

## A network model for primary production highlights linkages between salmonid populations and autochthonous resources

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**Abstract.** Spatial variation in fish densities across river networks suggests that the influence of food and habitat resources on assemblages varies greatly throughout watersheds. Conceptual models predict that in situ primary production should vary with river characteristics, but the influence of autochthonous resource availability on the capacity for river reaches to support fish is poorly understood. We estimated primary production throughout the South Fork and Middle Fork of the John Day River, Oregon, by measuring diel cycles in dissolved oxygen (DO) during July 2013. Using these data, we (1) evaluated the extent to which juvenile salmonid abundance and resource limitation correlated with areas of high gross primary production (GPP), (2) developed models to predict GPP from both site-level measurements and remotely sensed data, and (3) made predictions of GPP across the entirety of the Middle Fork John Day River (MFJD) network and assessed the utility of these spatially continuous predictions for describing variation fish densities at broad scales. We produced reliable estimates of GPP at sites where DO loggers were deployed using measurements of solar exposure, water temperature, and conductivity measured at each site, as well as surrogates for these data estimated from remote sensing data sources. Estimates of GPP across fish sampling sites explained, on average, 58–63% of the variation in juvenile salmonid densities during the summer sampling period, and 51–83% during the fall sampling period, while continuous network predictions of GPP explained 44% of the variation in fish densities across 29 km of the MFJD. Further, GPP explained nearly half of the variation in juvenile steelhead dietary resource limitation, as inferred from bioenergetics modeling results. These results comprise a first effort at quantifying variation in autochthonous production across an entire river network and, importantly, provide a much-needed food-web context for guiding more effective fish and habitat management.

**Key words:** bioenergetics; conductivity; network model; *Oncorhynchus mykiss*; *Oncorhynchus tshawytscha*; primary production; riverscapes; solar radiation; stream salmonids; water temperature.

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### INTRODUCTION

Primary production is a principle source of energy for consumers and a dominant control on the structure and function of ecosystems globally. In freshwaters in particular, major ecosystem properties, such as species richness (Guégan et al.

1998, Dodson et al. 2000), secondary production (Downing et al. 1990, Finlay 2011), and food-web structure (Takimoto and Post 2013), vary predictably with increasing autochthonous production. Aquatic primary production, in turn, ranges widely across scales due to variation in the availability/presence of nutrients and light (Mulholland

et al. 2001) or the strength of cascading trophic interactions (Strong 1992, Borer et al. 2005), among other factors. Given its influential role, understanding how primary production, and its association with aquatic biota, varies across space is fundamental to contemporary ecosystem theory and effective watershed management (Woodward and Hildrew 2002, Barquín et al. 2015).

Existing work provides a basis for describing spatial variability in productivity in relative terms, particularly for streams. The seminal river continuum concept (Vannote et al. 1980), for example, posits that aquatic primary production forms the dominant energy base in mid-sized streams, relative to smaller headwater streams or larger lowland rivers in which allochthonous resources prevail. Although these predictions have some empirical support (Finlay 2011, but see Winterbourn et al. 1981), riverscape-scale models of food-web structure and ecosystem function remain largely conceptual and provide little insight into productivity in specific numerical terms, despite the fact that well-developed tools exist for quantifying aquatic production and ecosystem metabolism at local scales (e.g., Demars et al. 2015). This is in stark contrast to the state of knowledge for terrestrial ecosystems, for which a wealth of data on primary production exists and supports a variety of biological assessments at different spatial and temporal scales (see Šimová and Storch 2017 for a recent review).

Despite gaps in knowledge, there is a pressing need for accurate estimates of aquatic production both at local scales and for entire stream networks, particularly within a river-restoration context. Firstly, restoration practitioners increasingly recognize that the success or failure of particular management strategies can depend on how system changes interact with or are mediated by the structure and function of biological communities (e.g., Power et al. 1996, Bellmore et al. 2017). Accordingly, Naiman et al. (2012) provide a recent and compelling argument in favor for pursuing river restoration with an explicit ‘food-web perspective’ in mind. Secondly, efforts to recover endangered fish (e.g., Pacific salmon, *Oncorhynchus* sp., in the U.S. Pacific Northwest) rely heavily on assumptions about the capacity of particular habitats to support fish (e.g., Wheaton et al. 2018), often with little data on the inherent productivity of habitats. Thus, quantitative insight

into primary production for entire riverscapes offers a powerful means to estimate fish production or carrying capacity at unprecedented scales (e.g., McGarvey and Johnston 2011). More locally, however, a spatially explicit and continuous view of productivity can shape the where and what for specific on-the-ground restoration actions, for example, helping to distinguish sites that may be good candidates for physical habitat restoration (e.g., woody debris addition; Roni et al. 2014) vs. nutrient addition (e.g., salmon carcass addition; Collins et al. 2015).

While there are obvious benefits to integrating productivity considerations into watershed restoration and fisheries management, lotic fish ecologists have historically viewed habitat through a physical rather than biotic (or combined) habitat lens (Wurtsbaugh et al. 2015). This emphasis, which contrasts with research traditions in standing waters, is perhaps a result of three factors. First, physical disturbance (e.g., floods, drought-related low-flow extremes) is a hallmark feature of streams, and indeed influences fish populations and communities, in some systems (Jensen and Johnsen 1999, Sabo et al. 2010), to such an extent that there may be little reason to consider biotic habitat attributes, such as productivity. The second reason is historical—an early emphasis on physical factors in studies of stream fish–habitat relationships, spurred in part by policy needs (e.g., Minns et al. 2011), may simply have narrowed the scope of inquiry for the discipline in general (Graham and Dayton 2002). A final, practical reason is that stream food webs are inherently complex, which poses significant challenges to efforts aimed at assessing habitat productivity in a manner that is meaningful to fish, tractable, and cost-effective. At their base, for instance, stream food webs are fueled by a mix of both in-stream and riparian primary production (e.g., Jardine et al. 2012). Once basal energy pools are assimilated and available to fish via secondary (invertebrate) production, the strength of in-stream trophic pathways may be diminished by terrestrial invertebrate subsidies (e.g., Baxter et al. 2005). This complexity is further compounded by a potentially high degree of spatiotemporal variability in energy flow and food-web structure in riverine systems (Woodward and Hildrew 2002, Finlay and Kendall 2007, Kiffney et al. 2014). In sum, reliably estimating habitat productivity is a difficult and costly task.

Nonetheless, fish-habitat restoration efforts are likely to be more effective if productivity considerations are factored into the planning and design process, as different strategies will be prescribed under an assumption of biotic vs. abiotic habitat limitation (Rosenfeld 2003). Yet, strategies for recovering populations of threatened or endangered Pacific salmon in the Columbia River Basin, where a large-scale and costly habitat-restoration program is currently underway, are formulated largely without a food-web or productivity context (Naiman et al. 2012). To address this deficiency, here we present an approach that allows for the accurate and cost-effective estimation of stream-habitat productivity at both local and network scales. More specifically, our goal was to develop a tool for making spatially explicit predictions of habitat productivity that could be used to inform habitat recovery efforts and limiting factor analyses centered around two anadromous salmonids of concern (steelhead/rainbow trout, *Oncorhynchus mykiss*; and Chinook salmon, *Oncorhynchus tshawytscha*) in two tributaries to the John Day River Basin, Oregon: the Middle Fork John Day River (MFJD) and Murderers Creek. The specific objectives of our study were fourfold: (1) to quantify spatial variation in gross primary productivity (GPP) across the MFJD and Murderers Creek watersheds; (2) to evaluate relationships between GPP and three physicochemical predictors (i.e., light, temperature, and conductivity) that were measured in situ but that can also be acquired for any point in the river network from existing geospatial data sets; (3) to link spatial patterns in primary production to the distribution and abundance of *O. mykiss* and Chinook salmon; and (4) to make continuous, spatially explicit predictions of GPP for the MFJD and Murderers Creek stream networks. In doing this work, we focused exclusively on the MFJD and Murderers Creek watersheds, but we provide a framework that can be readily adapted to any watershed.

