Olympic torrent salamanders, no captures were available in either the treatment or reference reach in each stream each year, precluding calculation of ESs and statistical analyses (Table 7).

Tailed frogs: Over 160 larval tailed frogs captured were suitable for SMI calculations, i.e., had no injuries or malformations. Mean SMI estimates varied by $\leq$11% among shade levels pre-treatment and were largest in the no-shade and reference reaches (Table 7). Mean SMI estimates post-treatment were the same for all reaches, except references, where they were 13% lower. Pre- to post-treatment, a decrease of 11% and 25% occurred in the no-shade and reference reaches, respectively, and did not change elsewhere.

However, mean ranked ES of larvae differed from 42 to 143% pre-treatment ($P = 0.003$-0.62) with the largest differences between the low-shade reaches and each of the no-and intermediate-shade reaches (Fig. 8a). However, ES estimates differed from only 0 to 2% ($P = 0.001$-0.94) post-treatment with the largest estimate for the low-shade level. Mean ES increased

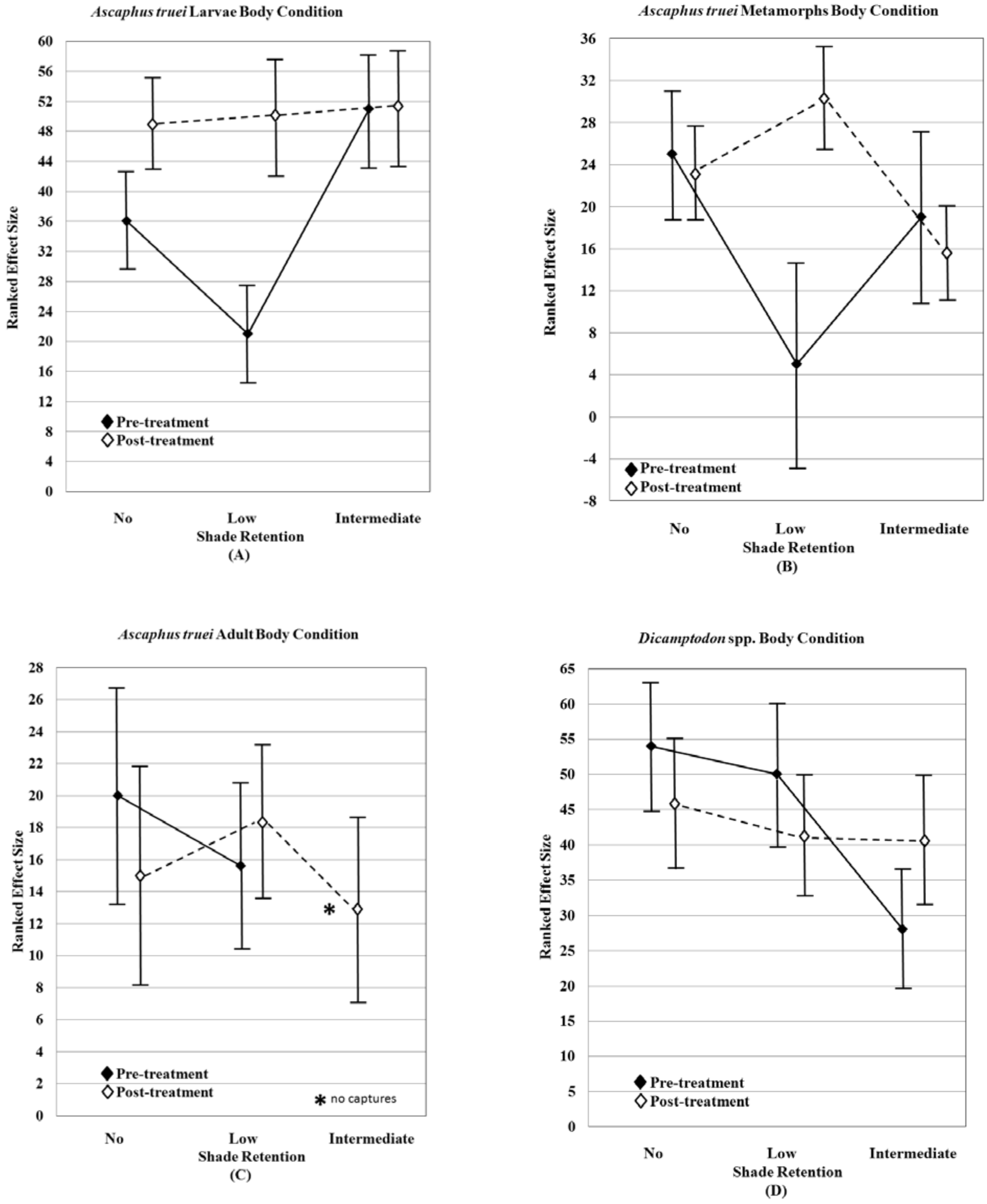

Fig. 8. Mean (SE) ranked effect size (treatment-reference) for body condition estimates (g) of tailed frog (*Ascaphus truei*) larvae (A), metamorphs (B) and adults (C), giant salamanders (*Dicamptodon* spp.; D), and two torrent salamanders (*Rhyacotriton* spp.; E, F) for stream reaches randomly assigned to one of three levels of shade retention for both pre- and post-treatment periods (two years each) for 25 streams in northwest Oregon and western Washington. Sampling occurred from 2004-2009.

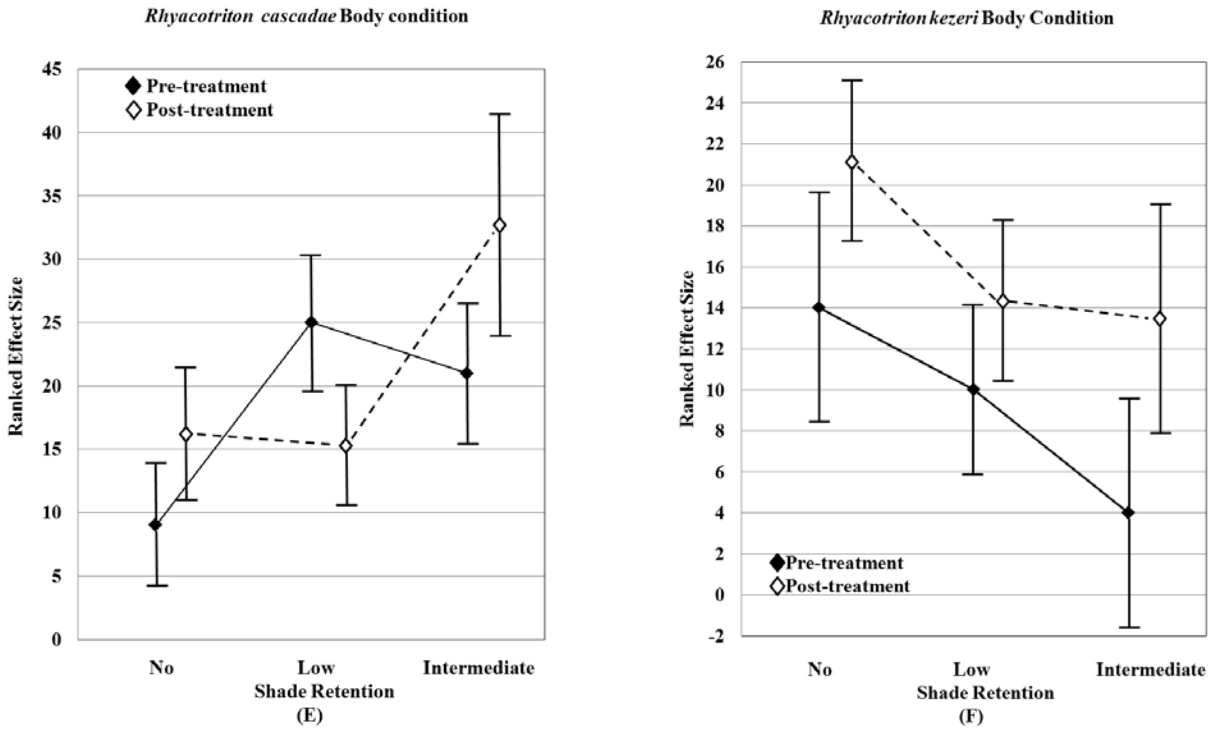

Fig. 8. Continued.

36% and 138% pre- to post-treatment at the no-(*P* = 0.07) and low- (*P* = 0.001) shade levels, respectively, but declined by 4% (*P* = 0.91) in the intermediate reaches, resulting in a significant (*P* = 0.04) interaction term.

Forty-seven tailed frog metamorphs were analyzed and their mean SMI estimates differed from 0 to 30% among reaches for the pre-treatment period, with the greatest difference between the intermediate-shade reaches and the low- and reference reaches (Table 7). Mean SMI estimates differed 8 to 30% post-treatment with the greatest differences between the intermediate-shade and reference reaches. The SMI increased 20% from pre- to post-treatment periods for the low-shade reaches and did not change for the other reaches.

Mean ranked ES estimates differed among reaches 37 to 420% pre-treatment (*p* = 0.07-0.45) with the largest difference between the low- and no-shade reaches (Fig. 8b). Post-treatment ES estimates differed 35 to 94% (*p* = 0.008-0.20) with the largest difference between the low- and intermediate-shade reaches. ES estimates declined by 13% and 19% (*p* = 0.74 and 0.64) for the no-shade and intermediate reaches, respectively, pre- to post-treatment, but increased 520% (*p* = 0.02) for the low- reaches, resulting in a non-significant interaction term (*p* = 0.13).

