**Using population models to predict aquatic invertebrate community assemblages in the Colorado River below the Glen Canyon Dam**

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*Introduction*

As anthropogenic influences on riverine system increase, by damming or by reduced steam flow due to climate change, understanding how changes in flow regime impact aquatic communities is crucial to the conservation and management of these ecosystems (Larned et al., 2010; McMullen et al., 2017; Palmer & Ruhi, 2019). Process-based models, which link species’ underlying biological mechanisms, like survival and fecundity, to environmental conditions, such as stream flow, offer a method to analyzing and understanding flow-ecology relationships (Palmer & Ruhi, 2019; Tonkin et al., 2019). Previous mechanistic models that link populations to flow regime have been successful in recovering observed population dynamics, and with increasing access to high performance computers, can be used to predict population changes under a variety of future scenarios (Tonkin et al., 2019). Analysis of model outputs can provide important conservation insights related to life stage bottlenecks, keystone species identification, and vital rates that drive ecosystem-level responses to flow regime (Tonkin et al., 2019). Process-based models can be applied to riverine ecosystems of conservation interest, like the Colorado River, and can be used to forecast ecosystem responses to proposed management strategies that would otherwise be time-consuming and expensive to conduct.

The Colorado River, which runs through Colorado, Utah, Arizona, Wyoming, California, and Mexico has multiple dams along its mainstem including Glen Canyon Dam in northern Arizona. Glen Canyon Dam, completed in 1959, functional in 1964, produces up to 1320 mwh (megawatts per hour) and has changed the environmental characteristics of the Colorado River downstream of the dam from a turbid, warm, aridland river to a cold, clear river that runs between 227 and 396 m3s-1 (cubic meters per second), as dictated by the electricity demands of nearby cities (Bureau of Reclamation, 2021a; Bureau of Reclamation, 2021c; Kennedy et al., 2016). The construction of the dam has altered the temperature regime of the river, homogenizing the water temperature and homogenizing the pre-dam temperature fluctuations. Invertebrates are known to have temperature-dependent growth and development rates (Sweeney and Vannote, 1980). However, increased temperatures in the summer months, combined with lower reservoir levels, and is predicted to increase the water temperature of dam releases in the summer months. How this forecasted temperature change will impact the invertebrate community in the Colorado River, after decades of mostly homogenized water temperatures) is unknown.

In order to optimize the energy supply from Glen Canyon Dam, there is high variation in water release, with a difference of about 169.9 m3s-1 each day (Bureau of Reclamation, 2021a; Kennedy et al., 2016). This practice is called hydropeaking, and it causes a wave that propagates down the length of the river, creating an ‘intertidal’ zone to which aquatic insects are not adapted (Kennedy et al., 2016; Moog, 1993). Hydropeaking reflects no natural flow regime and is an ecologically unpredictable phenomenon that disrupts aquatic insect life cycles and patterns of recolonization (Poff et al., 1997). In the Colorado River below Glen Canyon Dam, eggs cemented on near-shore substrate may be exposed to air and desiccate because of hydropeaking waves. This phenomenon, as well as environmental changes like decreased water temperature, reduced seasonal flooding, and reductions in sediment transportation from upstream reaches has reduced the abundances of ecologically important taxa in the orders Ephemeroptera, Plecoptera, and Trichoptera (Kennedy et al., 2016; Cross et al., 2010). In addition, the combination of hydropeaking and altered environmental conditions has caused shift in aquatic macroinvertebrate community assemblages, allowing non-native species, like the New Zealand Mudsnail, to colonize reaches of the mainstem river (Cross et al., 2010). New Zealand Mudsnails, among other aquatic bound non-native species, are not the preferred prey of terrestrial consumers, like birds or bats. Instead, these terrestrial organisms prefer to prey on native species that have aerial phases, like Ephemeroptera, Trichoptera, Plecoptera, or Diptera species (Cross et al., 2011).

Experimental high flows events (HFEs) have been implemented to facilitate the sedimentation of sandbars, beaches, and other habitats, as well as to provide a research opportunity for the study of biotic and abiotic processes in rivers during flood events (Patten et al., 2001). Nine high flow events have taken place (March 1996, November 2004, March 2008, November 2012, November 2013, November 2014, November 2015, November 2016 and November 2018), all of which met or exceeded a peak flow of 1034 m3s-1 between 24 and 168 hours, almost three times higher than high base flows (Bureau of Reclamation, 2021b). Studies on these events have shown that the spring-time high flow event reduced non-native macroinvertebrate abundances and favor aquatic insects that are of bioenergetic value to fish (Cross et al., 2011). However, the long term impact of these events is unknown.