## METHODS

### Study area

To describe watershed-scale variation in GPP and evaluate its importance to juvenile salmonids, we first evaluated the feasibility of predicting GPP at the reach and network scales using a

multiple regression approach and readily available data on solar exposure, water temperature, and water chemistry from either habitat monitoring programs or remotely sensed data source. Subsequently, we leveraged data on salmonid densities from the Integrated Status and Effectiveness Project (ISEMP) to determine the extent to which juvenile salmonids were associated with primary production at the reach scale (i.e., measured GPP) and network scale (i.e., predicted GPP). We identified 24 sites in two semi-arid watersheds in the John Day River Basin, Oregon, USA, wherein we collected data on diel oxygen concentrations, fish populations, and aquatic and riparian habitats (Fig. 1). The MFJD and Murderers Creek watersheds are both monitored annually under ISEMP and the Columbia Habitat Monitoring Program (CHaMP) to assess fish populations and aquatic habitat conditions (Bouwes et al. 2011, CHaMP 2013). These programs provide detailed information on the abundance and growth of anadromous and resident *O. mykiss* and juvenile Chinook salmon, as well as physicochemical conditions (e.g., water temperature, alkalinity, and conductivity), riparian structure, and channel structure. To leverage these existing data sets, we selected study sites to estimate primary production and investigate relationships between primary production and fish populations from those previously sampled by CHaMP and ISEMP. To maximize contrast and independence among sites, we further constrained site selection within this frame to ensure a range of geomorphic reach types (based on the River Styles classification; Brierley and Fryirs 2005, O'Brien et al. 2017) and land use, channel width, and vegetation cover conditions were reflected in our study.

Study sites were selected in the MFJD ( $n = 16$ ) and Murderers Creek ( $n = 8$ ) watersheds. Our MFJD sites were located in the MFJD Intensively Monitored Watershed (IMW; Bennett et al. 2016), a sub-basin of the MFJD in which salmonid populations and aquatic habitats have been intensively sampled as part of the Integrated Status and Effectiveness Monitoring Program (Bennett et al. 2016, Wheaton et al. 2018). The MFJD IMW constitutes an 827-km<sup>2</sup> watershed, ranging in elevation from ~1050 m to 1900 m. Riparian vegetation in the MFJD watershed takes two predominate forms. Where channel gradient is

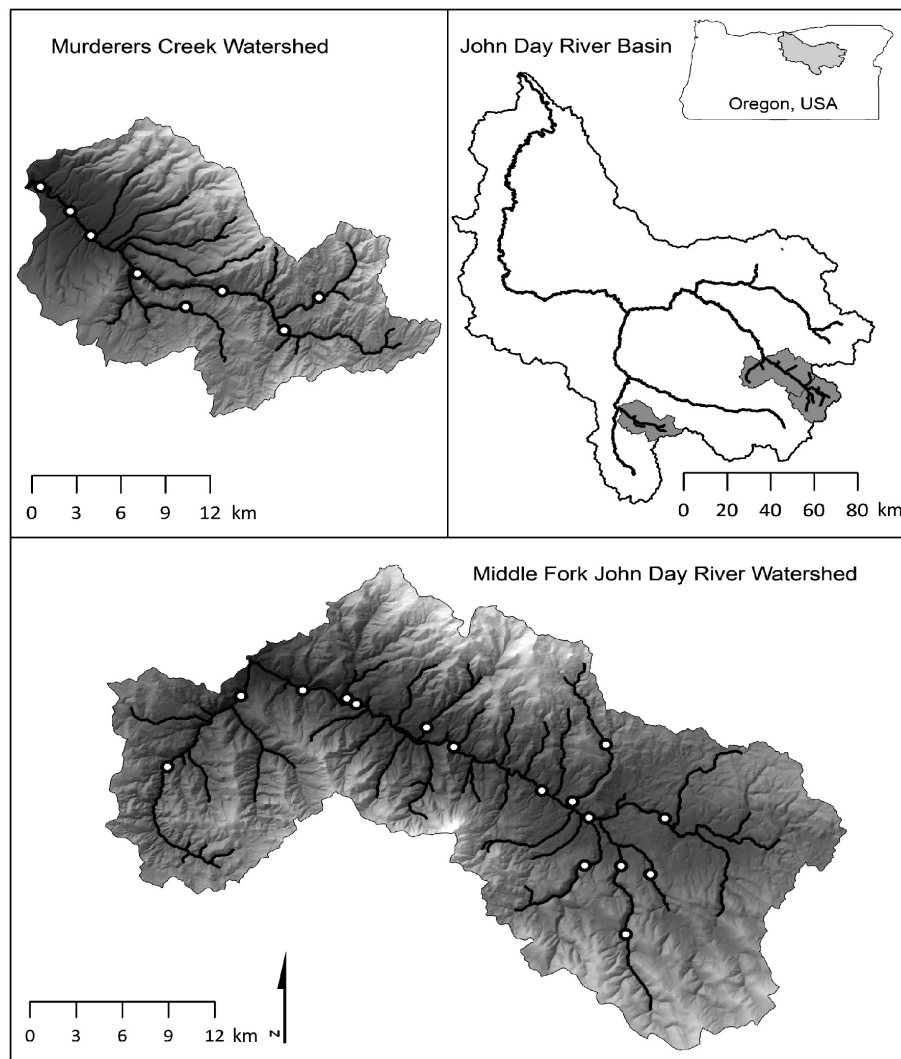


Fig. 1. Map of study area with sites where primary production, fish, and habitat were sampled shown as white circles.

low (~1.0–1.5%), vegetation is dominated herba-  
ceous vegetation with patchy willow (*Salix* spp.),  
redosier dogwood (*Cornus sericea*), and alder  
(*Alnus* spp.). Where channel gradients exceed  
2.0%, vegetation is dominated by mature ponderosa  
pine (*Pinus ponderosa*), lodgepole pine  
(*Pinus contorta*), Douglas fir (*Pseudotsuga men-  
ziesii*), or western larch (*Larix occidentalis*), and  
channel margins are more continuously vegetated  
with shrub species. Murderers Creek is a tributary  
to the South Fork John Day River (SFJD), draining  
a watershed area approximately 344 km<sup>2</sup> that ranges  
in elevation from ~890 m to

1790 m. Vegetation on Murderers Creek is domi-  
nated by ponderosa pine in high-elevation  
reaches, while low-elevation sections of the creek  
flow through open valleys vegetated with herba-  
ceous vegetation with a narrow corridor or of  
shrub species along stream banks.

Middle Fork John Day River and Murderers  
Creek provide habitat for an evolutionarily signifi-  
cant unit of *O. mykiss*, listed as threatened under  
the U.S. Endangered Species Act (ESA), and one  
of the last robust wild populations of spring Chi-  
nook salmon in the Columbia River Basin (Carmi-  
chael et al. 2001). In addition to the previously

mentioned salmonid species, longnose dace (*Rhinichthys cataractae*), reidside shiner (*Richardsonius balteatus*), longnose sucker (*Catostomus catostomus*), mountain whitefish (*Prosopium williamsoni*), and sculpin (*Cottus* spp.) are present throughout various portions of the study area. For more detailed information on the study area and fish populations present, see McMillan et al. (2012), Tattam et al. (2013), and Weber et al. (2014).

Stream food webs supporting salmonid populations are fueled by both autochthonous (primary production) and allochthonous (detritus and invertebrate inputs) energy sources (Vannote et al. 1980, Wipfli and Baxter 2010). Therefore, for GPP to influence salmonid populations, secondary production of aquatic invertebrates using this resource would need to be present in sufficient densities to represent a reliable prey resource for salmonids. Previous studies within the John Day watershed established that detritivorous and grazing macroinvertebrates were abundant throughout the watershed (Li et al. 1994, Tait et al. 1994). Further, Tait et al. (1994) demonstrated significant relationships between solar exposure and riparian vegetation, and densities of aquatic invertebrates. Here, we selected study reaches across a range of riparian vegetation communities that would support secondary production derived from aquatic and detrital pathways and having average July and August water temperatures that support salmonid populations (12–22°C; Appendix S1).