A total of 24 adult tailed frogs were suitable for analysis. However, not all cells of the data matrix had SMI estimates and some treatment effects could not be analyzed. Mean SMI estimates for adults differed 8 to 35% across reaches pre-treatment, with the no-shade reaches having the greatest estimate. Mean SMI differed 0 to 16% among reaches post-treatment with the intermediate-shade reaches having the greatest estimate. Body condition estimates increased 10% in the intermediate-shade reaches and declined from 2 to 42% in the remaining reaches between pre- and post-treatment periods (Table 7).

Mean ranked ES estimates differed by 25% (*p* = 0.59) between the reaches, but could not be calculated for the intermediate-shade reaches pre-treatment due to a lack of captures (Fig. 8c). Post-treatment estimates differed from 15 to 38% (*p* = 0.44-0.82), with the largest difference between the low- and intermediate-shade reaches. Mean ranked ES declined 33% for the no-shade reaches (*P* = 0.57) and increased 13% for the low- reaches (*P* = 0.67), pre- to post-treatment. The interaction term was not significant (*P* = 0.78).

Giant salamanders: We captured over 2,170 giant salamanders suitable for body condition analyses. Mean SMI estimates for giant salamanders differed from only 0 to 3% across shade levels pre-treatment, with the only difference occurring between reference reaches and all other reaches (Table 7). Post-treatment SMI estimates differed by 0 to 6 % among reaches, with the greatest difference between the low-shade and both the no- and intermediate-shade reaches. SMI increased three percent from pre- to post-treatment for the low-shade reaches and declined three percent in all other reaches.

Mean ranked ES estimates were more variable and differed 8 to 93% among reaches pre-treatment (*P* = 0.02-0.72) with the largest differences between the intermediate and both the no- and low-shade reaches (Fig. 8d). Differences among reaches post-treatment were smaller (0-10%) and greatest between the no-shade and each of the low- (*P* = 0.69) and intermediate- (*P* = 0.71) reaches. Pre- to post-treatment declines of 17 to 19% occurred in the no-and low-shade reaches (*P* = 0.47 and 0.48, respectively), but increased by 54% (*P* = 0.21) in the intermediate-reaches, resulting in a non-significant (*P* = 0.46) interaction term.

__Cascade torrent salamanders__: Over 470 Cascade torrent salamanders captured were appropriate for condition analyses. Mean SMI estimates differed from 0 to 27% across reaches, pre-treatment and were greatest for the low-shade reaches (Table 7). In contrast, SMI estimates differed by only 0 to 9% across reaches post-treatment, with equivalent estimates for the low-, intermediate-, and reference reaches and the no-shade reaches having the lowest estimate. Mean SMI estimates did not change pre- to post-treatment, except at the low-shade level, where it declined by 17%.

Mean ranked ES estimates were more variable and differed from 38 to 164% across reaches pre-treatment (P = 0.01-0.50) with the greatest differences between each of the low- and intermediate- reaches compared to the no-shade reaches (Fig. 8e). ES estimates differed from 7 to75% among reaches post-treatment with the estimate for the intermediate reaches greater than each of the no-and low-shade reaches (P = 0.07 and 0.05, respectively). Pre- to post-treatment ES increased 33% for the intermediate-shade reaches (P = 0.28) and 54% for the no-shade reaches (P = 0.19), but declined by 81% for the low-shade treatment (P = 0.07). These trends resulted in a significant (P = 0.10) interaction term.

__Columbia torrent salamanders__: Mean SMI estimates of over 250 Columbia torrent salamanders differed from 0 to14% pre-treatment with the no-shade and reference reaches greater than the low- and intermediate-shade reaches (Table 7). Post-treatment, mean SMI estimates for this species were the same across all reaches, resulting in a 14% decline in the no-shade and reference reaches and no change elsewhere.

Mean ranked ES estimates were more variable with pre-treatment differences ranging from 40 to 250% (P = 0.15-0.87) with the ES for the intermediate-shade reaches smaller than each of the low- (*P* = 0.34) and no- (*P* = 0.16) shade reaches (Fig. 8f). Post-treatment ES estimates differed 0 to 50% (*P* = 0.11-0.94) with the estimate for the no-shade reaches greater than each of the low- (*P* = 0.19) and intermediate reaches (*p* = 0.23). Pre- to post-treatment estimates increased 40 to 250% and was greatest for the intermediate-shade reaches (*P* = 0.18) and least for the low-shade retention level (*P* = 0.45), resulting in a non-significant (*P* = 0.65) interaction term.

<u>Olympic torrent salamanders</u>: Too few captures (53) of Olympic torrent salamanders existed to calculate an ES for each period/treatment combination (Table 7). Mean SMI estimates differed 0 to 25% across all reaches, pre-treatment and were greatest for the intermediate-shade reaches followed by the low-shade reaches (Table 7). Estimates differed from 6 to 22% among reaches post-treatment increasing with increasing shade retention. Mean SMI estimates increased by 6% for the low-shade reaches and 38% for reference reaches pre- to post-treatment, but declined by 5% in the intermediate reaches.

In summary, mean SMI estimates were relatively uniform within taxa differing by $\leq$0.3 g among reaches both pre- and post-treatment, except for tailed frog adults and Olympic torrent salamanders. The intensity of shade reductions did not consistently parallel the magnitude of raw SMI estimates. Post-treatment, mean raw SMI estimates were often greatest at intermediate levels of shade retention, except for Columbia and Olympic torrent salamanders, the latter of which had too few data to confidently evaluate. Ranked ES estimates differed among reaches for both pre-treatment and post-treatment periods in a complex fashion, with no consistent relationship between reduction in shade and increases or decreases in SMI estimates. However, all tailed frog life stages, giant salamanders, and Cascade and Columbia torrent salamanders exhibited positive increases in body condition at one or more reduced shade levels, but only tailed frog larvae and Cascade torrent salamander changes were statistically significant.

Amphibian growth rates: Residence time of individuals placed in the enclosures varied from ≤ one week to >18 weeks. Depending on the year, 75-226 individual tailed frog larvae were in the enclosures for a minimum of four weeks. In addition, 40-112 tailed frog metamorphs, 52-146 giant salamanders, 26-97 Cascade torrent salamanders, 42-101 Columbia torrent salamanders, and 52-82 Olympic torrent salamanders also met that criterion.

With some exceptions (17%), the mass of most individuals of each species/life stage combination declined while in the enclosures during the pre-treatment period (Table 8). In contrast, growth rates were positive for 33% of species/life stage/treatment categories, post-treatment. When excluding tailed frog metamorphs, because they typically lose mass, those estimates become 25% and 40%, respectively.

***Tailed frogs*:** Growth rates for tailed frog larvae differed among reaches by 200-1,900% pre-treatment with larvae in the no-shade reaches experiencing positive growth and those in other reaches loosing mass. Growth rates differed among reaches from 33 to 525% post-treatment with mass gains in all reaches, except the references, with the greatest gain in the no-shade reaches. Tailed frog larvae growth rates increased from pre- to post-treatment periods 613 to 1000% in the low- and intermediate-shade reaches, respectively, but declined 59% in the no-shade reaches and 433% in the reference reaches.

Mean ES estimates differed 225 to 300% among reaches pre-treatment with the largest

Table 8. Mean(SE) growth rate (mg change/week) of five taxa of stream associated amphibians held in in-stream enclosures for pre- and post-treatment periods (2 years each) at four shade levels for headwater streams in northwest Oregon, southwest Washington, and the Olympic Peninsula, Washington. Streams were sampled during July-September 2004-2009.

Species and	Pre-treatment shade level				Post-treatment shade level			
development stage	No	Low	Intermediate	Reference	No	Low	Intermediate	Reference
Ascaphus truei								
Larvae	19 (15)	-17 (14)	-1 (3)	-3 (4)	12 (4)	3 (4)	9 (4)	-16 (6)
Metamorphs	-48 (20)	-36 (16)	-27 (16)	-57 (18)	-43 (20)	-46 (15)	-54 (15)	-44 (9)
Dicamptodon spp.	16 (12)	-10 (10)	-9 (16)	-32 (20)	18 (17)	-5 (12)	-27 (24)	-12 (6)
Rhyacotriton cascadae	-11 (6)	-2 (9)	0 (16)	-1 (5)	-15 (9)	-36 (15)	-8 (12)	-23 (6)
R. kezeri	7 (18)	-16 (7)	-2 (6)	-1 (19)	13 (12)	-7 (10)	0 (5)	-11 (6)
R. olympicus	-2 (2)	-3 (3)	-24 (14)	0 (4)	0 (4)	6 (4)	-8 (2)	-3 (3)

difference between the no-shade reaches and each of the low- (*P* = 0.03) and intermediate-reaches (*P* = 0.15) (Fig. 9a). Effect size estimates were more variable post-treatment, differing 39 to 316% with the largest differences between both the no-shade and intermediate reaches and the low- reaches (*P* = 0.01and 0.10, respectively). Effect size increased 150 to 1,000% across all reaches from pre- to post-treatment periods being greatest for the intermediate-shade reaches (*P* = 0.02) followed by the no-(*P* = 0.07) then low- (*P* = 0.09) shade reaches, resulting in a non-significant (*P* = 0.2) interaction term (Fig. 9a).

