Discussion

GPP

A recent study by (Mejia et al. 2018) estimated metabolism in streams in the same habitat as the present study and with similar methodology with the exception that the streams were not headwaters. Most of the GPP values I estimated (0.007 to 0.707 g O2 m-2 d-1) were within the range reported by (Mejia et al. 2018) (0.02 to 2.53 g O2 m-2 d-1). This however is not what would be expected given that the lowest solar radiation estimation by (Mejia et al. 2018) per day (7.2 mol PAR m-2 d-1) was more than twice the highest value I determined for any of my sites (3.5 mol PAR m-2 d-1 which appear consistent with other headwaters (e.g. (Roberts et al. 2007) and GPP is heavily dependent on light (Odum 1956).

All of the streams in my study were almost certainly light limited with respect to GPP. Light limitation is the strongest factor controlling GPP below 3.5 mol PAR m-2 d-1 and GPP is severely limited below 2.2 mol PAR m-2 d-1 according to (Warren et al. 2017) who also conducted their study in a similar environment to mine. All but one of my sites were at or below the 2.2 mol PAR m-2 d-1 threshold with the highest being 3.5. This suggests that very low GPP values should result from low PAR values.

GPP is also heavily dependent on nutrients (Bernot et al. 2010) and the DIN in my study was relatively low with a mean of less than 0.02 mg N L-1 compared to 0.10 mg N L-1 for (Mejia et al. 2018). A large study conducted in Great Britain found that primary production in headwaters is often limited by DIN concentrations (Jarvie et al. 2018) and another extensive study of temperate streams in the USA suggests that DIN below 0.04 mg N L-1 exhibits depressed levels of chlorophyll (Dodds et al. 2002), chlorophyll is often used as a proxy for GPP since (Ryther 1956). The mean SRP was much higher however in my sites (0.022 mg P L-1) than (Mejia et al. 2018) (0.003 mg P L-1) which may help to explain my unexpectedly high GPP values although this is appears unlikely based on the low light and nitrogen concentrations.

Additionally, (Mejia et al. 2018) showed that GPP increases with increasing catchment area. The catchment area of the streams in my study were not determined, however the average stream discharge was far less (17.7 vs 420.2 L s-1) suggesting that the catchment area was also much less. The GPP values in my study again were not reflective of this.

ER

Ecosystem respiration values in my study also appear to be questionable. (Mejia et al. 2018) reported that ER also increases with catchment area as well as discharge, PAR, and temperature. The values I have measured or estimated for all of these potential determinants were less for my study and yet the ER values I obtained (mean of -10.287 g O2 m-2 d-1) were far greater in magnitude than what (Mejia et al. 2018) reported (mean of -1.25 g O2 m-2 d-1).

Although it appears that the explicit values produced by the models that estimated metabolism may not be trustable, it remains a possibility that the relative order of values may be preserved. Assuming that the relative order of values was preserved, it would be expected that the relationships observed here would be similar to the relationships discovered in other studies. Small forested headwaters are known to display net heterotrophic metabolism meaning that the respired oxygen is much greater than the produced oxygen (Allan and Castillo 2007). My metabolism predictions displayed this relationship with R>>P. It is also expected that GPP and ER will display a strong positive relationship (Hall et al. 2016) which my metabolism predictions also found.

Although some of the expected relationships were indicated by the predictive inverse modeling, the environmental predictors found by the metabolism GLZM’s do not appear to affirm the ordering of values. Both of the GPP and ER models (GLZM’s) found stream depth to be a main effect while the ER model also found stream slope and the GPP model found sampling period. Stream depth is a variable that is put directly into the inverse modelling used to derive metabolism and slope is part of the equation used to derive a *K*600 which is also put directly into the inverse model. This leaves sampling period (when samples were taken) which is not suggestive of any relationship that may inform the reliability of the inverse modeling results. It is conceivable that although slope and depth were inverse model inputs, these physical parameters still had the most profound effect on metabolism, although this appears unlikely.

As discussed above, if metabolism was generally limited by low PAR and DIN it may be difficult to identify other drivers. Depth appears easier to rationalize as deeper streams may generate more metabolism simply because of the increase in physical dimensions of the stream. Slope presents itself with more difficulty though. If stream slope were a driver of ER, the mechanism seems obscure. Steeper slopes could lead to more soil erosion (Renard et al. 2017 Oct 19) and thus potentially more nutrients or carbon in the stream, however neither nutrients nor DOC were part of the GLZM outcomes. If increasing slope allows for more light penetration through the canopy then this would be expected to reveal itself as PAR, canopy openness, and/or increased temperature, a relationship which has not revealed itself in the data. This leads to the conclusion that although the relative ordering of metabolism values may reflect reality, this assumption is quite tenuous.