### Field measurements

*Primary production.*—We measured primary production using a single-station, open-channel method (Grace and Imberger 2006). In each watershed, we recorded dissolved O<sub>2</sub> (DO) and water temperature continuously at 10-min intervals using miniDOT loggers (Precision Measurement Engineering, Vista, California, USA). Sampling in the MFJD was conducted during 29 June–8 July 2013, and sampling in Murderers Creek was conducted during 10–18 July 2013. In the MFJD, where we were unable to concurrently measure DO and water temperature owing to logger availability, we deployed miniDOT loggers randomly at eight of the 16 previously selected sites during one of two consecutive 5-d periods. Loggers were deployed at all sites for

several days (five in MFJD, eight in Murderers Creek) to ensure that diel DO profiles were recorded for at least two days with consistent, optimal production conditions (i.e., minimal cloud cover; initially assessed optically by W.C. Saunders; verified with solar radiation data; data not provided). Between consecutive deployments and following deployment at Murderers Creek, we submerged all loggers in a 5-gallon bucket with constant aeration for 16 h to verify consistency among loggers and accuracy of measurements under conditions that approach 100% oxygen saturation.

We used data from miniDOT loggers to calculate diel change in DO concentration and subsequently used a modified version of the daytime regression method to estimate primary production (Grace and Imberger 2006, Atkinson et al. 2008, Grace et al. 2015). We used the Bayesian Single-station Estimation program (BASE; Grace et al. 2015) to simultaneously estimate primary production, stream respiration, and reaeration for each 10-min period during which DO was measured in the field. Gross primary production was modeled as a function of solar input ( $I$ , measured model input; notation follows Grace et al. 2015), the ability of primary producers to use incident light ( $p$ ), and a light use efficiency factor ( $A$ ). Stream respiration ( $R$ ) was corrected for water temperature ( $T$ , measured model input) using a temperature-dependence factor ( $\theta$ ). Reaeration ( $K$ ) was also temperature-corrected and depended on the deficit or surplus of DO ( $D$ , calculated as the difference between measured O<sub>2</sub> concentration and O<sub>2</sub> concentration at 100% saturation, derived from field measurements). Thus, unlike other open-channel metabolism approaches requiring field methods for estimating  $K$ , reaeration is a computational solution in BASE. Dissolved oxygen concentrations at 100% saturation were corrected for water salinity (measured once at each site) and barometric pressure. The BASE program uses a Markov chain Monte Carlo (MCMC) method (chain length = 10,000 iterations, burn-in = 1000 iterations used here) to estimate values for the model parameters  $p$ ,  $A$ ,  $R$ ,  $\theta$ , and  $K$  (i.e., those not measured in the field; see Grace et al. 2015). For subsequent statistical analysis, we averaged estimates of GPP from daily models fit with the BASE program for which the  $r^2 > 0.7$  and posterior predictive check (PPC) fell between 0.1 and

0.9, to ensure a high correlation between measured and modeled DO data as well as overall model fit (Kery 2010). We converted estimates of GPP from the BASE program ( $\text{g O}_2\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ ) to aerial rates ( $\text{g O}_2\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ) based on the mean water depth calculated from a stream cross section located at the location of the miniDOT logger deployment.

Solar radiation ( $\text{watt}/\text{m}^2$ ) was measured at 10-min intervals at two permanent weather stations (CS300-L Pyranometer; Campbell Scientific, Logan, Utah, USA) located along the MFJD and used as an index of light intensity. Weather stations were located in wide valleys with an unobstructed view of the sky. To account for vegetation and topographic shading at individual sites, we calculated site-specific solar radiation data by discounting all solar radiation measurements, collected at 10-min intervals at the nearest weather station, by the average solar access, measured within sites using a SunEye 110 (Solmetric Corporation, Sebastopol, California, USA). We verified that solar radiation data collected in the MFJD were appropriate for use in Murderers Creek by comparing hourly measurements of solar radiation collected in the Murderers Creek watershed on 15 July 2013 during 0430–2030 h (510 Solar Irradiance Meter; Test Products International, Beaverton, Oregon, USA). The use of centralized solar radiation measurements likely proved sufficient (based on minimum model fit criteria) owing to the standardization of when DO data were collected, relative proximity (65 km), and similarity in elevation and aspect of the two watersheds studied (Fig. 1). Barometric pressure was measured concurrently with solar radiation at each of the two permanently established weather stations (Vaisala Weather Transmitter WXT520; Campbell Scientific). We verified the accuracy of barometric pressure measurements recorded in the MFJD watershed for use in the Murderers Creek watershed using a Brunton ADC Pro meter (Brunton, Louisville, Colorado, USA) and following the same procedure used to validate solar radiation. Water salinity was measured at each site at the time of miniDOT logger deployment (EC400; Extech Instruments Corporation, Nashua, New Hampshire, USA).

*Physical measurements.*—The CHaMP program measures a wide array of physical and chemical

attributes at each of its monitoring sites. We provide a brief description of the methods used to measure site attributes used in this study here. However, Bouwes et al. (2011) provide in-depth details for all sampling protocols. Site visits conducted by the CHaMP program occurred during July–August, but were not conducted in conjunction with DO sampling (within 3–4 weeks after DO sampling). Solar access, used to correct for site-specific topographic and vegetation shading (see *Primary production*), was measured at each site using a Solmetric SunEye by capturing images of the portion of the sky with solar exposure at 11 locations spaced evenly throughout the study site. We calculated the average solar access for each site as the mean of each individual estimate of solar access for the period of May–October. Site-specific solar access data for the Big Boulder Creek sampling site were not available, so we used estimates of solar access from a CHaMP site located on a nearby tributary, Camp Creek. For estimation of GPP from DO data, we used water temperature measurements provided by the miniDOT loggers. However, to predict GPP from individual site characteristics (see *Statistical analysis*), we calculated mean July water temperatures from hourly water temperature measurements recorded by TidbiT temperature loggers deployed at each site (Onset Computer Corporation, Bourne, Massachusetts, USA). Water conductivity (EC400; Extech Instruments Corporation) and alkalinity (Alkalinity Test Kit; LaMotte Company, Chestertown, Maryland, USA) were measured by the CHaMP program 100–300 m above the location of the logger deployment.

*Fish populations.*—To evaluate the relationships between GPP and juvenile *O. mykiss* and Chinook populations (hereafter referred to as salmonid populations) in the MFJD and Murderers Creek watersheds, we used two independent data sets on fish abundance (mark–recapture and snorkeling), fish consumption, and distribution collected during the summer 2013. First, at individual sample sites we used mark–recapture data on individual fish collected by the ISEMP program during summer (July) and fall (October) 2013. Densities (fish/m) of *O. mykiss* and juvenile Chinook salmon and growth rates of *O. mykiss* >60 mm total length (TL) were determined by implanting individuals with passive integrated transponder tags (PIT tags), and conducting a

two-pass Lincoln-Peterson mark-recapture estimate of abundance, modified by Chapman (1951), during the summer and fall sampling periods. Fish densities were standardized by the length of the survey reach, as juvenile salmonids are strongly associated with bank-attached features (e.g., under cut banks, woody debris, streamside vegetation, gravel bars; see Cramer and Ackerman 2009a, b). Additionally, we evaluated both continuous (site width) and categorical (tributary vs. mainstem) stream size variables in our analysis of fish density (see *Statistical analysis*) to account for any width-related influence on local abundance. Summer growth of *O. mykiss* was determined by the change in mass for fish captured in the same reach during July and October sampling ( $n = 273$  individuals). Using these data and a bioenergetics modeling approach (e.g., Hansen et al. 1993, Hartman and Kitchell 2008), we estimated the degree of resource limitation experienced by *O. mykiss* at sites of varying productivity. More specifically, we inferred limitation using model estimates of the proportion of the theoretical maximum consumption value (Pval; ranging from 0 to 1) consumed by fish. We estimated Pval for individual fish recaptured at sites in the MFJD and Murderers Creek watersheds by scaling theoretical estimates of maximum consumption (a function of fish size and water temperature; see Hansen et al. 1993) to empirically derived consumption rates consistent with observed growth rates, temperature, and diet during the study period. We ran bioenergetics models using observed data on site-specific water temperature, diet data from Weber et al. (2014), and bioenergetic parameters from the literature (From and Rasmussen 1984, Rand et al. 1993, Myrick 1998, Van Winkle et al. 1998). Pval provides a normalized measure of fish consumption that integrates across the entire energy budget of a fish normalized across size and temperature, and thus provides a relative measure of fish performance that is comparable among populations or streams. This approach has recently been used to evaluate the importance of prey availability and environmental factors on salmonid performance at regional (e.g., Weber et al. 2014) and global scales (e.g., Budy et al. 2013). Data on salmonid densities (fish/m) were available for 19 sites during summer 2013 and 16 sites during fall 2013, while data on resource

limitation were estimated from observed individual growth rates at 15 sites.

