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Creating a Mass-Balanced Food Web Model for a Generalized Restored Estuary in the Puget Sound

Pen Johnson

ESCI/HNRS Capstone Project

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Abstract

Historical anthropogenic modifications have been documented to have negative effects on the estuarine environments of Puget Sound. Over the last three decades there has been an increase in efforts to restore these estuarine environments through both passive and active means. This increase in restoration has been predicted to have positive effects on survival of juvenile Chinook salmon, which is an ecologically and culturally important species in the Salish Sea. The goal of this project was to use Ecopath with Ecosim to create a mass-balanced food web model of a generalized restored estuary to help further understanding of the potential effects of restoration practices on the diet matrices and biomass estimates of juvenile Chinook salmon and juvenile Chinook salmon prey. The model consisted of 8 functional groups: 1 primary producer group, 3 invertebrate groups, 2 fish groups, 1 bird group, and 1 detrital group. Biomass, abundance, and demographic data was obtained from the literature or from individual stock assessments conducted for principal ecosystem components. The model created is a vast simplification of a true estuary within Puget Sound and would benefit from the addition of more functional groups to fully understand the impact of restoration on juvenile Chinook salmon, and juvenile Chinook salmon prey.

Introduction

Historically, there have been modifications to the floodplains and channels of estuarine environments in Puget Sound. These anthropogenic modifications include the removal of snags, diking, ditching tidelands and diverting water to maintain water flows (Collins, 1998). These modifications have had negative effects on estuarine environments, including loss of sediment replenishment, reduced habitat complexity, and the loss of wetland areas (Collins, 1998). It has been shown that estuarine habitats contribute to juvenile salmon growth and survival patterns throughout their life history (Chalifour et al., 2019; David et al., 2016; Reimers, 1969). Salmonids have been documented to be an important species in Puget Sound because they play an essential role in cycling nutrients from the ocean to freshwater streams (Bennett, 2019). In addition to being an ecologically important species, salmonids are a culturally important species for indigenous communities in the Salish Sea (Thornton & Deur, 2015). This combination of ecological and cultural importance has prompted the restoration of estuaries in the Puget Sound in the last three decades (Furlong, 2017; Hinston & Hood, 2004). Currently there is increasing interest in researching how the previous restoration actions have affected the estuaries and the organisms that inhabit them and understanding whether they are providing the needed habitat and prey resources for salmon.

Summary of Restoration Practices

Restoration practices can be divided into two categories active and passive recovery (Elliott et al., 2007). Active recovery involves continuous human interaction in restoring ecological function to the impacted environment (Elliot et al, 2017). Examples of active recovery include the re-creation of a previous (unimpacted) environment, re-introduction of key species, and reclamation of land (Elliott et al., 2007). Passive recovery includes minimal human involvement and assumes that recovery will occur in the

ecosystem once the stressors have been removed and sustaining processes have been restored (Elliott et al., 2007). The estuarine restoration practices occurring in Puget Sound are a combination of both active and passive recovery. The Wiley Slough Estuarine Restoration Project implemented active recovery practices in the initial phase and passive recovery practices in the second phase (Furlong, 2017). The initial phase was the construction of setback dikes and the installation of a new tide gate, and the second phase left Wiley Slough to recover with the stressors (seaward dikes) removed and tidal exchange restored. (Furlong, 2017). A similar approach was used in the habitat restoration for Fir Island, an estuarine marsh also located in the Skagit River Delta (Hinston & Hood, 2004).

These restoration projects had primary objectives of restoring channel habitat for juvenile salmonids and to restore native marsh vegetation to support detrital food chains for juvenile salmonids (Furlong, 2017; Hinston & Hood, 2004). The restoration process restored tidally connected channels and helped with the re-introduction of tidal influences. With these aspects restored, it was assumed that it would be supportive of juvenile salmonid populations (Furlong, 2017). These primary objectives align with the assumption that recovery is truly successful then the community established will be similar in species composition, population density, population size, and biomass structure to that previously present or present at a comparable unimpacted and unaffected site (Elliott et al., 2007). It has been decades since many of these restoration projects started and there has been an increase in efforts to evaluate the recovery progress (Simenstad & Cordell, 2000), while recognizing that rebuilding ecosystem structures and sustaining processes takes time.

This project has a goal of being a part of those increased efforts by maintaining a focus of restoration evaluation through a mass balance model food web model of species in an expected restored estuary in Puget Sound (Vasslides et al., 2017). A mass balance model could help address the question if the current restoration meets the definition of recovery that has been outlined in the literature through the biomass structure and energy flow (Elliott et al., (2007). My major objectives for this project were to:

1. Assimilate available data on species abundance, vital rates, and diets into a trophodynamic model framework.
2. Identify significant data gaps that could potentially constrain model development and/or increase uncertainty in the outputs.
3. Create a resource to increase understanding about salmon food resources in estuaries, and whether restoring sites provide adequate prey that reference sites are known to.