I aim to apply a mathematical modelling approach to assess how aquatic invertebrate populations will respond to specific flow management scenarios related to the highlighted gaps in knowledge. I will implement the outlined analytical approach in the Colorado River below Glen Canyon Dam. Using the approaches of Lytle et al. (2017) and Rogosch et al. (2019), I will usethree population matrix models that reflects the biological responses of three different aquatic invertebrate taxa that represent well-defined trait-groups within the Colorado River ecosystem. We will investigate how increases in summer temperatures impact invertebrate population abundance, how temperature impacts population-level HFE responses by comparing the long-term effects of spring and fall HFES, and how changes in hydropeaking intensity interplay with different flow regimes.

**Methods**

*Model Structure*

Stage-structured population models use matrix multiplication to incrementally step populations forward in time (Eq. 1):

in which ***n****i(t)*, the stage-class abundances for species *i* at time *t* are multiplied by ***Ai****(t)*, the transition matrix for that species under certain environmental conditions over time *t*, which results in ***n****i(t+1)*, the stage-class abundances for species *i* in the next time step (Caswell, 2001).

The transition matrix ***Ai****(t),* which includes vital rate information for species *i* with stages classes *j* = 1, 2, 3 (Eq. 2):

in which species-stage specific vital rates like fecundity *Fji*, species-stage specific transition probabilities from stage *j* to stage *j+1*, *Gji*, and the probability of remaining in a specific stage, *Pji* are represented.

In this model, vital rates, like transition probability and fecundity, can change in response to environmental scenarios, according to the functions derived from the literature developed below. By allowing the transition matrix to vary timestep to timestep depending on river discharge and water temperature, we can model a dynamic environment.

*Timing of Emergence*

For most insects emergence timing is influenced by the accumulation of degree days. Each taxon has a specific threshold of degree days (*Di threshold*) that cohorts must accumulate before they can emerge.

In order to calculate how many degree days each emerging cohort has accumulated we can use the equation below:

When we set *D(t)total* equal to *Di threshold* and solve for *n*, we calculate the number of timesteps required to reach threshold *Di threshold*, which biologically represents the number of timesteps to reach Stage 3.

*Fecundity*

Because cohorts that remain in a larval stage for longer tend to grow to a larger body size at emergence, and larger body size at emergence is linearly related to per capita fecundity (Taylor et al. 1998), we can then generally scale per-capita fecundity to general body size at emergence. For *P. antipodarum*, which can start reproducing in Stage 2, per capita fecundity for Stage 2 and Stage 3 is the mean number of offspring for each size class.

*Recruitment Limits and Density Dependence*

All species are assumed to operate under density dependent fecundity, in which we adjust reproductive output based on the total abundance of all stages following a logistic relationship

in which stage-specific fecundity is modified by the relationship between total *N* for species *i* at time *t* and carrying capacity at time *t* (Rogosch 2019).

The starting abundance at which total recruitment limitation occurs for each species is estimated based on food availability in a given reach (i.e. low, medium, high). Both Baetis and *P. antipodarum* are scraper-grazers that thrive in areas with lower turbidity, while hydropsychids are collector-gatherers that create a net that catches fine-particulate organic matter (FPOM), which is unrelated to turbidity but is dependent on upstream production (Vieira et al. 2006., Brockhuizen et al. 2001).

*Flood Disturbance Response*

Disturbance-adapted insects also often see a brief increase in carrying capacity in response to disturbances, which can be represented by increasing R in proportion to the disturbance magnitude post-disturbance accordingly

In which *R0* represents post-disturbance carrying capacity in individuals at time *t*, *Rpre* represents the pre-disturbance carrying capacity, *rd* represents maximum carrying capacity after a large disturbance (McMullen 2017). *Qf* is a modifier that describes the relationship between disturbance magnitude and carrying capacity, which is determined by the equation

in which Qmin is the minimum disturbance magnitude to influence *Ri,t* and *a* is the half-saturation constant for that relationship (McMullen 2017, Table 1). We also allow *Ri,t* to return to *Ri.b*, which represents baseline *Ri* in the absence of disturbances following

in which g is a shape parameter that determines the rate at which *Ri,t* returns to *Ri,b* and τ is the number of timesteps since the disturbance (McMullen 2017. Figure 2). *Ri,b*, although a constant in this model for the sake of simplicity, in future iterations it could fluctuate as a function of varying productivity in the system.

In addition to brief increases in recruitment limit, there is also immediate mortality caused due to flood pulse disturbances. To calculate flood mortality relationship, we fit a negative exponential equation to data from the literature (Table 1)

Where *h* and k are species specific shape modifiers for the negative exponential function and *Q* is disturbance magnitude (McMullen 2017, Table 2).