To test whether network predictions of GPP (see *Network prediction of GPP*) were associated with fish densities, we used spatially extensive snorkel data collected by Blanchard (2015). For more details on survey protocols, see O'Neal (2007) and Blanchard (2015). Snorkel-based estimates of fish densities were conducted during July–August 2013 at or close to base flow conditions. Snorkel estimates of salmonid densities were calibrated at 12 CHaMP sites that were concurrently sampled with electrofishing gear, and densities estimated with mark-recapture sampling. Snorkeling was conducted in 51 locations, consisting of 2–6 consecutive 100- to 300-m reaches, throughout the MFJD and all major salmonid-bearing tributaries in the study area (total survey area, 30.74 km). Salmonid densities were estimated for each reach and, for subsequent analysis purposes, averaged within prediction segments associated with our network GPP model (see *GPP–Fish relationships*).

Preliminary screening of data revealed outliers in both our abundance and growth data sets that warranted censoring some observations from further analysis. First, extreme temperatures ( $>25^{\circ}\text{C}$ ) in the mainstem MFJD caused a 10-fold increase in juvenile Chinook between 29 June and 3 July 2013 in the lower reaches of Vinegar and Granite Boulder creeks (Blanchard 2015), which likely provide thermal refugia (e.g., Bilby 1984, Sutton and Soto 2012). Additionally, we excluded growth estimates from one mainstem site in the MFJD owing to a limited number of recaptured fish and their small size.

### Statistical analysis

We evaluated the potential to predict GPP at monitoring sites as a function of (1) in situ measurements and (2) globally available (GIS) analogs of site-level measurements, with the ultimate goal of predicting GPP continuously throughout a stream network as a means of describing spatial variability in potential food resources available to juvenile salmonids. Subsequently, we used a linear modeling approach to evaluate the importance of GPP in describing spatial variation in salmonid densities and growth in the MFJD and Murderers Creek at sites where DO was measured for estimating GPP. Finally, we determined whether continuous predictions of GPP throughout the MFJD

River network were associated with salmonid densities.

*Site-specific prediction of GPP.*—We used multiple linear regression to examine abiotic factors controlling GPP across sample sites in the two study watersheds and develop a predictive model for GPP at specific monitoring sites. Although the factors controlling GPP are complex, and potentially synergistic (e.g., Beaulieu et al. 2013), much of the research to date points to light availability (e.g., Mulholland et al. 2001, Roberts et al. 2007), temperature (e.g., Demars et al. 2011, Griffiths et al. 2013), and nutrient availability (e.g., Lamberti and Steinman 1997, Bernot et al. 2010) being among the primary drivers of potential GPP in lotic systems. Our goal was to determine whether we could predict GPP at sites where DO loggers were deployed using proxies for these three controlling factors that can be easily measured as part of a fish or aquatic habitat monitoring program (e.g., CHaMP). As part of its annual monitoring, CHaMP collects data on two proxies for stream nutrients (i.e., alkalinity and conductivity; Biggs and Price 1987, Jacoby et al. 1991). We constructed independent models to predict GPP at monitoring sites using each of these nutrient proxies, as well as the average summer solar exposure (SunEye data, measured as a percentage) and the average water temperature during DO logger deployment. A primary assumption of multiple regression is that measurements are independent, which spatial data often violate. We accounted for spatial patterns in the independent variable by incorporating predictor variables that might drive flow-connected (temperature and nutrients) and landscape-based (solar radiation) spatial autocorrelation in GPP. While it may be possible to build predictive network models based on autocorrelation structures (e.g., SSN models; Isaak et al. 2014), which inherently address non-independence, such models are data-intensive, beyond the capabilities of our sample size and spatial coverage of observations, and naïve of mechanisms driving spatial covariance. By including spatially varying predictors that influence GPP, our approach inherently addresses autocorrelation issues, and arguably offers more mechanistic approach.

We based inferences about the ability to make site-specific predictions of GPP based on the top-performing model, selected using Akaike's

information criterion corrected for small sample size (AICc; Burnham and Anderson 2002), among a set of 11 candidates which ranged in complexity from single- to three-predictor models. We validated our top-performing model using a jackknifing procedure (Dixon 1993) wherein we iteratively removed individual sites from the data set, refit models to the remainder, and predicted GPP for the withheld site. We assessed the validity of our site-scale predictive model for GPP by quantifying the correlation between the mean jackknifed GPP predictions and mean daily GPP estimates from DO logger data. We validated that the assumptions of multiple regression were met by visually inspecting residual plots to assess linearity and homoscedasticity, and normal quantile plots to assess normality.

*Network prediction of GPP.*—We constructed a model to predict GPP continuously across the network and evaluated how well predictions from this model correlated with fish densities throughout the *O. mykiss*-bearing portion of the MFJD watershed. We used multiple linear regression to model observed GPP as a function of accumulated solar radiation, mean July water temperature, and conductivity (base on site-scale model selection results; see *Results*). In contrast to site-scale models, which used field measurements, independent variables were calculated using remotely sensed (GIS) data sources so that we could predict GPP continuously throughout the river network.

To account for reductions in solar radiation resulting from topographic and near-stream vegetative shading, we created a hybrid elevation model based on a 10-m digital elevation model (DEM; USDA NRCS Geospatial Data Gateway [<https://datagateway.nrcs.usda.gov>]) and vegetation height data (2011 Existing Vegetation Height [EVH]; LANDFIRE land cover data [<https://www.landfire.gov>]). We converted LANDFIRE EVH data (30 m resolution) to a 10-m DEM wherein elevation values within 10 m of MFJD streamlines were set equal to 0 m (i.e., to represent solar access in open channels). We merged these data with the bare earth DEM to form a final DEM from which to estimate total accumulated solar radiation (positive integer). Solar radiation accumulated during the period 1 July–31 August was calculated at points spaced 250 m apart along the MFJD stream network following



the procedure outlined by Rich et al. (1994) and Fu and Rich (2002), using the Solar Radiation toolbar in ArcGIS 10.1 (ESRI 2012). Data were log-transformed for analysis.

We calculated mean July water temperature for river segments as the average of daily mean water temperature (DMWT) for July modeled for the John Day River by McNyset et al. (2015). McNyset et al. (2015) predicted DMWT as a function of land surface temperature, measured by the U.S. National Aeronautics and Space Administration's (NASA) Moderate Resolution Imaging Spectroradiometer (MODIS) satellites. We predicted mean July water temperatures for every confluence-to-confluence stream reach. We used Olson and Hawkins' (2012) random forest model to predict conductivity as a function of geologic, climatic, soil, topographic, atmospheric deposition, and groundwater variables. We estimated conductivity at points spaced 500 m apart along the stream network. We merged data for all independent variables in both the MFJD and Murderers Creek watersheds onto a single stream layer that we segmented into 1-km reaches. For solar radiation and conductivity, which we estimated at a finer spatial resolution, we averaged all available data to produce a single estimate for each independent variable for each 1-km river segment.

We validated the network-scale GPP model using the jackknifing procedure described above, only this time by quantifying the correlation between the mean GPP values for 1-km prediction segments and the mean DO logger-based GPP estimates for the corresponding segment. Residual and normal quantile plots were visually assessed to determine whether multiple regression assumptions were met. Following validation, we predicted GPP for the *O. mykiss*-bearing portion of the MFJD using parameter estimates derived from fitting the multiple regression model to the entire data set of DO logger data.