Tailed frog metamorphs lost weight in the enclosures during both pre- and post-treatment periods, as expected (Table 8). However, mass changes differed more among reaches pre-treatment (33-111%) than post-treatment (5-24%) and mass changes increased (11% and 30%) only in the no-shade and reference reaches and decreased in the low- and intermediate reaches (28% and 100%) between pre- and post-treatment periods.

Mean ES estimates differed 1,000 to 2,300% among reaches pre-treatment with the largest difference (*P* = 0.37) between the intermediate- andlow-shade reaches (Fig. 9b). Differences between reaches post-treatment ranged from 80 to 300% with the largest difference (*P* = 0.18) between the low- andintermediate-shade reaches. ES increased from pre- to post-treatment periods 1,000% (*P* = 0.67) in thelow-shade reaches, but declined 200 to 228% (*P* = 0.32-0.10) in the no- andintermediate-shade reaches, respectively. These trends resulted in a non-significant (*P* = 0.39) interaction term.

***Giant salamanders*:** Growth rates of giant salamanders were primarily negative during both pre- and post-treatment periods, except in the no-shade reaches (Table 8). However, growth

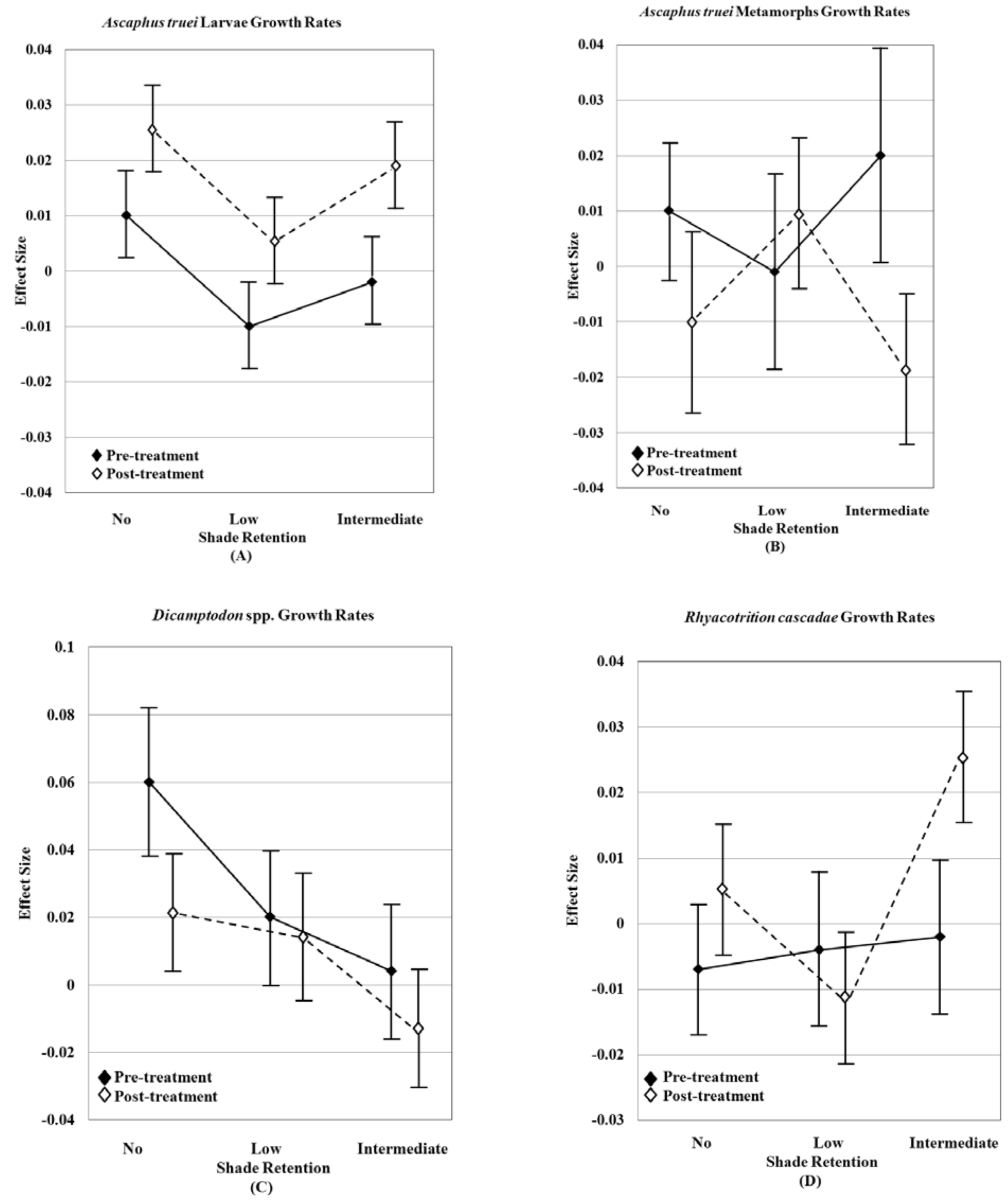

Fig. 9. Mean (SE) effect size (treatment-reference) for growth rates (g/week) of tailed frog (*Ascaphus truei*) larvae (A) and metamorphs (B), giant salamanders (*Dicamptodon* spp.; C), and three torrent salamanders (*Rhyacotriton* spp.; D-F) held in in-stream enclosures in stream reaches randomly assigned to one of three levels of shade retention for both pre- and post-treatment periods (two years each) for 25 streams in northwest Oregon and western Washington. Sampling occurred from 2004-2009.

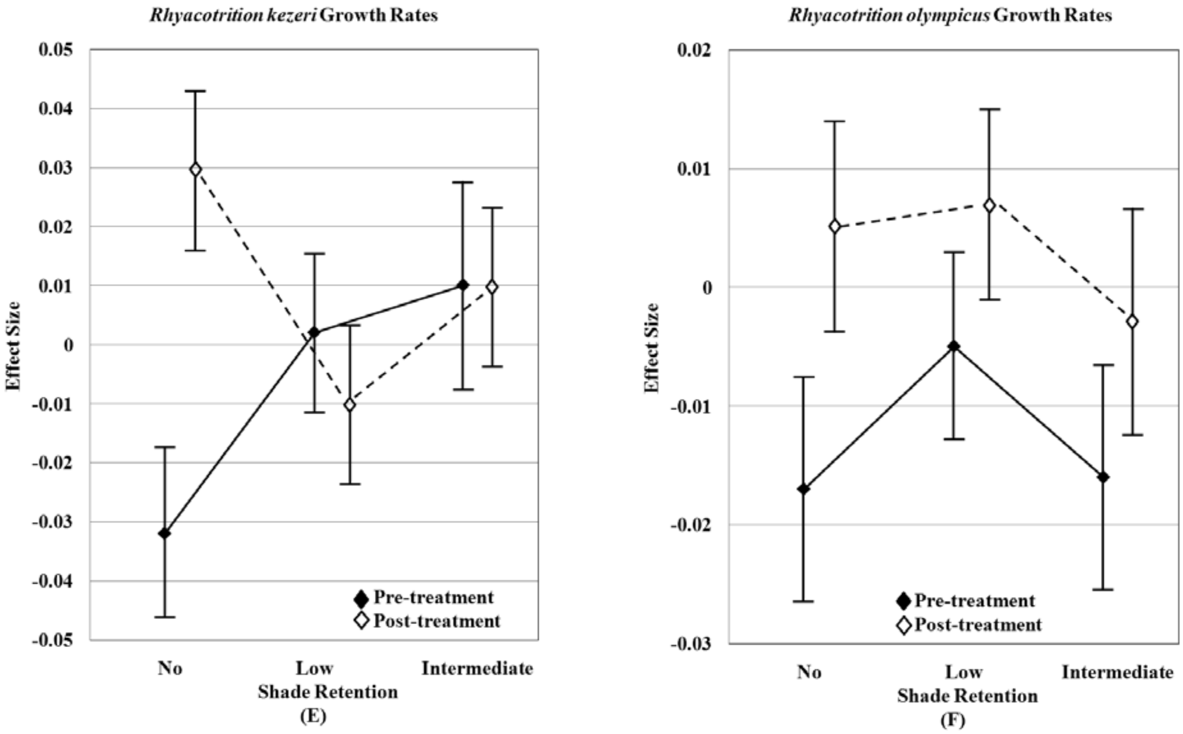

Fig. 9. Continued.

rates increased in the no-shade (13%),low-shade (100%), and reference reaches (107%) from pre-to post-treatment periods. Growth rates differed by 11-200% across reaches pre-treatment, and were more variable (140-250% differences) post-treatment.

In contrast, mean ES estimates were positive for all reaches, pre-treatment and differed from 480 to 1480% with the largest difference (*P* = 0.06) between the no-shade and intermediate- reaches (Fig. 9c). Estimates differed from 23 to 262% post-treatment with the largest difference (*P* = 0.24) between the low- and intermediate-shade reaches. Furthermore, ES decreased 35 to 408% pre- to post-treatment with the largest decline in the no-shade reach (*P* = 0.52) and the least in the low- reaches (*P* = 0.82), resulting in a non-significant (*P* = 0.72) interaction term.

<u>Cascade torrent salamanders</u>**:** Growth rates of Cascade torrent salamanders were negative for all reaches in both periods, except at the intermediate-shade level pre-treatment where there was no change (Table 8). Growth rates differed more across reaches (100-1,000%) pre-treatment than post-treatment (87-350%) and declined from pre- to post-treatment periods in all reaches with the largest declines in the reference and low- reaches.