The trout GLZM found colder minimum daily water temperature and canopy openness to be important factors determining fish biomass. Each of the trout biomass estimates fall within the range of a large data set compiled by (Benjamin and Baxter 2012) who included data for the same subspecies of cutthroat and brook trout I sampled. The estimates I have provided are overwhelmingly due to cutthroat which are known to be a species heavily dependent on cold mountain streams (Isaak et al. 2016). Cutthroat are quite capable of existing in warmer water than where I found them but they are often outcompeted by rainbow trout at warmer temperatures (Bear et al. 2007) which may be part of the reason for this finding. The same relationship exists in my data with minimum, mean, and maximum water temperatures illustrating the robustness of this finding. The canopy openness effect in the GLZM was significant as an interaction with colder water. This finding is also well supported in the literature (Kaylor and Warren 2017a), (Martens et al. 2019 Feb 18) with (Kaylor and Warren 2017b) finding that the majority of vertebrate biomass in the streams they studied, including cutthroat trout, was accounted for by canopy openness alone.

No relationship was found between trout biomass and GPP, ER or the PR ratio which may be substantive or an artifact of metabolism inverse modeling inaccuracies. The trout biomass estimation and GLZM appear to be consistent with previous empirical tests which is evidence indicating either the inverse modeling was flawed, the sample size was too small, or there was indeed no relationship with stream metabolism. (Marcarelli et al. 2011) posit the idea that heterotrophic streams display a decoupling between ER and secondary productivity which may be why I did not find a connection here either. The authors did nonetheless, find a positive relationship between the PR ratio and secondary production in streams and suggest that carbon from GPP may be more responsible for supporting animal growth than allochthonous carbon. I did not detect this linkage and if there was a significant connection here, my data would depict a negative relationship. (Marcarelli et al. 2011) found this relationship with aquatic invertebrates and not fish though, perhaps this relationship is obscured at higher trophic levels. These conclusions are open to question however given the somewhat problematic metabolism estimations.

Discuss what to change

Future studies that attempt to estimate headwater whole stream metabolism using diel oxygen curves without using gas tracers to estimate the gas exchange may be better served by altering the methods presented here. Using the inverse modeling to estimate the gas exchange is likely a preferable technique although model results with a negative gas exchange, negative GPP, and positive ER will still need to be left out of the analysis. Increasing the initial sample size to compensate for this eventual loss of data may offset the loss. Increasing the sampling rate of the instruments to 1 minute or less is also recommended to increase the resolution of the data. These changes have the benefit of relatively simple methodology although it may still be limited to streams of lower slopes (Hall Jr. and Madinger 2018).

Another possibility may be to use an equation to derive the gas exchange value involving more parameters than slope. A meta-analysis by Palumbo and Brown (2014) which evaluated 18 different equations affirm that using equations that have slope as a parameter are less biased than equations which do not have slope as a parameter. They then suggest an equation from Thackston and Dawson (2001) for streams within the same depth and velocity range as the streams in my study which curiously does not include a slope component. This seeming contradiction may be because small steep streams behave uniquely or little effort has been put forth to extend predictive power to them and thus the meta-analysis had little to work with. Interestingly none of the equations include a component for stream bed roughness. Other studies including Ulseth et al. (2019) demonstrate that increasing the stream bed roughness to depth ratio causes large increases in gas exchange because of the increased turbulence which is typical of low order mountain streams. The same study also suggests that stream slope above 4% causes disproportionate increases in gas exchange because air bubbles begin to form and become entrained in the water column. This study does not suggest an equation to use for my application, however there appears to be much work attempting to extend equations for predictions of gas exchange rates to headwater mountainous streams and this may be expected in the near future.

Other techniques for estimating the gas exchange rate in headwaters likely exist for future studies of this kind. Pennington et al. (2018) found that the gas exchange rate can be calculated from the simultaneous measurement of both DO and CO2. This technique involves more instrumentation and more complex calculations but is uninvasive and produces a time-series of the gas exchange rate such that if environment conditions change which alter the gas exchange (e.g. flow variation, surface wind movement) this change will be accounted for. Another promising and creative avenue of research in this area makes use of sound. Morse et al. (2007) reasoned that turbulence drives gas exchange in steep streams (Chanson and Toombes 2003) and turbulence has acoustic properties (Leighton 2012). This led them to compare the sound coming from a stream at a standardized distance to measured gas exchange from gas injections. This study found a strong linear relationship between gas exchange and sound levels and has the benefit of using inexpensive equipment and simple methodology.