*GPP–Fish relationships.*—We used multiple linear regression to evaluate factors influencing salmonid densities (combined density of *O. mykiss* and juvenile Chinook, fish/m) measured when oxygen was sampled (summer) and during the fall, independently. To account for the potential influence of channel width on fish densities, we constructed linear models including GPP, and site location (categorical variable representing

tributary and mainstem reaches, also a proxy for size) or bankfull channel width (continuous variable) as potential independent variables. We designated sites as either tributary or mainstem sites since (1) use of tributary habitat by juvenile Chinook is typically lower than that of mainstem habitat (Quinn 2011), (2) these river reaches provide greater surface area per unit length than tributary reaches, and (3) we hypothesized that GPP would play a greater role in influencing salmonid densities in mainstem sites owing to reduced riparian vegetation. Designation of sites in the headwaters of both the MFJD and Murderers Creek as either mainstem or tributary habitat was based on the average bankfull width (<5 m is tributary; mainstem otherwise). This cutoff was based on the average bankfull width of tributaries in the MFJD watershed. We included bankfull channel width as an independent variable since both GPP (independent variable) and salmonid density (response variable) were expected to be influenced by channel size, and we sought to determine whether GPP was a better predictor of fish densities than channel width alone. We determined the ability of models to explain variation in salmonid density based on coefficients of determination ( $r^2$ ) and AICc. We evaluated the significance of independent variables by determining the sum of the AICc model weights for all models incorporating parameters for specific variables (cumulative  $w_i$ ). Lastly, to investigate relationships over a broader spatial extent and range of GPP and fish abundance conditions, we evaluated the relationship between estimates of GPP derived from our network model and snorkeling estimates of fish density using linear regression.

## RESULTS

Throughout the MFJD and Murderers Creek basins, estimates of GPP ranged from 0.007 to 3.639 g O<sub>2</sub>·m<sup>-2</sup>·d<sup>-1</sup> (Appendix S1), a nearly 400-fold difference between our most and least productive sites. On average, estimates of GPP were similar in the MFJD (mean = 1.045 g O<sub>2</sub>·m<sup>-2</sup>·d<sup>-1</sup>, SE = 0.323) and Murderers Creek (mean = 0.779 g O<sub>2</sub>·m<sup>-2</sup>·d<sup>-1</sup>, SE = 0.191;  $t = 0.56$ ,  $P = 0.6$ ). Estimates of GPP were about sixfold greater at mainstem sites (mean = 1.839 g O<sub>2</sub>·m<sup>-2</sup>·d<sup>-1</sup>, SE = 0.321) than at tributary sites

(mean = 0.253 g O<sub>2</sub>·m<sup>-2</sup>·d<sup>-1</sup>, SE = 0.083;  $t = 5.54$ ,  $P < 0.001$ ). On average, GPP increased by 0.211 g O<sub>2</sub>·m<sup>-2</sup>·d<sup>-1</sup> with each 1-m increase in bankfull width ( $t = 5.65$ ,  $P < 0.001$ ). At these sites, mean July water temperature ranged from 11.9 to 21.5°C (mean = 16.7, SE = 2.6), solar access ranged from 48% to 99% (mean = 68.6, SE = 14.0), conductivity ranged from 49 to 390 μS (mean = 183, SE = 106), and alkalinity ranged from 44 to 332 ppm (mean = 127, SE = 80.0). We observed fish densities ranging from 0.01 to 3.26 fish/m during the spring sample period and 0.28 to 3.47 fish/m during the fall.

### Predicting GPP from site measurements

Physicochemical variables explained a significant portion of variation in mean daily GPP across sites, and when combined in a predictive model performed well for the two basins. Among the 11 candidate models considered, the top model for predicting GPP included site-level measurements of temperature, solar exposure, and conductivity (Table 1). However, this model ranked similarly to a reduced model with only solar access and water temperature ( $\Delta\text{AICc} = 0.75$ ) and one with solar access, water temperature, and alkalinity ( $\Delta\text{AICc} = 1.64$ ). Overall, the most important variables, among those included in the analysis, in describing differences in GPP measurements were solar access (cumulative  $w_i = 0.95$ ) and mean July water temperature (cumulative  $w_i = 0.75$ ). Between the two proxies for nutrient availability, conductivity (cumulative  $w_i = 0.48$ ) was a more important variable than alkalinity

(cumulative  $w_i = 0.22$ ). However, given the small distinction between the three top models, our data indicate that both nutrient surrogates were of minor importance for predicting GPP across the MFJD and Murderers Creek. We ultimately used the top-ranked model for predictive purposes, in which mean daily GPP was positively associated with solar access (slope = 0.0387; SE = 0.0135) and mean July water temperature (slope = 0.135; SE = 0.073) and weakly associated with conductivity (slope = -0.0016; SE = 0.001). Linear regression between field measurements of and jackknifed GPP predictions indicated that there was a strong correlation between observed GPP and modeled GPP values ( $r^2 = 0.53$ ; Fig. 2A), with an RMSE = 0.716. However, predicted values of GPP tended to be lower than observations at sites where measured GPP was highest (Fig. 2A).

### Predicting GPP from globally available variables

Using remotely sensed estimates of solar radiation, July water temperature, and conductivity, we fit a multiple regression model, analogous to the top site-level model, to predict mean daily GPP throughout the entire *O. mykiss*-bearing portion of the MFJD stream network; it explained 45% of the variation in the observed GPP values ( $P = 0.001$ ; Fig. 2B). Similar to the site-level model, GPP values were positively correlated with July water temperature (slope = 0.322, SE = 0.075) and log-transformed solar radiation (slope = 0.59, SE = 0.353) and only weakly influenced by conductivity (slope = -0.0007, SE = 0.002). However,

Table 1. Model selection results for the 11 models evaluated to predict mean daily gross primary production with independent variables measured at monitoring sites during 2013.

Model	-2 LogL	AICc	$\Delta\text{AICc}$	$w_i$
Solar access + temperature + conductivity	39.48	49.7	0	0.329
Solar access + temperature	43.19	50.45	0.75	0.226
Solar access + temperature + alkalinity	41.13	51.34	1.64	0.145
Solar access + conductivity	44.23	51.49	1.79	0.134
Solar access + alkalinity	45.98	53.24	3.54	0.056
Solar access	48.67	53.27	3.57	0.055
Temperature	50.14	54.73	5.03	0.027
Temperature + conductivity	48.75	56.01	6.31	0.014
Temperature + alkalinity	48.85	56.11	6.41	0.013
Alkalinity	63.89	68.49	18.79	0
Conductivity	65.2	69.79	20.09	0

Note: The -2 log-likelihood (-2 LogL), Akaike's information criterion adjusted for small sample size (AICc), difference in AICc ( $\Delta\text{AICc}$ ), and Akaike weights ( $w_i$ ) are shown for each model.

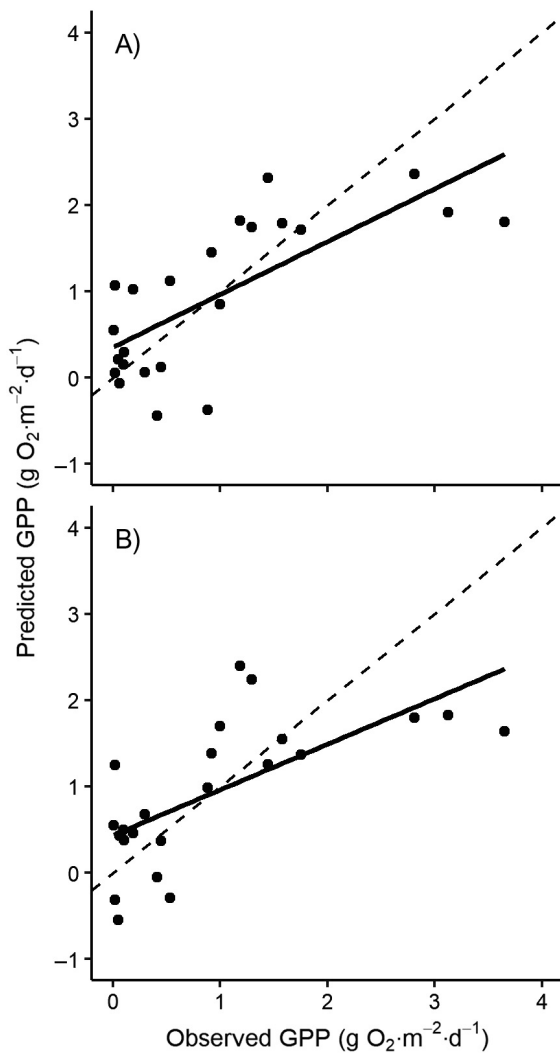


Fig. 2. Linear regressions of mean daily gross primary production (GPP) observed at monitoring sites against mean GPP predicted after jackknifing the top-performing model predicting GPP based on solar access, water temperature, and conductivity, using site-level measurements of predictors (A) or predictors from remotely sensed data sets (B). Dotted lines show 1:1 line.

removing conductivity parameter from the network model resulted in a  $\Delta\text{AICc} = -0.2$ , indicating relatively high support for both models, so we retained this variable for making GPP predictions across the river network to maintain consistency with the site-level model. Results from jackknife validation revealed that the network prediction model performed nearly as well as the model using site-based independent variables

(slope = 0.836,  $r^2 = 0.43$ , RMSE = 0.788). In its network-scale application, this model produced predictions that ranged from  $-0.67$  to  $2.61$   $\text{g O}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  across the MFJD (Fig. 3).