Mean ES estimates were also negative for all reaches pre-treatment and differed from 100 to 250% among reaches with the largest difference (*P* = 0.70) between the intermediate- and no-shade reaches (Fig. 9d). Effect size estimates differed from 310 to 400% post-treatment with the greatest difference (*P* = 0.10) between the intermediate- and no-shade reaches. Effect size increased 240% and 1,304% in the no-shade and intermediate reaches (*P* = 0.34 and 0.06), respectively and declined 175% in the low- reaches (*P* = 0.64) pre- to post-treatment, resulting in a non-significant (*P* = 0.33) interaction term.

__Columbia torrent salamanders__**:** Columbia torrent salamander mean growth rates were negative for all reaches and periods, except for the no-shade reaches pre-treatment, and the no-and intermediate-shade reaches post-treatment (Table 8). Growth rates differed among reaches from 100 to 1,500% pre-treatment and 57 to 286% post-treatment. Growth rates increased 86 to 129% in all but the reference reaches where growth rates declined (1,000%). The greatest increases were in the low- (145%) and the intermediate-shade reaches (100%).

Differences among reaches in mean ES were more variable pre- (350-100%) than post-treatment (217-521%, Fig. 9e). The largest difference between reaches in both the pre- (P = 0.13) and post-treatment (P = 0.10) periods was for the no-shade and low- reaches. From pre- to post-treatment periods, ES increased by 110% for the no-shade reaches (P = 0.01) and declined by 400% for the low- reaches (P = 0.71), and 29% for the intermediate- reaches (P = 0.93). These trends resulted in a significant interaction term (P = 0.10).

__Olympic torrent salamanders__**:** Growth rates of Olympic torrent salamanders differed 50 to 1,100% among reaches pre-treatment and were negative in all reaches, except references where animals maintained mass (Table 8). Post-treatment changes in mass were positive in the low-shade reaches, and negative in the intermediate and reference reaches, but mass did not change in the no-shade reaches resulting in a 167 to 300% difference among reaches (Table 8). Pre- to post-treatment, growth rates increased 100% in the no-shade reaches, 300% in the low- reaches, and 200% in the intermediate reaches, but declined 100% in the reference reaches.

Mean ES estimates differed from 6 to 240% pre-treatment with the greatest differences (P = 0.20-0.24) between the low-shade reaches and all of the others (Fig. 9f). Post-treatment, ES estimates differed from 40 to 317% and were positive for all treatments except the intermediate-shade reaches, with the largest difference between the low- and intermediate reaches (*P* = 0.29). Mean ES estimates increased 240 to 633% from pre- to post-treatment periods with the largest increase for the intermediate-shade reaches (*P* = 0.10) followed by the no-(*P* = 0.09) and low-shade reaches (*P* = 0.28), resulting in a non-significant (*p* = 0.33) interaction term.

In summary, most individuals of each taxon and development stage lost mass while in the enclosures. Trends in growth rates among reaches post-treatment were mixed and variable with some taxa maintaining or gaining mass in some reaches, most often at moderate levels of shading, and others losing mass in all reaches. However, based on differences between pre- and post-treatment periods, mean ES estimates for tailed frog larvae and Olympic torrent salamanders exhibited positive changes in growth rates at all reduced shade levels. The other torrent salamander species and tailed frog metamorphs also showed positive changes in mass at one or more reduced shade levels, with the no-shade reaches having the most positive changes. Based on ES estimates, only giant salamanders had negative growth rates for all reaches. In addition, some of the largest increases in growth rates occurred at the intermediate- levels of shade retention, particularly for tailed frog larvae and Cascade torrent salamanders. Based on the interaction term, only changes in the Columbia torrent salamander mass appear clearly attributable to a treatment effect.

DISCUSSION

The overarching objective of this study was to document the response of headwater stream communities to variation in vegetation shading, focusing on six species of SAAs and the mechanisms that led to those responses. We sought to create a complete gradient in irradiance reaching streams through a multi-treatment (Steury et al. 2002) study design. Despite the vagaries and imprecision of spherical densiometers (Cook et al. 1995, Nuttle 1997) the levels of PAR reaching stream surfaces over the post-treatment period indicate that this goal was largely met.

Stream energetics/predictions

Our experimental procedure converted some stream reaches that were primarily heterotrophic before shade reductions to autotrophy as exhibited by the large increases in periphyton AFDM and declines in detritus following treatment implementation, particularly at the no-shade level. We expected this change to have large effects on primary and selected secondary consumers. In addition, we expected that effects could vary linearly or as a quadratic function over the gradient of shade we created, depending on the response variable (Kiffney et al. 2003, Hill et al. 2010, Ohta et al. 2011) and site conditions. Based on post-treatment ES estimates, we observed linear, quadratic (U- or bell-curves), and asymptotic trends, depending on the response variable. Light and water temperature had an inverse linear response to shade level; periphyton and vegetation drift primarily asymptotic, macroinvertebrate drift bell- and U-curves, and SAAs all three patterns (Figs. 3-9).

We also anticipated that the largest biotic effects of the treatments would be on periphyton accrual (positive), the abundance of macroinvertebrate scrapers (positive; Hill et al. 2010, Ohta et al. 2011), shredders (negative; Cummins et al. 1989), and tailed frog larvae (Kiffney et al. 2004), and perhaps metamorphs (both positive). In addition, we expected that tailed frogs and possibly some salamanders (MacCracken 2002) would also exhibit better body condition and greater growth rates in stream reaches with less shade (Kiffney et al. 2004, Mallory and Richardson 2005).

Macroinvertebrates

Some predictions may have been met based on the results of the ES analyses. Within the macroinvertebrate community, gatherers exhibited the greatest response to our light manipulations at intermediate-shade levels, with ES estimates increasing 15 to 45%, but declining slightly (6-7%) at the greatest light level (Appendix 2). Significant interaction terms regardless of metric (g/m^3 or g/day) supports attributing this pattern to the treatment gradient. Generally, gatherers exploit detritus deposited in eddies and against stream bed material (Merritt and Cummins 1996) that is created by both the feeding of shredders on CPOM and the physical breakdown of plant and animal material. Increases in periphyton at the intermediate-shade level likely account for the response of gatherers that we observed; also being greatest at that level of shade retention.

Shredding insect ES estimates declined by 18-42% at the lowest level of canopy retention with slight changes (–2% to 1%) at the higher levels of canopy retention (Appendix 2). This is in line with the view that shredder population size, species composition, and life histories are tightly coupled to riparian area vegetation composition and disturbance regimes (Cummins et al. 1989), but the mixed significance of interaction terms for the two different metrics calls into question either a direct link to treatments or the efficacy of the g/day metric. Our results suggest that shredders were not limited by declines in allochtonous subsidies until canopy reduction fell below the low-shade level (≈ 30% cover).

Scraper ES estimates were mostly positive and increased with shade reductions with the greatest increases (2-24%) at moderate light levels (30-70% shade, respectively) consistent with the light:nutrient hypothesis (Appendix 2). However, the lack of significant interaction terms makes the link to treatment effects ambiguous.

Macroinvertebrate predators declined from pre- to post-treatment periods in the no-shade reaches (Table 9). Though not definitive, the decline in predators may reflect the decline in shredder abundance in the no-shade reaches. Detailed studies on selection of macroinvertebrate prey by macroinvertebrate predators for the region are lacking, but most studies suggest that predators are opportunistic (Hildrew et al. 1985, Giller and Sangpradub 1993, Lancaster and Robertson 1995). Prior to treatment implementation, shredders were the most abundant macroinvertebrate class based on ranked ES estimates, but fell to fifth post-treatment.

Amphibian overview

Depending on the metric (counts, SMI, or growth rates), all SAAs and development stages exhibited at least one significant difference among reaches for the pre-treatment period. This was likely due to inherent differences among streams within blocks that reflects variation in abiotic (geology, elevation, aspect) and biotic (riparian vegetation, stream subsidies, SAA densities) factors, and that may have also been influenced by management history (Mallory and Richardson 2005, Kroll 2009, Leuthold et al. 2012). Though we selected streams that ran through forest stands resulting from silvicultural practices that were in use about 50 years ago, substantial site-specific variation existed in the structure of both riparian and surrounding upland stands associated with each stream in terms of dominant and co-dominant overstory trees, understory vegetation, and ground cover. Moreover, enough differences existed in management regimes between state and private forest landowners to contribute additional variation. For example, state forests in Oregon and Washington are managed primarily for revenue for schools, prisons, hospitals, etc. whereas corporate private lands are managed to maximize investor returns. States also promote compatible multiple uses and make concessions to integrate multiple uses into forestry programs whereas most other uses of corporate forest lands are secondary to timber production. Thus, characteristics such as rotation ages, harvest unit sizes, use of chemicals, etc. may vary between the two. Interacting natural processes and management-induced variation likely contributed to the pre-treatment differences we observed, not only in SAA metrics (Kroll 2009), but also in other response variables (periphyton and some macroinvertebrate classes) exhibiting significant differences.

Pre-treatment variation could influence post-treatment responses of amphibian taxa to shade reductions and changes in pre-existing differences following treatment would also be indicative of a treatment effect. Shade reductions either did not change pre-treatment differences (2 of 15), resulted in a switch in the rank order of ES estimates among treatment levels (2 of 15), or eliminated the differences (i.e., no post-treatment significant differences; 10 of 15) (Table 9). These patterns suggest that most (12 of 15) of these pre-treatment differences (i.e., those that were changed or eliminated post-treatment) were influenced by vegetation cover. These types of changes occurred most often for pre-treatment differences in amphibian body condition (8 of 12) and counts of giant salamanders (5 of 12) and tailed frogs (4 of 12) (Appendix 2). For those differences that changed, reaches with the largest ES estimate maintained that rank, whereas the other two switched their rank order.