*Hydropeaking Disturbance Response*

Hydropeaking causes desiccation of eggs laid along the rivers edge. We calculated the percent eggs surviving hydropeaking as

in which *r* represents location of oviposition along a cross section of the river, with 0 being the river edge and 1 being the center of the river, and shape-parameter c = 2 (Kennedy et al. 2016 We modify that equation to be a modifier of survival related to hydropeaking index (HI), where a higher HI represents a more intense hydropeaking regime (Dibble, 2015).

*Transition Probabilities*

For hydropychid and baetid spp, we allowed water temperatures to decrease stage duration, while colder temperatures increased stage duration. We calculate *Pi* and *Gi* following Birt et al. 2009:

Where *σi* is stage specific survival and *S(t)i,j* is stage *j* duration for species *i* at timestep *t*.

In order to allow *P. antipodarum* to fit our stage-structured model we created three size-based bins. Stage 1 represent pre-reproductive individuals (smaller than 3.2mm). Stage 2 are small reproductive individuals (3.2 mm to 3.954 mm) and Stage 3 are large reproductive individuals (larger than 3.954 mm).

Table 1: Summary of model parameters

|  |  |
| --- | --- |
| Parameter | Description |
| t | Timestep |
| F(t)i,j | Fecundity for species i in stage j at timestep t |
| G(t)i,j | Probability of species i transitioning from stage *j* to stage *j+1* at timestep *t* |
| P(t)i,j | Probability of species i of remaining in stage *j at* timestep *t* |
| Ni,t | Total population abundance at timestep t for species i |
| Ni,pre | Population abundance pre-disturbance at timestep t for species i |
| Ri,t | Recruitment limitation abundance at timestep t for species i |
| Ri,pre | Pre-disturbance R at timestep t for species i |
| Ri,d | Maximum post-disturbance R for species i |
| Ri,0 | Post-disturbance K at timestep t for species i |
| Ri,b | Baseline R (in the absence of disturbance) for species i |
| Qt | Disturbance magnitude at timestep t |
| Qf | Disturbance magnitude carrying capacity relationship |
| Qmin | Minimum Disturbance magnitude |
| a | Half-saturation constant |
| b | Scaling modifier for disturbance-mortality relationship |
| h | Modifier for disturbance-mortality relationship |
| g | Rate that Ri,t returns to baseline Ri,b |
| τ | Timesteps post minimum disturbance |
| T(t) | Temperature in °C at timestep t |
| whydro | Percent of eggs surviving hydropeaking |
| r1, r2 | Range of oviposition locations within the river |
| c | Shape parameter for whydro |
| D(t)total | Total number of degree days accumulated within a given number of timesteps (t) |
| Di,threshold | Degree day threshold for species i |
| n(t) | Number of timesteps required to accumulate Di,threshold at timestep t |
|  |  |

*Model Parameterization*

*Fecundity:* Per capita fecundity for Hydrospyche spp was calculated by taking fecundity per female from Willis Jr & Hendricks (1992) and dividing by 2, assuming a 1:1 sex ratio. In the case of hydropsychids, we use a *DHYOS threshold*= 1680 (Hauer & Stanford 1982) and we use

to relate per-capita fecundity to *n* timesteps taken to emergence (95% CI from Willis Jr. & Hendricks, 1992). For Baetis, *DBAET threshold* = 1356 (Lee et al. 2013) and we use

to relate per-capita fecundity to degree days (minima and maxima from Degrange, 1960).

For *P. anitpodarum*, we used supplemental material from McKenzie et al., 2017, we calculate the linear relationship between mean Stage size (mm) and fecundity:

For the two reproductive stages, we calculated the mean fecundity. Like other invertebrates, *P. antipodarum* fecundity is driven by temperature. Dybahl and Kane (2005) report maximum fecundity between 16 and 19 C, with no fecundity below 9 C (Bennett et al. 2015). Using this information, we fit a power function to scale fecundity to temperature:

These temperature adjusted fecundities are then multiplied by 0.655, based on data that 95% of *P. antipodarum* are female and assuming 30% newborn mortality rate, since it is unlikely that 100% of newborn individuals survive (Zaranko et al. 1997).

*Flood Disturbance Response* – we fit our immediate mortality response to flood events with data from the literature listed in Table 2.

*Hydropeaking Disturbance Reponse* - We assume that r1 = 0.4 and r2 = 0.6 for hydropsychids based on observation that Hydropsyche species prefer to oviposit closer to the middle of the channel, while Baetis spp prefer to oviposit on the river edge (Miller et al 2020). For Baetis, we set r1 = and r2 =, which are values from Kennedy et al. (2016). Because *P. antipodarum* are fully aquatic and are relatively unaffected by hydropeaking, we assume r1 = 0.9 and r2 = 1.