Because GPP predictors were themselves modeled variables, we evaluated the goodness of fit of the network models for each of the three independent predictors. Overall, models used to predict temperature, solar radiation, and conductivity across the MFJD and Murderers Creek networks performed reasonably well. Prediction from network model used to predict stream temperature, which was calibrated using temperature logger data in both watersheds, accounted for the majority of the variation in reach-scale measurements ( $r^2 = 0.73$ ,  $P < 0.001$ ). Predictions of solar radiation ( $r^2 = 0.43$ ,  $P < 0.001$ ) and conductivity ( $r^2 = 0.31$ ,  $P = 0.005$ ), which lack watershed-scale calibration, explained a smaller but still significant proportion of the variation in reach-scale measurements.

#### GPP–Fish relationships

Salmonid densities and the degree of resource limitation of *O. mykiss* were significantly positively correlated with GPP measured at monitoring sites across the MFJD and Murderers Creek basins. The top model for describing variation in salmonid density at monitored sites during both summer and fall fish sampling periods included parameters for average daily GPP and tributary/mainstem designation. The average daily GPP was significantly correlated with the total density of salmonids (fish/m) estimated during both summer and fall sampling periods (Fig. 4). However, associations between mean daily GPP and juvenile salmonid densities were stronger for mainstem sites, during both summer ( $t_{\text{summer}} = 3.82$ ,  $P_{\text{summer}} = 0.007$ ,  $r_{\text{summer}}^2 = 0.63$ ) and fall ( $t_{\text{fall}} = 5.46$ ,  $P_{\text{fall}} = 0.003$ ,  $r_{\text{fall}}^2 = 0.83$ ) sampling periods, than for tributary sites ( $t_{\text{summer}} = 3.24$ ,  $P_{\text{summer}} = 0.02$ ,  $r_{\text{summer}}^2 = 0.58$ ;  $t_{\text{fall}} = 2.68$ ,  $P_{\text{fall}} = 0.04$ ,  $r_{\text{fall}}^2 = 0.51$ ). Models that included the categorical tributary/mainstem variable ranked higher than models that included bankfull width as a continuous variable to account for stream size ( $\Delta\text{AICc} = 8.3$ ). The top model for salmonid density during the summer sampling period included an interaction between tributary/mainstem designation and GPP ( $\Delta\text{AICc} = 2.1$ ), while the top model for the fall sampling period included an additive effect of site

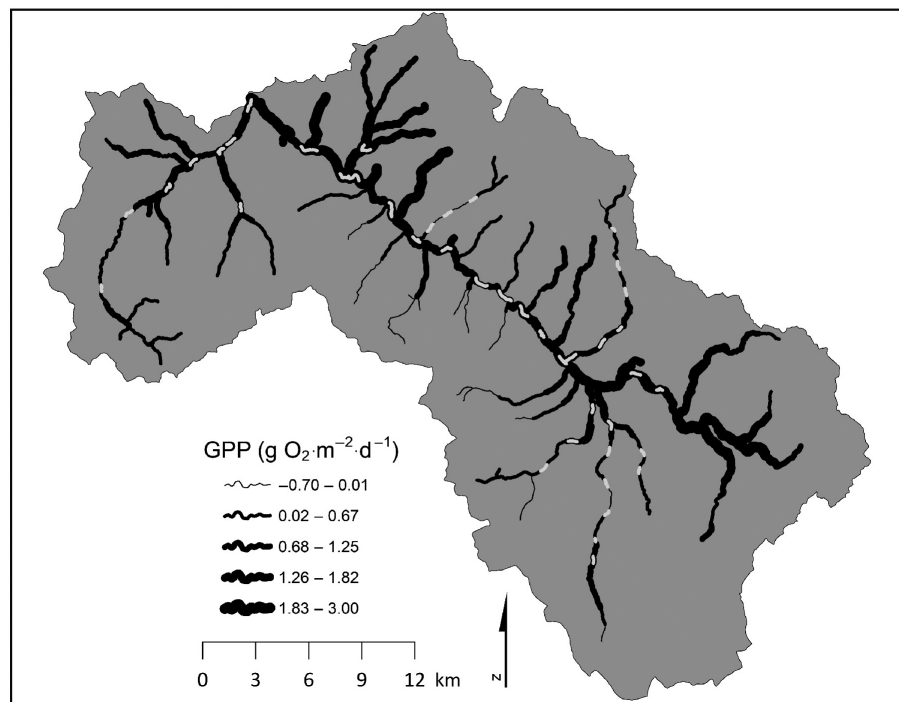


Fig. 3. Map of the MFJD Basin showing gross primary production (GPP) predicted using proxies of solar access, water temperature, and conductivity derived from remotely sensed data. Channel widths indicate the magnitude of predicted GPP. Stream reaches highlighted in light gray denote areas surveyed by snorkeling to estimate salmonid densities.

designation and GPP ( $\Delta\text{AICc} = 2.0$ ; Fig. 4). Estimates of  $P_{\text{val}}$  for of *O. mykiss* during summer were also positively correlated with average daily GPP ( $t = 3.42$ ,  $P = 0.005$ ,  $r^2 = 0.45$ ; Fig. 5).

Predictions of GPP using our network prediction model explained 44% of the variation in snorkeling estimates of fish densities conducted throughout 29.24 km of the MFJD (Fig. 6). Further, network predictions of GPP explained more variation in fish densities than temperature alone and the GPP model was more strongly supported ( $\Delta\text{AICc} = -5.2$ ).

## DISCUSSION

Across the MFJD River and Murderers Creek, GPP during mid-summer varied by greater than two orders of magnitude, ranging from relatively unproductive reaches ( $\sim 0.01\text{--}3.6 \text{ g O}_2\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ) characteristic of cool, well-shaded streams to moderately productive open-canopy systems ( $\sim 2.0\text{--}3.6 \text{ g O}_2\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ; Mulholland et al. 2001,

McTammany et al. 2007, Griffiths et al. 2013). Furthermore, across the two watersheds GPP was strongly correlated with both density and consumption rates of juvenile salmonids. Our study represents one of the more extensive surveys to evaluate within-watershed spatial variation in GPP ( $n = 24$ ; see Marcarelli et al. 2011) and is unique in that a primary goal was to evaluate linkages between rates of GPP and densities of juvenile salmonids in riverine ecosystems (Wurtsbaugh et al. 2015). We demonstrate that relatively simple models constructed from either site-level measurements of physicochemical stream attributes (such as those commonly collected by large-scale habitat monitoring programs) or surrogates thereof derived from remotely sensed data sources provide an efficient means to describe spatial variation in GPP at the watershed scale. The ability to measure or predict spatial variation in GPP can provide context for numerous ecological investigations and provides a cost-effective means to integrate food