Also depending on the metric, all SAA taxa and development stages exhibited a positive response to at least one level of shade reduction based on ES pre- to post-treatment comparisons that were statistically different. Positive responses occurred most frequently for the no-shade treatment (4 of 5) and exhibited the same frequency of response for the low- and intermediate- (3 of 5) shade reaches (Appendix 2). For all reaches combined, the majority of pre- to post-treatment changes were positive (10 of 15), four were negative and one was equivocal (Appendix 2). Negative responses to shade reductions were observed for counts of Cascade torrent salamanders and giant salamanders (no- and intermediate-shade reaches, respectively), body condition estimates for Cascade torrent salamanders (low-shade reaches) and growth rates for Columbia torrent salamanders (low-shade reaches) (Appendix 2).

Detection probability

We found some large differences in estimates of detection probabilities (p) for some amphibian species in the low- and intermediate-shade treatment reaches in both pre- and post-treatment periods. However, p was unrelated to either species abundance (r = –0.01 to 0.20) in contrast to McCarthy et al. (2012) or the time between the initial search of a plot and subsequent resampling (r = –0.03 to 0.29). Differences in p that we detected further illustrate the effects that site-specific characteristics can have on amphibian studies. Our results indicate that p should be estimated for studies of SAAs to produce unbiased results (Kroll 2009), contrary to Welsh's (2011) assertions, which were partly based on preliminary results of this study.

Counts

Abundance (based on detection probability-corrected raw counts) of all taxa, except Olympic torrent salamanders, increased from pre- to post-treatment periods in the reference reaches as well as most treatment reaches suggesting that conditions for SAAs improved throughout the region during 2006-2007. The most plausible mechanism for this pattern is an overall increase in amphibian populations due to greater survival and/or reproduction between the two periods. One could also postulate either differential movement of amphibians into treatment reaches from adjacent reaches, or better sampling conditions during the post-treatment period. Differential movement of amphibians into treatment reaches is highly implausible because the same pattern also occurred in reference reaches, so one would have to invoke a mechanism in which differential movement in both treatment and reference reaches occurred over all study streams. The better sampling condition hypothesis is equally implausible in view of the lack of change in reference reaches. Consistent with our supposition that environmental conditions were favorable for SAAs during 2006 and 2007 is the large increase in 2007 in coastal giant salamander densities reported by Leuthold et al. (2012) in paired third-order watersheds in southwestern Oregon. Trends in Olympic torrent salamander abundance during the post-treatment period are consistent with this explanation, but trends in tailed frogs in the Olympic blocks are not.

Tailed frogs

Shade treatments did not appear to influence tailed frog ES estimates of abundance enough to override other sources of variation. Tailed frogs are a relatively long-lived anuran with a relatively low reproductive rate and it would likely take several years for populations to respond to shade manipulations as long as the manipulations did not result in direct mortalities (e.g., from extreme water temperatures).

Body condition estimates for tailed frog larvae showed the greatest response of the variables measured to our shade manipulations, increasing in both the no-and low-shade reaches as predicted (Appendix 2). Presumably, algal abundance in the no-shade reaches was great enough to more than compensate for greater structural carbon and lower digestibility, i.e., tailed frog larvae may have been able to ingest more algae per unit time in those reaches than in more shaded reaches. Alternatively, differing light levels favor different species and structural forms of diatoms (Hill et al. 2011b, Lange et al. 2011) and those that increase in high light environments may be favored or more easily assimilated by tailed frog larvae. Kiffney et al. (2004) also reported greater response (growth rates and survival) of tailed frog larvae to full sun than moderate levels and found a strong linear correlation ($r \geq 0.7$) between those two metrics and chlorophyll *a* concentrations in periphyton, which in turn was a function of light intensity. However, they did not speculate about the basis of the relationship.

In contrast to the above, growth rates of larval tailed frogs in in-stream mesocosms in this study increased in both the low- and intermediate-shade reaches from pre- to post-treatment periods (Appendix 2) . In contrast to body condition estimates, this finding is consistent with the light:nutrient hypothesis. Inconsistencies between these two response metrics as well as with the results of Kiffney et al. (2004) may be due to a number of factors (e.g., methods, sampling asymmetries, site conditions) and suggests that measurements that reflect primarily current conditions (growth) and past conditions (energy stores) may be needed to fully evaluate the effects of altering habitat.

Body condition estimates for free-ranging tailed frog metamorphs declined in the no-shade reaches and increased in the low- reaches, consistent with the light:nutrient hypothesis (Appendix 2). Body condition of metamorphs is likely carried over from the larval stage (Chelgren et al. 2006, Davis and Maerz 2009) and apparently tailed frog metamorphs in the low-shade reaches were able to store and retain more energy than those in the no-shade reaches. This finding is important in that greater mass and body condition at metamorphic climax results in greater survival, fitness, and physical performance in anurans (Goater 1994, Newman and Dunham 1994, Goater and Vandenbos 1997). However, growth rates of tailed frog metamorphs did not differ in relation to shade manipulation. In general, anurans at metamorphic climax cannot feed and the accompanying physiological and morphological changes result in a decline in mass. Thus, we would not expect a change in stream subsidies to have a direct effect on growth rates of metamorphs. Both food levels (periphyton) and temperature showed large increases in the no-shade reaches in the stream, precisely in the reverse direction of body condition estimates (Appendix 2). Though not presented here, temperature profiles for stream reaches had considerable intervals of time (>20 days) during which stream temperatures range over 14° C, temperatures rarely selected by first- and second-year larval Coastal tailed frog in a thermal gradient (de Vlaming and Bury 1970). This may suggest that despite increased periphyton levels, food resources either were poorer in quality, less used or less well assimilated; a bioenergetic pattern with parallels in salmonid fishes (Brett et al. 1969, Leach et al. 2011).

Overall, our results for tailed frogs in terms of trends in body condition estimates and growth rates are at least partly consistent (i.e., at the lowest shade levels) with the potential for bottom-up control of tailed frog populations; and at worst, do not clearly support alternatives. However, ES estimates of abundance are consistent with this interpretation only for the intermediate-shade reaches, which suggests that if this interpretation is part of the explanation, one or more additional factors complicate the pattern (Appendix 2). Tailed frogs are preyed on by American dippers (*Cinclus mexicanus*; Morrissey and Olenick 2004) both species of giant salamanders sampled in this study (Bury 1968), red-legged frogs (*Rana aurora*; Jones and Raphael 1998), and garter snakes (*Thamnophis* spp.; Karraker 2001); cutthroat trout

(*Oncorhynchus clarki*) are suspected predators also (Daugherty and Sheldon 1982). Increased light levels may increase larval susceptibility to predation, particularly by diurnal/crepuscular predators like American dippers and nocturnal predators when there is a full moon and clear skies. However, we cannot evaluate the impact of predation and it is unknown whether any of these predators can actually limit tailed frog populations.

Captures of post-metamorphic tailed frogs were too few to conduct a meaningful analysis and provide reliable inferences about treatment effects. Sampling mature adults that spent their entire life in a single treatment reach would likely reveal the true effects of shade reductions on the species (Mallory and Richardson 2005). However, to accomplish this our study would have had to continue for several more years and efficiently target adults for sampling with pitfall traps (Matsuda and Richardson 2005), night spotlighting (Diller 2011, pers. comm.), or some other method.

Mallory and Richardson (2005) conducted a study with tailed frog larvae in British Columbia with an experimental design similar to ours. They examined the effects of two light levels (full sun and complete shade), nutrient additions (N and P), and six levels of tailed frog density in three sizes of in-stream enclosures; sampling chlorophyll *a* concentration, periphyton AFDM accrual, and tadpole growth rates. Estimates for all response variables were greater under the full sun treatment. They also reported density-dependent effects on tadpole growth rates at 14-29 tadpoles/m^2. We maintained a density of 23-35 tadpoles/m^2 in our enclosures, which may have contributed to limiting growth rates, based on the negative values we obtained. Mallory and Richardson (2005) also reported an effect of the enclosures themselves on the response variables, which was also related to enclosure size. This appeared to be the case in this study for maximum water temperature as enclosure estimates were warmer in 12 of 16 comparisons with stream temperatures and periphyton accrual was also consistently greater in enclosures than in streams (Appendix 2). These data indicate that conditions in enclosures differed from the streams, most obviously due to reduced water flow (J. MacCracken, pers. observ.) and perhaps macroinvertebrate densities, etc. and as Mallory and Richardson (2005) pointed out, enclosure effects could confound comparisons among studies that use different enclosure designs. Our enclosure design was constant, but due to year-to-year changes in manufacturer's specifications and availability of different models of the plastic boxes, the size of our enclosures varied.

Giant salamanders

The abundance of giant salamanders increased in the no-shade reaches following shade reductions, but shade reductions generally appeared to have little effect on either body condition or growth rates (Appendix 2). In general, the response of giant salamanders to the opening of forest canopies due to timber harvest has been mixed (Murphy and Hall 1981, Hawkins et al. 1983, Bisson et al. 1996, Steele et al. 2003, Kiffney and Roni 2007) and varies by species. Coastal giant salamanders have either responded positively to canopy reductions (Murphy and Hall 1981, Adams and Bury 2002, Steele et al. 2003, Kiffney and Roni 2007) or exhibited little change (Hawkins et al. 1993), probably due to site-specific characteristics. On the other hand, the two studies that differentiated Cope's giant salamanders found little effect of canopy openings on that species (Bisson et al. 1996, Steele et al. 2003). Because we did not differentiate between the two species, interpretation of our results is compromised. The increase in the no-shade reaches suggests that our study sites may have been dominated by coastal giant salamanders and supports the findings of other studies of this species if that is true. Steele et al.