*Transition Probabilities*- Transition probabilities for hydropsychids were calculated from Willis Jr & Hendricks, 1992, Table 3. Larval instars I and II were grouped to create Stage 1, larval instars III through V and the pupal stage was grouped to create Stage 2, and adults and eggs were grouped to create Stage 3. Based on observation by Willis Jr & Hendricks 1992, Stage 1 duration can vary depending on temperature by the number of timesteps required to reach *D(t)threshold*. Similarly, Baetid transition probabilities are derived from survival rates reported in Werneke 1992 and stage duration is calculated from timesteps required to reach *D(t)threshold* for Baetis spp assuming that Stage 1 and Stage 2 stage durations are equal and that Stage 3 stage duration is one timestep:

Since *P. antipodarum* are ovivioparous and size at birth is 0.5 mm, we can calculate the duration of each stage from the equation on Cross et al. 2010, Figure 3. We assumed the individuals above 3.95mm remain in that size class for about 7 timesteps, thus limiting the lifespan of a modeled snail to 1 year, the longest that a cohort of *P. antipodarum* has been tracked (Dybdahl and Kane, 2005).

Transition probabilities for *P. antipodarum* are calculated from Cross et al. 2011 which suggests a probability of survival of 80 – 100%. Not much is known about total lifespan of *P. antipodarum*. Because of this, we applied Birt et al. 2009 equations, assuming survival for each stage is 0.9 (overall survival = 0.729) and assuming that the total lifespan of a *P. antipodarum* is one year. There is no temperature dependent transition probabilities.

Table 2: Literature reviewed to fit flood mortality relationships

|  |  |  |  |
| --- | --- | --- | --- |
| Flood Response Literature | Hydropsyche spp. | Baetis spp. | *P. antipodarum* |
|  | Kimura et al. 2011; Bond and Downes 2000 | Robinson et al. 2003; Consoli et al 2022 | Bennett et al. 2015; Cross et al. 2011 |

*Validation with Historical Drift Data*

We validated each species population model by comparing model outputs to historical observed abundance data from the Grand Canyon Monitoring and Research Center (GCMRC), using publically available temperature and discharge time series for three different sites (Colorado River at Less Ferry, Colorado River above Diamond Creek confluence, Green Riverbelow Flaming Gorge Dam). We compared the association between model output and observed abundances using a Spearman rank sum correlation (Rogosch et al., 2019). Additionally, we calculated root mean square error and coverage to determine that amount of the 95% confidence interval of the model output that matches observed data points.

*Experimentation with High Flow Experiment timing*

Although flows below Glen Canyon Dam are seasonally homogenized compared to the pre-dam flows, Glen Canyon Dam does occasionally release large amounts of water from time to time, called High Flow Experiments (HFE) (Melis et al. 2011). These HFEs have historically occurring in either fall (November) or spring (March). A major management question is whether HFE timing effects aquatic invertebrate populations and if they mitigate invasive *P. antipodarum* populations. To test this, we compared three 100 year scenarios comparing randomized fall HFEs, randomized spring HFEs, and a timeseries with no HFEs. We compared change in population abundance for each species, including Baetid mayflies that currently do not occur below Glen Canyon Dam (Kennedy et al. 2016).

*Perturbation analysis to test sensitivity*

Weekend reduction in hydropeaking: In addition to schedule HFEs, Glen Canyon Dam has also piloted (adopted?) experimental weekend reductions in hydropeaking intensity to improve aquatic invertebrate recruitment. To test how the presence of absence of reduced hydropeaking on summer weekends. We compared change in population abundance for each species (How best to compare significance?).

Perturbation Analysis to test sensitivities: As the depth of Lake Powell decreases and lake water temperatures increases due to continued drought in the Southwest, water outflows in the summer are projected to increase in temperature (Get REF from TK). To understand the sensitivity of this model to increases in summer water temperatures, we can run 20 scenarios increasing summer water temperatures by 10% (see Regan et al., 2003). We tested the sensitivity of each population model to changes in hydropeaking, by iteratively running 20 scenarios with +- 10% of the Hydropeaking Index of Glen Canyon Dam and plotting the change in abundance. We then tested the sensitivity of the models to flood response, running 20 scenarios with increasing and decreasing mortality due to floods by +- 10%, following Lytle and Merritt, 2004. We can analyze sensitivity by taking the slope of the average population size in response to the aforementioned perturbations. Elasticity is calculated as the logarithm of sensitivity. We retained and interpreted sensitivities and elasticities with a R2 > 0.3 (Lytle et al. 2017).

*Model Iterations*

For each scenario described for HFE and hydropeaking experiments, as well as the perturbation analysis, we ran the model 100 years out for 1000 iterations to converge on an average value, using the first 10 years as burn-in (Lytle et al. 2017).