Intro

When viewing mountainous regions from high elevation small grooves can be seen in the hillsides which often conceal narrow headwater streams. These almost impossibly thin ribbons of water are regularly enshrouded by a dense canopy of trees and their presence is only inferred based on the steep concave nature of the terrain. These are the very starting points of a fluvial network that becomes a much more apparent feature of the landscape as these dendritic channels coalesce into larger rivers. When viewed from their banks, headwater streams present themselves as modest rivulets with steep banks winding around large rocks and tree roots. They are often kept cool and shaded by the canopy above, where previous years’ leaves litter the ground and have accumulated in small pools (personal observations). Most of these leaves will appear sturdy and intact but some may show the invariable signs of decomposition where fungi, bacteria and aquatic insects have left little but the skeletonized remains (Suberkropp 1980). Occasionally small fish can even be seen darting around and jostling for positions within the current, seeking the best position to feed on small insects and other morsels that are unlucky enough to be caught drifting downstream (Hughes 1992).

Headwaters are vital components of stream networks which contribute substantially to the water quality and biodiversity of larger, more conspicuous waterways (Alexander 2007, Meyer 2007). Although individually these streams may be meager, en masse they form almost 80% of the system’s total length and more than 70% of the land surface is drained by them (Colvin 2019). A succinct definition for headwater streams has not been completely agreed on although they are broadly understood as less than 3 m wide, and have an average discharge of less than 57 L s-1, being generally 1st order streams (not yet confluenced with another stream) and drain a catchment of less than 100 ha (Richardson 2007). Material that enters these small headwater streams begins to be transformed by the biological, physical, and chemical processes there and conveyed downstream where it impacts the inhabitants and processes of much wider channels (Vannote 1980). Certain species of fish use headwaters continually or as refuges from heat and predators and may depend on them as rearing habitat for their young while some aquatic invertebrates are found nowhere else (Meyer 2007).

A small forested headwater stream ecosystem contains an integrated community of organisms which displays a distinct structure peculiar to that habitat. The amount of light reaching the stream is often much less than downstream reaches where the channel width is sufficient to part the canopy of trees. Little solar radiation is typically left available to stimulate large amounts of photosynthesis in the primary producers or photoautotrophs, such as algae, that inhabit the stream. There is however, usually an abundance of plant matter mostly in the form of leaves or pine needles. This plant material known as allochthonous (from the outside) organic matter, serves largely as the energetic foundation for headwater ecosystems. Consequently, these ecosystems are known as net heterotrophic. The plant matter is typically first colonized by aquatic fungi which begin to consume the leaves and spread throughout them shortly followed by bacteria which starts to form a thin slimy biofilm. The leaves are composed almost entirely of hydrocarbons which the biofilm slowly breaks down and liberates through digestion. The scant nutrients such as phosphate and nitrate are absorbed for critical cellular processes while some of the hydrocarbons are used for the structure of the biofilm. Some of these hydrocarbons are also broken down completely and used as an energy source while the residual carbon dioxide is exhausted to the aquatic environment through respiration. Many aquatic invertebrates seek out these biofilm laden leaves and begin shredding them to ingest the most nutritious and soft parts. Other invertebrates may patiently wait for discarded particles of food to be delivered to them by the current or actively collect small scraps from the stream bed. A few are predatory which spend their time hunting for other invertebrates which have found themselves vulnerable. This whole food web is overshadowed by the presence of fish which regularly occupy the top trophic level who continuously monitor the water column for anything that may fit in their mouth.

The activities of all of the aerobic organisms in a stream reach can be evaluated with a metric of stream metabolism. Stream ecosystem metabolism is the combination of gross primary production (GPP) and ecosystem respiration (ER). GPP by photoautotrophs uses the energy in light to fix the carbon in CO2 into organic hydrocarbons which releases O2. ER is the reverse of this process and is the mineralization of organic hydrocarbon to CO2 which consumes O2. This consumption of O2 represents the use of energy by organisms in the stream (methods stream ecology ch34). Stream metabolism is therefore a comprehensive measure which sums the activity of virtually all of the organisms in a stream (Meijia 2019). The top predators living in streams are most often fish (stream ecology ch6) and in In the Pacific Northwest headwaters these fish are generally trout (Family Salmonidae) (Richardson 2007).