(2003) surveyed streams within our Texas Cr. and Beacon Rock blocks in the Cascade Range and captured nearly equal numbers of the two species (221 Cope's, 212 coastal) over two years of sampling, but in streams that had both species, coastal giants outnumbered Cope's by 10-20%. This could explain the increase in abundance in the no-shade reaches and lack of differences in the other reaches and for the other metrics.

Cascade torrent salamanders

Cascade torrent salamanders showed some of the largest responses to shade reductions of any species. Abundance, body condition, and growth rate ES increased in the intermediate-reaches and estimates were greater in those reaches than the no- and low-shade reaches following shade reductions (Appendix 2). Steele et al. (2002) sampled streams across a forest age gradient (0-94 years) in or near our Texas Cr. and Beacon Rock blocks and had the lowest captures in streams in forests 0-24 years of age and the greatest captures in streams in forests 25-60 years old. They noted the relationship between captures, forest stand characteristics associated with successional stages, and trends in light penetration levels. The results of this study and Steele et al. (2002) are consistent with the predictions of the light:nutrient hypothesis in that abundance, body condition, and growth rates peaked at moderate light levels. Furthermore, these findings suggest a bottom-up trophic cascade for these west Cascade Range stream ecosystems. No predators of larval or post-metamorphic torrent salamanders have been documented (Petranka 1998) and torrent salamanders placed in aquaria with a giant salamander were captured, but quickly expelled (Rundio and Olson 2001).

In contrast to our results, Russell et al. (2005) did not find a relationship between Cascade torrent salamander abundance or occupancy and stand age at the stream reach (10 m) scale, but they did report a positive relationship with forest age (0-90 years) at the landscape scale (2.58 km^2), a result at least partially consistent with that of Steele et al. (2003). However, neither of these studies or others published before 2009 estimated detection probabilities.

Columbia torrent salamanders

MacCracken (2002) found that Columbia torrent salamanders had greater body condition, but lower densities in streams where the overhead tree canopy had been reduced, retaining 50-70% in the Coast Range of southwest Washington. In contrast, the only significant response of this species to shade reductions in this study was an increase in growth rates for the no-shade reaches (Appendix 2). We detected no statistically significant trends in body condition estimates for this species in this study, but this comparison may be confounded because MacCracken (2002) used the residuals body condition index which can be unreliable if a number of conditions are not met (Green 2001). However, ranked SMI ES estimates increased (40-250%) in this study across all shade levels, with the greatest increase in the intermediate-shade reaches (Appendix 2). Though this appears consistent with MacCracken (2002) and the light:nutrient hypothesis as well as a bottom-up trophic cascade, the non-significant interaction term for our data indicates that we cannot attribute this change solely to treatment effects. In contrast, Russell et al. (2004) did not find a relationship between Columbia torrent salamander abundance or occupancy and forest age or overhead cover in the Coast Range of Oregon.

Olympic torrent salamanders

Similar to Cascade torrent salamanders, Olympic torrent salamanders also increased in abundance in the intermediate-shade reaches and those reaches had significantly more salamanders than the low- reaches following shade reductions (Appendix 2). In addition, growth rates also increased more in the no-shade reaches than the other reaches, but the non-significant interaction term indicates an effect cannot confidently be tied to the treatment (Appendix 2). These trends appear consistent with the light:nutrient hypothesis and a bottom-up effect.

Body condition and growth rates

MacCracken and Stebbings (2012) suggested that changes in habitat that effect amphibian populations may become evident through indices of body condition before changes in demographic parameters can be detected. For relatively long-lived species with moderate reproductive rates like PNW SAAs, we would expect energy stores to fluctuate on a finer temporal scale than population numbers, barring a large mortality event or mass movements. In this study, we found more significant period × treatment interactions for count data (2) and body condition (2) than growth rate (1) estimates. Factors unrelated to habitat change can affect population size, e.g., predation and movements, but energy stores are largely a function of habitat quality. However, body condition may not always reflect habitat quality, depending on energy demands, food availability, life history stage, predation pressure, and other extrinsic factors. For example, Schultner et al. (2012) found that black-legged kittiwakes (*Rissa tridactyla*) did not maximize energy stores when given supplemental food during chick-rearing periods, presumably to reduce the energetic costs of frequent and extended foraging trips. Animals may also limit energy storage when long-distance movements are undertaken to reduce movement costs or when predation pressure is high in order to enhance maneuverability if attacked. As Schultner et al. (2012:9) noted, "…equating large energy stores with prime environmental conditions may oversimplify the natural situation." This could explain why body condition estimates for amphibians are sometimes equivocal, counterintuitive, and inconsistent with other metrics.

Growth rates as estimated in this study (change in mass) and others (Kiffney et al. 2004, Mallory and Richardson 2005) would fluctuate on an even finer temporal scale and could reflect energy stores more than actual growth. Relative changes in measures of total length, limb length, or head size may reflect changes in growth rates better than changes in mass.

Assuming that both body condition and growth rates largely reflect the assimilation of food resources, our results suggest that food resources for Cascade and Columbia torrent salamanders were enhanced in both the no- and intermediate-shade treatments (Appendix 2). Little is known about the foods of torrent salamanders (Petranka 1998) and the only information available is for *R. variegatus* (Bury 1970) and *R. kezeri* (O'Donnell and Richart 2012). Both these studies found a wide variety of food items in stomachs, suggesting the species are opportunistic. Linking greater body condition and growth rates of torrent salamanders in this study to the response of macroinvertebrates to shade reductions is hampered by our level of taxonomic resolution, but the drift of gathering collectors (which included Diptera - a major item found in Columbia torrent salamander stomachs [O'Donnell and Richart 2012]), increased significantly in the intermediate-shade reaches.

Water temperature

Numerous studies in the PNW have reported increases in water temperatures in small streams with reduced shading (Brown 1969, Johnson 2004, Danehy et al. 2005, Gomi et al. 2006). Steele et al. (2003) suggested that headwater streams were less susceptible to temperature increases associated with reduced shade due to groundwater inputs. Our results were not completely consistent with that conclusion, but Steele et al. (2003) conducted their study in relatively high elevation streams in and near our Beacon Rock and Texas Cr. blocks in the western Cascade Range (Fig. 1) and some of our steams in those blocks had the least amount of change in water temperature following shade reductions (1.0 vs. 1.5-2.0 °C). These inconsistencies point to an underappreciated recognition of the magnitude of site-specific effects.

Stream temperature increases have been implicated in the low numbers of stream amphibians in managed forests (Hawkins et al. 1988, Welsh and Lind 1996, Wahbe and Bunnell 2003, Olson et al. 2007). However, many studies have made only one-time, spot readings of stream temperature when sampling amphibians. This can be misleading because readings may be biased (up or down) relative to the temporal profile (for example, they cannot account for intervals of potential exposure to elevated temperatures) and spot measurements may miss cold-water refugia (Bilby 1984, Danehy et al. 2005, Groom et al. 2011). The laboratory derived critical thermal maxima for most amphibian species are about 10-15° C, higher than maximum temperatures recorded in many field studies (Brattstrom 1963, Bury 2008), and temperatures actually selected may be much lower (de Vlaming and Bury 1970). Pollett et al. (2010) found that occupancy of headwater streams by Cascade torrent salamanders was reduced when stream temperature was $\geq$14° C for 35 consecutive hours. The seasonal maximum and maximum seven-day moving average of most of our study reaches equaled or exceeded 14° C prior to shade reductions and all were occupied by one species of *Rhyacotriton* as well as tailed frogs. However, our water temperature estimates may not represent the entire 50-m reach as the thermistors were placed at the bottom of each reach and likely overestimate a reach-long average, particularly where ground water inputs are important.

The relationship between changes in levels of shading and changes in stream temperature is remarkably consistent among recent studies. We recorded an average increase in seasonal maxima of 4.0^{o} C following a 100% reduction in shade. Johnson (2004) also reported a 4.0^{o} C difference in temperature between streams with 100% artificial shading and those with no shading. In addition, Groom et al. (2011) found that the best model relating shade and stream temperature predicted a 2.0^{o} C change at 50% shading. A simple ordinary least squares regression of percent change in seasonal maximum temperature (y) as a function of percent change in shade (x) over all the reaches sampled in this study resulted in the following relationship: $y = -0.57 + 4.14(x)$, $r^2 = 0.85$.

Management Implications: Most studies that evaluated the potential effects of timber harvesting on headwater streams are limited in spatial and temporal scope, and few incorporate pre-harvest sampling. Thus, their scope of inference is limited, which often constrains their application when developing management plans and regulations, assessing species status, and for other purposes. In this study, we included pre-treatment sampling using a BACI design, kept our scope of inference broad by selecting sites from a large geographic area and a wide range of treatments that were replicated eight or nine times, and evaluated responses of SAAs from all three stream-associated genera known to occur in the PNW. In addition, we controlled for aspect, gradient, and parent lithology. Despite our efforts at controlling undesired variation, rarely accomplished in manipulative ecological experiments, site and yearly differences appeared to have a greater effect on response variable estimates in this study than shade reductions in 15 of 117 (4%) comparisons.