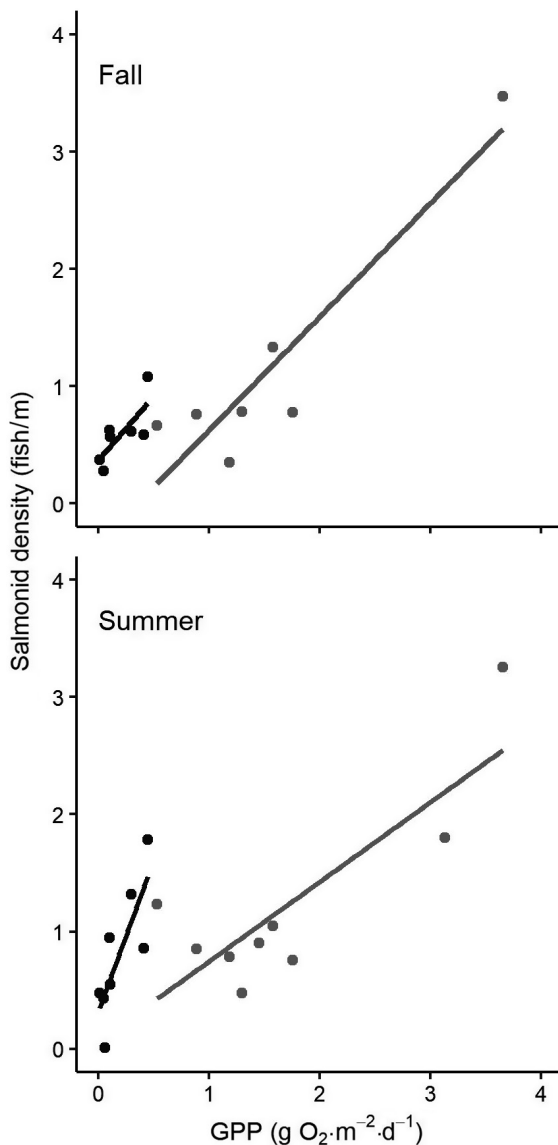


Fig. 4. Linear regression of salmonid density estimates for summer and fall 2013 and gross primary production (GPP) at tributary (black lines and symbols) or mainstem reaches (gray lines and symbols) throughout the MFJD and Murderers Creek watersheds.

web considerations into habitat restoration and fisheries management (e.g., Naiman et al. 2012).

#### Modeling gross primary production

Our multiple regression results indicating the importance of solar irradiance and water temperature as drivers of spatial variation in GPP corroborate a now extensive body of literature that

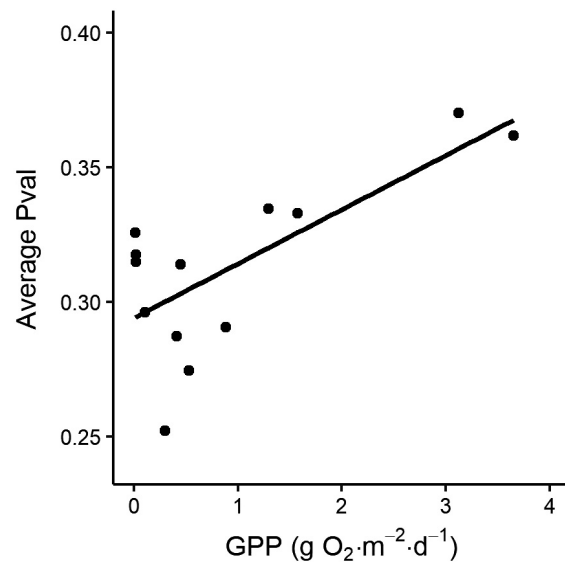


Fig. 5. Linear regression of the average proportion of maximum consumption (Pval) achieved by *O. mykiss* at monitoring sites during summer–fall 2013 against gross primary production (GPP).

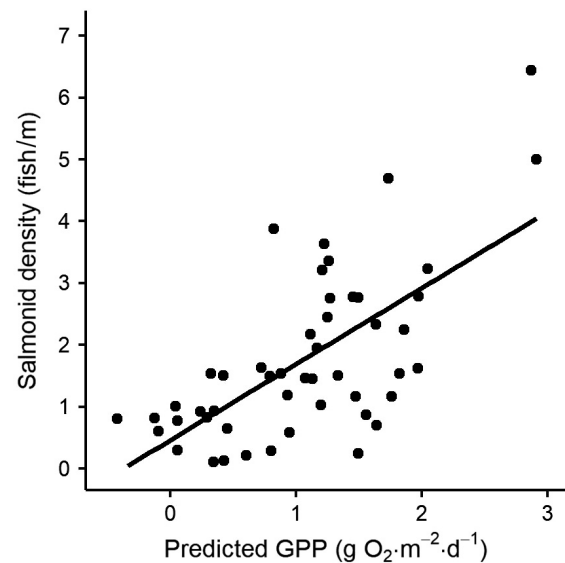


Fig. 6. Linear regression of salmonid density estimated with snorkeling during summer 2013 and gross primary production (GPP) predicted using a network predictive throughout the MFJD watershed.

identifies solar inputs and water temperature as dominant controls on GPP (e.g., Mulholland et al. 2001, Bernot et al. 2010, Griffiths et al. 2013). Most studies evaluating factors influencing GPP measure

solar irradiance, most frequently photosynthetically active radiation (PAR; e.g., Roberts et al. 2007, Beaulieu et al. 2013). However, we demonstrate that estimates of solar exposure (a measure that accounts for topographic and vegetative shading as well as geospatial position) and even canopy cover (e.g., Bunn et al. 1999, Mosisch et al. 2001) may be sufficient to describe variability in the amount of light reaching stream substrates in a watershed-scale application such as ours. This provides a low-cost alternative to expensive radiation sensors if GPP is to be estimated in many locations simultaneously. In contrast to recent regional comparisons of factors controlling GPP that identify nutrient concentrations (N and P) as potentially important factors influencing GPP (Lamberti and Steinman 1997, Mulholland et al. 2001, Bernot et al. 2010), we observed no significant relationship between either alkalinity or conductivity, proxies for nutrient concentration, and GPP. The underlying geology across which survey sites were distributed in the MFJD and Murderers Creek was relatively homogeneous, potentially yielding minor differences in nutrient concentrations across the survey sites. Alternatively, although fish populations have been shown to correlate with both alkalinity and conductivity (e.g., Kwak and Waters 1997), these measures may be poor surrogates for the nutrients most important to GPP. Ultimately, the importance of obtaining precise measurements of nutrient concentrations at survey sites likely increases as sites are distributed more widely and are distributed across more heterogeneous geology.

An important contribution of our research is that surrogates for solar input, water temperature, and conductivity derived from remotely sensed data were nearly as useful in predicting GPP as the site-level measurements themselves. Although the best performing multiple regression model to predict GPP from remotely sensed data tended to underpredict GPP at sites where GPP was measured, it accounted for nearly half of the variation in observed GPP. Since Fausch et al. (2002) encouraged fisheries professionals to develop an understanding of how fish populations interact with aquatic habitat throughout the riverscape, researchers have developed network models for water temperature (e.g., McNyset et al. 2015, Isaak et al. 2017) and physical habitat structure (e.g., Beechie and Imaki 2014, O'Brien et al. 2017), as well as integrating network

models of fish-habitat attributes to predict attributes of fish populations (Barquín et al. 2015, Wheaton et al. 2018). For example, network models developed for water temperature have greatly assisted efforts to model the effects of climate change (e.g., Isaak et al. 2015, Al-Chokhachy et al. 2016) and understand spatially structured fish habitat (Dauwalter et al. 2015).

The development of network models for GPP is a novel enterprise, with currently no published examples in the literature to our knowledge. Although the use of proxies for factors determining reach-scale rates of GPP derived from remotely sensed data produced predictive models that were slightly inferior to those based on site-level measurements of solar exposure, water temperature, and conductivity, these coarse proxies are needed to facilitate painting the network-scale picture of GPP. Our results suggest that simple models representing a few primary drivers of GPP may be sufficient to describe the extent of spatial variation in stream productivity. Further, the correlation between network predictions of GPP and fish density estimates collected as part of a large-scale snorkeling survey in the MFJD indicates that network models describing spatial variation in stream productivity may be a powerful tool for understanding factors determining the distribution and abundance of fish throughout river networks. However, one drawback to using remotely sensed data as inputs for empirical models is that much of the data are available at coarse resolutions and may not accurately represent local conditions at scales that are most meaningful to fish. For example, the LANDFIRE vegetation height data, used to account for potential reductions in solar radiation owing to vegetative shading, have a 30 m resolution, a coarseness that might exceed the width of riparian areas at some of our sites. Thus, although geospatial layers facilitate extrapolation to the network scale, drawing on coarsely resolved GIS data sets may require that tradeoffs in precision are made.