Methods

Ecopath with Ecosim (EwE)

Ecopath with Ecosim is a trophodynamic model in which functional groups are represented as biomass pools. These biomass pools are regulated by gains (consumption, production, and immigration) and losses (predation, fisheries, and emigration) (Christensen et al., 2005). Within the software there are two modules Ecopath, a static mass balanced model of the “reference” state of a food web, and Ecosim, a dynamic model in which biomass densities and vital rates change through time in response to perturbations. For this project only Ecopath was used as a modeling program. Ecopath functions as a series of linear equations that describe flows of mass into and out of the biomass pools, with the rates happening at annual steps. For each functional group l ,

$$BA_i = B_i * \left(\frac{P}{B}\right)_i * EE_i - \sum_{j=1}^n B_j * \left(\frac{Q}{B}\right)_l * DC_{ji} - Y_i - E_i \quad (1)$$

Where BA = biomass accumulation B_i = biomass, P/B = the production/biomass ratio (roughly equal to total mortality), and EE = ectotrophic efficiency (Christensen et al., 2005). The summation represents losses to all predators, B = biomass of j (the prey), Q/B the consumption-to-biomass ratio of group j and DC is the proportion of the group i in the diet of group j . Additionally losses due to Y = fishery yield and E = net migration can be included. This function is what drives this model, more specifically with four core parameters (biomass, P/B, Q/B, and EE), and the diet composition (defined in a matrix by proportion of prey) for each functional group. For the diet composition there was the assumption that for each functional group all nutrients were not going to be obtained within the system. This assumption is parameterized by the inclusion of a prey import group in the diet composition matrix for all consumer groups; this is an important component where functional groups use the model domain as one of several habitats.

Functional Groups

The generalized Puget Sound restored estuary model I developed has 8 functional groups, representing individual species and aggregations of species. This model includes 1 primary producer group, 3 invertebrate groups, 2 fish groups, 1 bird group, and 1 detrital group (Table 1). These functional groups were defined with the four core parameters and the diet composition (Table 2 & 3). Some groups migrate outside of the model domain; they include Chinook salmon (*Oncorhynchus tshawytscha*) and Trout spp. (*Salvelinus spp.*), as well as the bird predator. For simplification we assume no interannual variability in the timing or spatial extent of migrations, limiting temporal domain to one salmon outmigration season, ~March-June. Guilds were included or rejected based on criteria such as:

- Their importance in the diets of other groups,
- The potential effects that estuarine restoration has upon the represented guilds.
- Their ability to integrate ecological processes (e.g., species that move between habitat types and thus link the ecology of those habitats)
- Their importance to local communities for non-consumptive reasons

| Table 1. Functional Groups in the model with major representatives. | | |
|---|---|--|
| Functional Group | Common Name | Scientific Name |
| Major Bird Species | Great Blue Heron | <i>Ardea Herodias</i> |
| Salmonid Species | Juvenile Chinook Salmon | <i>Oncorhynchus tshawytscha</i> |
| Predator Fish Species | Trout (Bull Trout, <i>Salvelinus confluentus</i> , and cutthroat trout, <i>Oncorhynchus clarkia</i>) | <i>Salvelinus spp.</i> |
| Emergent Insect | Various arachnids | <i>Arachnida spp.</i> |
| | Various flies | <i>Insecta spp.</i> |
| | Various beetles | <i>Diptera spp.</i> |
| Benthic Invertebrates | Amphipods | <i>Amphipoda</i> |
| | Isopods | <i>Isopoda</i> |
| | Benthic insects | <i>Hyrosychidae, Culicidae, Chrionomidae</i> |
| Zooplankton | Various Copepods | <i>Copepoda</i> |
| | Various Mysids | Family Mysida |
| Phytoplankton | Diatoms | - |
| Detritus | - | - |

Species and Functional Group Descriptions

The four core parameters and diet composition for each functional group's pre-balance are described in this section and are represented in Table 2 & 3. Highlighted are the two values that were modified within the mass-balancing routine.