Several constraints limit conducting geographically broad manipulative experiments. Other than cost and logistics, the practice of frequentist statistical hypothesis testing and the peer-refereed publication process are also influential. It is not uncommon for ecologists to narrowly define an experimental unit and the study area in hopes of reducing background variation and increasing the likelihood of demonstrating a statistically significant effect, which is often perceived as a requirement for publication (Russell et al. 2012). Much has been written on the use and misuse of statistics in ecology (Johnson 1999, 2002, Anderson et al. 2000) and alternatives have been identified (Dixon and Ellison 1996, De'ath and Fabricus 2000, Burnham and Anderson 2002), but null hypothesis testing remains the dominant approach. Because forestry practices are regulated over broad geographies (e.g., by states or uniformly on federal lands across the PNW), the most relevant studies will also have to have broad application. As noted in the Introduction, studies of SAAs in the PNW are contradictory, likely due to a combination of the narrow focus of each and regional, local, and site-specific variation in habitat conditions.

A number of previous studies have also confounded the primary effects of timber harvest on headwater streams – reduced shade and increased fine sediment inputs – by not controlling for either and by sampling at sites where both variables can vary widely. We intentionally avoided manipulating vegetation with ground-based harvesting/skidding equipment by applying shade reduction treatments by hand to minimize increases of sediment input to study reaches and specifically examined responses to four levels of shade retention, attempting to cover the entire gradient in light levels. One of the purposes of that approach is to determine if thresholds in community responses to irradiance could be detected that would apply to riparian area management guidelines.

Over the last few decades, fixed-width buffers with limited or no manipulation have become the standard prescription to protect aquatic resources from forestry practices (Richardson et al. 2012). This approach has come under increasing scrutiny and found to create unnatural linear patterns of forest landscape structure, a decline in the complexity and diversity of riparian stands and networks, a potential decline in resiliency, and a loss of aquatic community structure and function that is associated with various types and intensities of disturbance (Kreutzweiser et al. 2012, Sibley et al. 2012). One proposed solution is to manage riparian forests in ways that emulate natural disturbances, acknowledging that a cautious, site-specific experiment-by-management approach is required (Sibley et al. 2012). Two of the primary natural disturbance regimes of riparian forests in the PNW are windthrow and channel realignment that create relatively small to moderate gaps in the forest canopy (Naiman et al. 1998). The results of our study provide some insight into the effects of disturbances that create similar-sized forest canopy gaps (≈ 0.1 ha) and potential guidance for gap management.

In areas of intensive forest management in the PNW, headwater riparian stands are often dominated by red alder (*Alnus rubra*)-salmonberry (*Rubus spectabilis*) communities (MacCracken 2002), but can also be composed entirely of conifers or mixed hardwood-conifer stands depending on past harvest practices and site conditions. Regardless of stand composition, dense shading limits stream productivity and to optimize stream productivity those stands may need thinning or have gaps created in them. Even in riparian areas dominated by hardwoods, decreases in canopy cover can result in positive responses in light-limited ecosystems, both aquatic and terrestrial (MacCracken 2002). Our results indicated that the productivity of streams with dense canopy cover (>70%) would be positively influenced by creating openings in the canopy which correspond to the low- to intermediate- ranges tested in this study. In addition, the intermediate-shade treatment level was more often associated with slightly greater improvements in stream productivity metrics and positive amphibian responses than the low-shade treatment level with the added benefit of smaller water temperature increases (mean ES seven-day moving average <1.0^{o} C as compared with 2.5^{o} C). However, this pulse of energy to streams will be relatively short-lived, particularly at greater shade retention levels, as remaining vegetation will re-occupy vacant growing space within two to ten years (Howard and Newton 1984, Newton et al. 1993, MacCracken 2002, Popescu et al. 2012). Nonetheless, canopy openings could provide several cohorts of SAAs with high quality habitat in terms of food resources that could increase their lifetime fitness. These forest canopy dynamics will likely result in a lagged response with some SAA populations peaking a decade or so after complete canopy closure (e.g., Steele et al. 2002, see also Findlay and Bourdages 2000 and Lövenhaft et al. 2004 for lagged responses by herptiles to road construction and urban development, respectively). Periodic reductions in shade over headwater channels on the time and spatial scale of commercial forest rotations in the PNW can increase short-term stream productivity with minimal on-site negative impacts given current regulations for private and state lands and also benefit downstream reaches (Bisson and Bilby 1998).

Regulations protecting headwater streams on state and private commercial forest lands differ by state. In Oregon, headwater streams are protected with a 3-10-m riparian management zone with specific vegetation retention and basal area targets depending on stream type and size. The effects of these rules on SAAs are unstudied. However, Russell et al. (2004, 2005) found that the majority of headwater streams in the intensively managed forests (0-80 year old second- and third-growth, naturally or artificially regenerated) they sampled in Oregon were occupied by torrent salamanders, including the highest density ever recorded for the Columbia torrent salamander (Russell et al. 2004) and evidence of successful reproduction (Russell et al. 2002).

In Western Washington headwater stream buffer prescriptions are too complex to describe in detail here, but rely on a combination of continuous buffers and patch buffers around specific stream features. At least 50% of the length of perennial headwater streams receives a 15-m wide unmanaged buffer on both sides of the channel starting at the junction with the fish-bearing segment. In addition, all sensitive sites (e.g., seeps, springs, stream origins, and tributary junctions) receive a ≥ 0.07 ha patch buffer, depending on the size and type of sensitive site. Thus, the scale of our experimental reaches (≈ 0.1 ha) is similar to that of the patch buffer and our results are most applicable to changes that could occur in patch buffers due to changes in vegetation cover. In addition, buffers may be required on greater than 50% of the channel length if buffers of sensitive sites and the junction with the fish bearing stream encompass more than the 50% length.

Even though marketable trees will not be retained in harvested reaches of headwater streams in western Washington, a 9-m stream-side equipment exclusion zone is required on both sides and should maintain the shrub layer and associated shading that could range from 0-100% depending on site conditions. Even though our experimental reaches will most often be substantially shorter than harvested reaches, our findings may be applicable to the open reaches created by these regulations depending on the characteristics of the shrub layer. Openings upstream of fully shaded buffered areas should provide salamanders residing in the stream within those buffers with increased macroinvertebrate prey through stream drift, at least at the interface of shaded and open reaches. However, those openings may do relatively little for larval tailed frogs residing in the buffers. The efficacy of the western Washington prescription is currently under investigation.

Application of our results at the watershed level should be undertaken with caution given the significantly large increases in water temperatures over a relatively short distance (50 m) at the lowest shade levels and the potential for cumulative impacts. However, green-up rules, constraints on harvest unit size, and locations with a more northerly aspect will act to reduce this potential.

Overall, our results indicate that different species (and life stages of SAAs) respond differently to changes in habitats resulting from reduced vegetation cover. For any specific shade level, ecoregion, and stream there were ecological winners and losers. These findings suggest that regulations could be tailored to a variety of situations, and Washington and Oregon already recognize the ecological differences between the west- and east-slope of the Cascade Range in regulation. Further refinements for west-side ecosystems may be warranted. Under a one size fits all approach, negative impacts will occur for some species at particular times and places, positive effects will be realized by others, and still others will be unaffected. Over time, as riparian forests move through successional stages this may balance out, but with further refinement it may be possible to reduce negative impacts, maintain or increase positive and null responses and increase the economic return of state and private forests. Situations that result in positive and null effects define the scope of possible management alternatives (Guthery et al. 2001) and “treatments” under an adaptive management framework.

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Appendix 1. Location and major physical and vegetation features of the sampling units in the study. The general location of blocks is shown in Figure 1. Dominant species codes are listed in Appendix II.

Ecoregion	Block	Reach	Treatment (% cover)	Latitude (DD)	Longitude (DD)	Elevation (m)	Aspect (°)	Gradient (°)	Dominant Species[a]
South Cascades	Beacon	Treatment	0	45.68539	-122.03196	734	153	15	TSHE/ALRU
	Rock	Reference		45.68607	-122.03248	745	147	15	TSHE/ALRU
		Treatment	30	45.70679	-122.02994	774	188	11	ALRU/PSME
		Reference		45.70777	-122.02658	796	218	12	ALRU/PSME
		Treatment	70	45.71371	-122.04448	563	170	10	TSHE/ALRU
		Reference		45.71469	-122.04406	670	194	11	TSHE/ALRU
	Texas Cr.	Treatment	0	45.70471	-122.19696	655	180	25	ALRU/PSME
		Reference		45.70414	-122.19852	702	180	24	ALRU/PSME
		Treatment	30	45.69526	-122.21708	448	206	18	ALRU/PSME
		Reference		45.69625	-122.21681	504	201	15	ALRU/PSME
		Treatment	70	45.70352	-122.19765	592	179	19	ALRU/PSME
		Reference		45.70488	-122.19817	699	188	18	ALRU/PSME
	Rock Cr.	Treatment	0	46.02393	-122.48784	567	213	15	TSHE/ALRU

Appendix 1. Continued.