In the western USA trout are regionally an important fish for recreational angling which has a sizable economy surrounding it (TCW 2010, Loomis 2012). Although the trout in first and second order headwater systems are not generally the target of anglers, these smaller systems present themselves with a more manageable size of stream to study and smaller streams exhibit connectivity with larger systems (Colvin 2019). A trend or relationship that exists in a small stream may not hold true as the stream widens (Richardson 2007) however it may be a place to begin hypothesis testing.

The presence of trout in a headwater stream may relate to overall stream metabolism. The respiration of trout will be included directly in the stream ER estimate (Hall 1972) and may also affect GPP due to a trophic cascade (Young 2008). A trophic cascade occurs when a change in the presence or activity of organisms at a particular trophic level affects the organisms of other trophic levels through indirect pathways. In the case of trout for example, more fish may relate to more GPP. More fish could consume and put more pressure on invertebrates which will in turn consume less algae which will allow for more algae growth and thus GPP. It also remains a possibility that ER, GPP and trout may relate to one another due to mechanisms that either increase or decrease production and metabolism of most trophic levels.

Organisms need an energy source and certain nutrients to maintain activity levels, grow and reproduce. Dissolved organic carbon (DOC) occurs in varying concentrations in streams and is readily absorbed and metabolized by stream microbial organisms (Findlay 1993). DOC is associated with moderate increases in GPP (cite) and larger increases in ER (Bernhardt 2002) but may decrease fish production at least in lakes (Benoit 2016). Nutrients such as nitrate and phosphate are also known to increase the metabolism of headwater microbes (Suberkropp 2009) and increase overall GPP (Mullholland 2001), ER (Pascoal 2005), and trout biomass (Artigas 2013). Light availability is the major stimulant of GPP (Warren 2017) and may also be associated with ER (Parkhill 1999) and trout (Warren 2018). Warming temperatures may also be associated with increased GPP, ER (Hill 2002) while having variable effects on trout (Coutant 2011).

A method for estimating stream metabolism that is currently receiving a lot of attention is the single station open diel oxygen method (methods 34). This method assumes that oxygen saturation at any particular time is a function of GPP, ER and the oxygen exchange rate between the air and water (Odum 1956). GPP and ER are often solved for using inverse modeling where the amount of light is assumed to be proportional to GPP and the remaining oxygen deficit is assumed to be ER. This will produce a modeled oxygen curve which can be compared to the measured oxygen curve for accuracy. To do this, light measurements and oxygen saturation must be measured frequently (commonly 5-15 minute intervals) along with temperature, salinity, and barometric pressure to calculate 100% saturation. The last remaining parameter required is the gas exchange or reaeration rate often reported as *K*600 in d-1 (600 refers to Schmidt number scaling used for comparison between different gasses).

The *K*600 may be estimated as a free parameter in the inverse modeling technique or measured directly. Estimating *K*600 as part of the model is adequate for streams with low slope and high light availability, however it is more accurate to measure gas exchange directly in shaded streams with higher slopes which are typical of headwater streams. Measuring gas exchange is done by diffusing a gas of choice into the stream at high volumes and measuring concentrations downstream from the injection point. This process may however require permits, be cost prohibitive, and the gas may have undesirable effects.

An alternative to measuring the gas exchange directly in headwater streams may be to estimate this value from physical attributes of the stream and relationships reported in the literature. Palumbo (2014) suggests that stream slope is the most accurate variable to include when predicting gas exchange in this way and Hall (2016) reports a *K*600 to stream slope relationship with an *R*2 of 0.89. Similarly in a later study Hall (2018) includes data from gas injections in small headwater streams which produces an *R*2 of 0.68. Using this relationship it may be possible to calculate a *K*600 from the slope of the stream which can then be used in the inverse modeling to estimate stream metabolism.

The goal of this study was to use estimates of stream metabolism with a derived gas exchange value to predict trout biomass in headwater streams and to investigate what water quality parameters best predict both stream metabolism and trout biomass.

*H*a1: Trout biomass will have a positive relationship with GPP.

*H*a2: Trout biomass will have a positive relationship with ER magnitude.

*H*a3: Trout biomass will have a positive relationship with stream nutrients.

*H*a4: GPP will have a positive relationship with stream nutrients.

*H*a5: ER will have a positive relationship with stream nutrients.