Table 2. Ecopath parameters pre-balance for the functional groups in the generalized restored estuary model. See the Species and functional group descriptions section for description of parameters. Boldfaced values were calculated by the mass-balancing routine in the Ecopath model.

| | Group name | Trophic level | Hab area (proportion) | Biomass in habitat area (t/km ²) | Biomass (t/km ²) | Production / biomass (/year) | Consumption / biomass (/year) |
|---|------------------|---------------|-----------------------|--|------------------------------|------------------------------|-------------------------------|
| 1 | Great Blue Heron | 3.789 | 1 | 0.01 | 0.01 | 0.11 | 61.1 |
| 2 | Bull Trout | 3.421 | 1 | 0.15 | 0.15 | 0.64 | 1.1 |
| 3 | Chinook Salmon | 3.155 | 1 | 0.081 | 0.081 | 4.5 | 14.8 |
| 4 | Emergent Insects | 2.364 | 1 | 28.5 | 28.5 | 18 | 32.6 |
| 5 | Benthos | 2.000 | 1 | 30.9 | 30.9 | 3.41 | 25 |
| 6 | Zooplankton | 2.000 | 1 | 129.41 | 129.41 | 15 | 75 |
| 7 | Phytoplankton | 1.000 | 1 | 85 | 85 | 160 | |
| 8 | Detritus | 1.000 | 1 | 10 | 10 | | |

Table 3. Diet Composition estimates for all eight model groups, Great Blue Heron, Bull Trout, Juvenile Chinook Salmon, Trout, Emergent Insects, Zooplankton, Phytoplankton, Detritus and Import. Import is defined as nutrients from outside the system. Prey are represented in the column, predators the row across.

| Prey/Predator | Great Blue Heron | Trout | Chinook Salmon | Emergent Insects | Benthos | Zooplankton | Phytoplankton | Detritus |
|-------------------------|------------------|-------|----------------|------------------|---------|-------------|---------------|----------|
| Great Blue Heron | | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Trout | 0.01 | | | 0 | 0 | 0 | 0 | 0 |
| Juvenile Chinook Salmon | 0.043 | 0.15 | | 0 | 0 | 0 | 0 | 0 |
| Emergent Insects | 0 | 0.45 | 0.4 | | 0 | 0 | 0 | 0 |
| Benthos | 0.1 | 0.05 | 0.2 | 0.2 | | 0 | 0 | 0 |
| Zooplankton | 0 | 0.15 | 0.3 | 0 | 0 | | 0 | 0 |
| Phytoplankton | 0 | 0 | 0.005 | 0.2 | 0.5 | 0.75 | | 0 |
| Detritus | 0 | 0 | 0 | 0.15 | 0.5 | 0.25 | 0 | |
| Import | 0.847 | 0.2 | 0.095 | 0.45 | 0 | 0 | 1 | 1 |

Great Blue Heron (*Ardea herodias*)

The Pacific Great Blue Heron (GBH) is a common non-migratory bird that is found in large concentrations in the coastal regions of the Pacific Northwest (Kenyon, 2005). Pacific Great Blue Heron feeds primarily on small fish in freshwater streams and estuarine marshes during their breeding season (March-June). Salmon smolt have been documented to be susceptible to heron predation, with an annual predation rate of 0.3-1.3% of all juvenile salmon out-migrating from 2008-2018 (Sherker et al., 2020). This species is protected under the Migratory Bird Treaty Act of 1918, making it important to monitor, potentially gaining from estuarine habitat restoration while also serving as a predator for the target of restoration activities, Pacific salmon.

I used data from the southern Puget Sound for the biomass estimates, and the (P/B) ratio (Preikshot & Cheney, 2015). The estimates used were data collected in 2012, which were the best current available values of these parameters in a restored estuary in Puget Sound (Preikshot & Cheney, 2015). For the consumption rates I used an allometric equation, which estimates daily energy requirements as a function of mean body mass (Birt-Friesen et al., 1989). In the allometric equation I used weight estimates for adult herons (Bennett et al., 1995). Then to account for assimilation efficiency I multiplied the daily energy requirement by 1.16 (Bennett et al., 1995). I then divided this new value by the energy density of the aggregate to yield the total mass consumed per day. I used energy density estimates, and I then multiplied the daily mass consumed by 365 days and divided it by body mass in grams to generate Q/B for Great Blue Heron (Hunt et al., 2000). This calculation process was based on the work done by Harvey (2010).

There was limited information available on the diet composition for GBH, but there were estimates for Chinook salmon diet percentage and benthic invertebrates diet percentage available. The best current and available estimates were from an Ecopath model focused on southern Puget Sound (Sherker et al., 2020; Preikshot & Cheney, 2015). The assumption was also made that trout would be considered a prey species (Eissinger, 2007). Import assumptions were based upon seasonal changes cause a shifting of prey availability and influencing heron foraging patterns, territoriality, and distribution (Eissinger, 2007)

Chinook Salmon (Oncorhynchus tshawytscha)

A focus for estuarine restoration is improvement of Chinook salmon habitat. This species was listed as a threatened species under the U.S. Endangered Species Act (Fisheries, 2021). Chinook Salmon is an ecologically an important species as well as culturally significant in the area, as detailed in the introduction.