		Reference		46.02529	-122.48718	610	187	19	TSHE/ALRU
		Treatment	30	46.01143	-122.45325	511	225	22	PSME/TSHE
		Reference		46.01163	-122.45259	513	208	13	PSME/TSHE
		Treatment	70	46.02341	-122.44988	567	222	17	ALRU/TSHE
		Reference		46.02431	-122.44905	610	193	10	PSME/ALRU
Coast Range	KM Mtn.	Treatment	0	46.38024	-123.53820	65	224	21	ALRU/TSHE
		Reference		46.38087	-123.53740	156	183	19	TSHE/ALRU
		Treatment	30	46.36103	-123.47655	314	193	17	ALRU/TSHE
		Reference		46.36200	-123.47609	318	202	21	ALRU/TSHE
		Treatment	70	46.35953	-123.47423	315	225	24	TSHE/ALRU
		Reference		46.35970	-123.47310	345	250	70	ALRU/TSHE
	Humbug Mtn.	Treatment	0	45.91600	-123.67700	362	153	13	ALRU/TSHE
		Reference		45.91746	-123.67844	388	140	13	ALRU/TSHE
		Treatment	30	45.89016	-123.72037	326	144	10	ALRU/TSHE
		Reference		45.88993	-123.72100	344	147	11	ALRU/TSHE

Appendix 1. Continued.

		Treatment	70	45.88095	-123.69739	300	218	10	TSHE/ALRU
		Reference		45.88231	-123.69699	304	207	10	TSHE/ALRU
	Soapstone Cr.	Treatment	0	45.79903	-123.88137	335	151	25	TSHE/PSME
		Reference		45.79959	-123.88245	339	171	13	TSHE/PSME
		Treatment	30	45.83788	-123.85273	387	186	17	TSHE/PSME
		Reference		45.83861	-123.85299	431	155	21	TSHE/PSME
		Treatment	70	45.78962	-123.89407	341	194	10	TSHE/PSME
		Reference		45.79100	-123.89400	341	156	12	TSHE/PSME
Olympics	Waketickeh Cr	Treatment	0	47.60458	-123.00734	628	100	4	ALRU/TSHE
		Reference		47.60509	-123.00830	632	180	5	ALRU/ACMA
		Treatment	30	47.60232	-123.06597	505	154	32	THPL/PSME
		Reference		47.60365	-123.06609	538	197	35	ALRU/TSHE
		Treatment	70	47.58063	-123.06123	304	116	17	ALRU/THPL
		Reference		47.58170	-123.06155	283	127	15	ALRU/ACMA
	Sund Cr.	Treatment	0	47.43532	-123.15615	233	116	4	ALRU/TSHE

Appendix 1. Continued.

	Reference		47.43569	-123.15799	239	85	4	ALRU/TSHE
	Treatment	30	47.45435	-123.15811	185	95	6	ALRU/TSHE
	Reference		47.45459	-123.15962	433	97	7	ALRU/TSHE
	Treatment	70	47.45944	-123.13631	178	97	8	ALRU/PSME
	Reference		47.46001	-123.13686	200	160	16	ALRU/PSME
Jorsted Cr.	Treatment	30	47.52435	-123.10975	242	142	20	ALRU/ACMA
	Reference		47.52507	-123.11100	275	142	10	ACMA/ALRU

[a]TSHE = *Tsuga heterophylla* (Western hemlock), ALRU = *Alnus rubra* (Red alder), PSME = *Pseudotuga menziesii* (Douglas-fir), THPL = *Thuja plicata* (Western red cedar), and ACMA = *Acer macrophyllum* (Big leaf maple)

Appendix 2. Effect size (90% confidence interval) for physical and biotic variables at 3 levels of shade retention (no-, low-, intermediate-) based on pre-treatment and post-treatment (2 years each) contrasts for 25 streams in northwest Oregon, southwest Washington and the Olympic peninsula that were sampled from 2006-2009. Sign of the effect size (-,+) indicates direction of response. *P*-value is for the period × treatment interaction. We regarded $\alpha \leq 0.1$ as significant (see text). For each shade level: * *P* = 0.1, ** *P* <0.1-0.01, *** *P* <0.01-0.001, **** *P* <0.0001.

	Shade level			
Variable	No	Low	Intermediate	*P*
Photosynthetically active				
radiation (μmols/m^2/sec)	589**** (505–673)	422**** (343–501)	210**** (126–294)	0.0001
Water temperature (^{o}C)				
Stream				
Seasonal maximum	3.0**** (2.0–4.0)	1.5** (0.5–2.5)	0.5 (-0.5–1.5)	0.001
7-day maximum[a]	2.5**** (1.5–3.5)	2.0**** (1.0–3.0)	0.5 (-0.5–1.5)	0.0001
Enclosure[c]				
Seasonal maximum[b]	-10.0 (-31.0–11.0)	8.0 (-13.0–29.0)	15.0 (-5.0–35.0)	0.03
7-day maximum	-17.0 (-37.0–3.0)	-2.5 (-23.5–18.5)	9.0 (-11.0–29.0)	0.11
Periphyton accrual (g/m^2 AFDM)[b]				
Stream	28** (8–48)	27** (8–46)	26** (6–46)	0.23
Enclosure	12 (-11–35)	12 (-9–33)	4 (-16–24)	0.78

Appendix 2. Continued.

Stream drift[b]				
Coarse particulate organic matter				
g/m^3	-63***	-10	-7	0.19
	(-102– -54)	(-48–28)	(-46–32)	
g/day	-30	-15	-1	0.75
	(-69–9)	(-53–23)	(-40–38)	
Fine particulate organic matter				
g/m^3	-32	20	-8	0.43
	(-71–7)	(-18–58)	(-49–33)	
g/day	-32	14	16	0.42
	(-70–6)	(-22–50)	(-23–55)	
Macroinvertebrates				
Filtering collectors				
g/m^3	-18	-3	20	0.72
	(-57–21)	(-41–35)	(-19–59)	
g/day	-12	4	28	0.66
	(-50–26)	(-34–42)	(-11–67)	
Gathering collectors				
g/m^3	-14	84****	31	0.008
	(-52–24)	(48–120)	(-7–69)	
g/day	-13	63***	37	0.06
	(-51–25)	(27–99)	(-1–75)	

Appendix 2. Continued.

Predators				
g/m^3	-42**	23	-15	0.22
	(-81– -3)	(-15–61)	(-56–26)	
g/day	-25	17	9	0.59
	(-64–14)	(-22–56)	(-32–50)	
Scrapers				
g/m^3	-1	9	19	0.91
	(-40–38)	(-29–47)	(-20–58)	
g/day	23	4	40**	0.56
	(-15–61)	(-32–40)	(2–78)	
Shredder				
g/m^3	-69***	-4	1	0.09
	(-107– -31)	(-40–32)	(-37–39)	
g/day	-33	19	-4	0.46
	(-71–5)	(-19–57)	(-43–35)	
Total mass				
g/m^3	-38	16	29	0.20
	(-77–1)	(-22–54)	(-12–70)	
g/day	-6	22	35	0.55
	(-45–33)	(-16–60)	(-4–74)	
Total count of individuals				
$number/m^3$	-41**	-2	31	0.47
	(-79– -3)	(-38–34)	(-7–69)	
number/day	30	32	16	0.82
	(-9–69)	(-6–70)	(-23–55)	

Appendix 2. Continued.

Amphibian metrics				
Counts (number/reach)[e]				
Ascaphus truei	-2 (-7–3)	-3 (-8–2)	3 (-2–8)	0.74
Dicamptodon spp.	8*** (3–13)	1 (-4–6)	0 (-5–5)	0.08
Rhyacotriton cascadae	-5 (-10–0)	5 (0–10)	9** (4–14)	0.10
Rhyacotriton kezeri	2 (-1–4)	-1 (-4–2)	-2 (-7–3)	0.61
Rhyacotriton olympicus	-2 (-5–1)	-3** (-6–0)	5** (2–8)	0.06
Body condition (g)[b]				
Ascaphus truei				
Larva	15** (2–28)	32*** (17–47)	1 (-15–17)	0.04
Metamorph	-2 (-12–8)	26** (10–42)	-4 (-15–7)	0.13
adult[f]	-5 (-20–10)	3 (-7–13)		0.78
Dicamptodon spp.	-8 (-26–10)	-8 (-26–10)	14 (-4–32)	0.46
Rhyacotriton cascadae	7 (-1–15)	-10** (-18– -2)	11 (-4–26)	0.10
Rhyacotriton kezeri	7 (-3–17)	4 (-4–12)	10 (-1–21)	0.65

Appendix 2. Continued.

Growth (g/week)				
Ascaphus truei				
Larva	0.01** (0.00–0.02)	0.01** (0.00–0.02)	0.02** (0.01–0.03)	0.20
Metamorph	-0.02 (-0.05–0.01)	0.01 (-0.02–0.04)	-0.04** (-0.07– -0.01)	0.39
Dicamptodon spp.	-0.04 (-0.09–0.01)	-0.01 (-0.06–0.04)	-0.02 (-0.07–0.03)	0.72
Rhyacotriton cascadae	0.01 (-0.01–0.03)	-0.01 (-0.03–0.01)	0.03** (0.01–0.05)	0.33
Rhyacotriton kezeri	0.06*** (0.03–0.09)	-0.01 (-0.04–0.02)	0.00 (-0.03–0.03)	0.10
Rhyacotriton olympicus	0.02** (0.00–0.04)	0.01 (-0.01–0.03)	0.01 (-0.01–0.03)	0.33

[a] moving average of daily maximum temperature over 7 consecutive days.

[b] data rank-transformed.

[c] reference reaches amphibian instream enclosures.

[d] p-values for g/m^3 of stream flow and g/day, respectively.

[e] corrected for probability of detection.

[f] not enough adults were captured in theintermediate-shade reaches to estimate body condition.