While we demonstrate the utility of an empirical modeling approach to developing network models for GPP, mechanistic models of GPP (e.g., Bellmore et al. 2017) are able to account for time-series data on stream metabolism and provide a means to evaluate hypotheses about resource limitation, interactions among factors controlling

GPP, and the effects of habitat restoration on productivity. Such models may also better inform our understanding of factors controlling GPP that vary temporally (e.g., marine-derived nutrients from spawning salmon; Benjamin et al. 2016) and improve empirical attempts to continuously model GPP across riverine networks. However, owing to their more complex nature, these models require greater amounts of data both for parameter estimation and for model operation, and as a result are often limited in terms of the number of unique spatial locations for which they can be parameterized. These limitations make continuous interpolation of model results more difficult. Another alternative to the approach we outline here is that with the increasing prevalence of low-cost, accurate DO loggers, spatial stream network models (SSN; Isaak et al. 2014) may become more feasible for modeling GPP across riverine networks. Spatial stream network models of GPP could model the effect of factors controlling rates of GPP (e.g., light, nutrients, water temperature) such as in the present study, but would also account for any additional spatial autocorrelation among survey locations and thus may improve interpolation of model results. However, potential drawbacks to the SSN approach are that (1) larger, spatially distributed data sets are necessary for detecting underlying autocorrelation structures and (2) the potential for making model predictions outside of the original study frame is limited owing to a lack of information on spatial structure in new networks. Depending on the study goal, the multiple regression framework that we present here, while simple, may be sufficient to reliably identify regions of relatively high productivity within a watershed, perhaps even beyond our calibration. Furthermore, even in cases where more mechanistic food-web modeling approaches will be pursued, our approach provides a means for broadly characterizing a key response variable (i.e., GPP) to facilitate effective study design.

A number of ecologists have highlighted the need to develop a more complete understanding of how food webs are spatially structured across watersheds (Wipfli and Baxter 2010, McGarvey and Johnston 2011), as well as integrate this information into management and restoration efforts (Naiman et al. 2012, Wurtsbaugh et al. 2015). Numerous studies have documented the

importance of primary production in controlling food-web structure in aquatic systems (e.g., Forrester et al. 1999, Bunn et al. 2003, Parker and Huryn 2013), while others have pointed out that spatial heterogeneity in the controls of food-web structure is driven by heterogeneity in both terrestrial and aquatic landscapes (e.g., Polis et al. 1997, Thompson and Townsend 2005). Network models of GPP, and models predicting GPP over large spatial extents more generally (e.g., Running et al. 2004, Šimová and Storch 2017), provide a basis for testing theories on the influence of primary production on food-web structure and species abundance at the landscape/riverscape scale. Furthermore, spatially continuous predictions of GPP will help identify river reaches that are likely to subsidize riparian consumers via secondary production (i.e., emerging aquatic insects; Jackson and Fisher 1986, Nakano and Murakami 2001, Epanchin et al. 2010). Owing to the consistency with which light, water temperature, and nutrients are identified as factors controlling GPP in rivers and the relative simplicity of the modeling framework we outlined (in terms of both model construction and calibration), we believe that our approach provides a template for describing spatial variation in productivity across a wide variety of river networks.

#### *GPP–Fish relationships*

Beyond presenting a basis for quantifying GPP for an entire river network, our work also demonstrates tight coupling between primary production and salmonid abundance. In fact, GPP as a single variable predictor performed relatively well compared to many multivariate empirical models describing fish abundance (Fausch et al. 1988). Greater densities of juvenile salmonids were observed at river reaches with relatively high rates of GPP and may have resulted from increased secondary production of aquatic invertebrates at these sites, a primary prey resource for drift-foraging salmonids (e.g., Kiffney et al. 2014). Indeed, researchers have demonstrated positive relationships between GPP and invertebrate densities or production (e.g., Fisher and Gray 1983, Hall et al. 2010, Finlay 2011, Jardine et al. 2012) and between invertebrate and fish densities (e.g., Weber et al. 2014) demonstrating the intermediate linkage between GPP and fish populations in river ecosystems. Furthermore, previous studies

within the John Day watershed have demonstrated significant relationships between solar exposure, riparian vegetation, and densities of aquatic invertebrates (Li et al. 1994, Tait et al. 1994). However, these studies failed to find a significant relationship between this prey resource and salmonid densities, potentially owing to limited sample size ( $n = 5-7$  study reaches) and distribution of sampling effort or additional factors (e.g., water temperatures) being the primary factor limiting salmonid pupations.

While relationships between GPP and fish populations have been demonstrated for many lentic systems (e.g., Downing et al. 1990, Stockner and MacIsaac 1996), there have been relatively few studies evaluating the role of primary production and supporting fish populations in lotic systems (Wurtsbaugh et al. 2015). Bilby and Bisson (1992) observed higher fish densities in stream reaches traversing clearcuts, where GPP was greater, than in stream reaches with adjacent old-growth forest. Jardine et al. (2012) also observed a strong relationship between aquatic primary production and the proportion of energy fish derived from aquatic resources in rivers with limited floodplain connectivity. In addition to autochthonous production, terrestrial subsidies to aquatic systems in the form of leaf litter (Wallace et al. 1997) and terrestrial invertebrates (Nakano et al. 1999, Baxter et al. 2004, see Baxter et al. 2005 for a review) play important roles in structuring stream food webs. These allochthonous sources of energy to river food webs tend to be greatest for smaller channels, with high edge:perimeter ratios (see Baxter et al. 2005 for a review), and have the strongest influences on consumers in recipient habitats where productivity in the donor habitats greatly exceeds that of the recipient habitat (Polis et al. 1997, Nakano and Murakami 2001). However, in rivers with high rates of GPP, such as arid and semi-arid systems with limited canopy coverage (Lamberti and Steinman 1997), one might expect relatively strong linkages between autochthonous production and juvenile salmonids (e.g., Wilson et al. 2014), such as those observed in the present study. To date, there have been few comprehensive efforts to describe these two sources of energy for riverine food webs simultaneously (but see Bellmore et al. 2017), and thus, broad generalizations of the role of allochthonous vs.

autochthonous resources for structuring river food webs remain elusive.

The strong correlations observed between estimates of GPP and densities of juvenile salmonids suggest that when/where the rate of primary production is high, greater densities of juvenile salmonids can be supported through the duration of summer, within a reasonable temperature range (e.g., Tait et al. 1994). Indeed, data on salmonid growth between July and October at sites where estimates of GPP were high suggest that juvenile salmonids were less food-limited, evident from consistently higher estimates of Pval from bioenergetics modeling. However, in addition to the observed relationship between GPP and juvenile salmonid distributions, fish in the MFJD also responded to extreme water temperatures. During an eight-day period beginning 1 July 2013, maximum water temperature exceeded 25°C in portions of the mainstem MFJD and large numbers of juvenile salmonids, particularly Chinook salmon, migrated into the lower extent of two tributaries where maximum water temperatures were, on average, three degrees lower during this time period. Although we removed the two sites where we observed behavioral thermal regulation by fish, they highlight the fact that fish distributions across the landscape are often influenced by numerous factors simultaneously (e.g., White et al. 2014). Therefore, in order to explain spatial variation in fish densities, fisheries professionals need to make continuous predictions of both the physical aspects of fish-habitat and food-web attributes.

Although the approach outlined here provides a partial picture of the prey resources available to support riverine fish (i.e., neither detrital pathways nor terrestrial invertebrate subsidies were accounted for), we found that salmonid densities were closely correlated with estimates of GPP, even in a watershed where terrestrials contribute a significant proportion to the diets of juvenile salmonids (Weber et al. 2014). A primary goal of this research was to test whether relatively simple modeling approaches using the type of data that are routinely gathered by habitat monitoring programs (e.g., Columbia Habitat Monitoring Program, USFS Pacfish/Infish Biological Opinion Monitoring Program) can be used to predict GPP across river networks. Using this approach, we were able to identify portions of the MFJD



watershed characterized by relatively high rates of GPP. Managers could use this type of information to prioritize restoration of physical habitat to occur in these more productive reaches to ensure that fish have the necessary prey resources available to take advantage of restoration actions, or to determine whether the productive capacity of habitats would even support more than what is currently there (see Naiman et al. 2012).

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