In general, P/B estimates for fish species corresponds to the total mortality rate (Z) (Christensen & Walters, 2004). With this assumption I calculated total mortality using a non-equilibrium version of the Beverton Holt estimator of Z, based on mean length (Huynh et al., 2017). These calculations were done using the program Fish Base (Froese and Pauly 2000). The parameters length of first catch (L_c) the mean length (L_{mean}) I obtained from a study done on juvenile Chinook salmon in Puget Sound (Gamble et al., 2018). There is evidence supporting the resulting P/B estimates by other similar Ecopath analyses of juvenile Chinook salmon (Kenyon, 2005; Warren et al., 2014). There was limited availability for Q/B and biomass estimates for Chinook salmon and I used estimates taken from the Columbia River as the Columbia River basin has a comparable climate to the study area (C. J. Harvey & Kareiva, 2005).

Diet composition for Chinook salmon in an estuarine environment has been documented to be mostly flies, spiders, and other insects (Chalifour et al., 2019; Chittenden et al., 2018; Simenstad & Cordell, 2000). These groups were broken down into species and for emergent insects I used the estimates for Amphipods, Mysids, and Dipterans in the Nisqually Estuary to simplify the model (Woo et al., 2019). The diet proportions for benthos, and zooplankton as Chinook salmon prey were also determined based upon estimates in the Nisqually Estuary (Woo et al., 2019). Chinook salmon are categorized as carnivorous; thus, I maintained the diet composition of phytoplankton to be quite low. I decided that the prey import values for Chinook salmon could be assumed to be low as juvenile salmon have been documented to have a strong tendency to reside in tidal channel for a relatively long period of time (Levy & Northcote, 1982).

Trout (Salvelinus spp.)

This functional group is represented by bull trout and cutthroat trout, both of which are piscivorous salmonids known to be predators of juvenile Chinook salmon consuming salmon eggs, fry and carcass

flesh depending on the season (Guy et al., 2011). These species group also have a major presence in Puget Sound with the Skagit River Watershed containing 26 of the 27 bull trout populations with all four life histories present (Lowery & Beauchamp, 2015). Trout would also be a key species to monitor during estuary restoration as some populations are included in the listing under the Endangered Species Act (Fisheries, 2021). With this knowledge trout is important to include in this model, as understanding bull trout predation would inform the potential true effects on restoration on Chinook salmon.

There is limited data available for both the biomass and Q/B estimates for bull trout. There was an EwE model parameterized for the Salmon River Basin (Warren et al., 2014). I used both these estimates as the Salmon River Basin is comparable to an estuary located in Puget Sound. The process used for calculating P/B for bull trout was the same as the juvenile Chinook salmon functional group. For P/B calculations I used L_c and L_{mean} from studies done in the Dungeness and Elwha estuaries (Quinn et al., 2017).

There was also limited data about the exact diet composition of bull trout. Through the information provided on Fish Base, I estimated diet composition for benthic crustaceans, bony fish, insects, and mollusks as trout prey (Coad, 1995). I used Chinook salmon prey estimates for Skagit River Bull Trout (Guy et al., 2011). The age class for trout that resides in inter-tidal areas within estuaries are generally larger fish, and we assumed the import proportion of the diet composition to be 0.2 as there is a higher capacity for bull trout to be moving in and out of the assumed study area (Goetz et al., 2021).

Emergent Insects

Emergent insects have been documented to make up a high percentage of juvenile Chinook salmon diet and are key to species survival (Simenstad & Cordell, 2000; Woo et al., 2018, 2019). I pulled biomass estimates for Arachnida and Insecta (both major juvenile Chinook salmon prey species) from the Nisqually Estuary (Woo et al., 2019). This data was recorded for a 0.00049 m^2 area in dry weight biomass (mg), and I converted this to be in tons/km^2 . This conversion was done by multiplying the area by 10^6 and multiplying the dry weight biomass by approximately 10^9 . This biomass was still not accurate as it was dried samples. To amend this issue, I multiplied the dry weight biomass by 300% which was based off conversions done in a study done on emergent insects in the Atnarko River (Watkinson, 2001).

There was limited information for emergent insect Q/B, P/B and diet composition estimates for Puget Sound estuaries. There were riparian estimates available from a EwE model done for the Atnarko River Watershed (Watkinson, 2001). Diet composition was estimated based on the knowledge that there is a mix of both carnivores and herbivores emergent insects, with this assumption estimates for benthos and phytoplankton would be the same percentage (Watkinson, 2001). Prey imports for this model group was estimated to be low as the necessary nutrients would assumed be produced in place.

Benthos

Benthic invertebrates that were included in this model group were Amphipods and Isopoda, both of which are common in the diet of juvenile Chinook salmon (Woo et al., 2019). Both species are also key consumers of benthic primary producers and detritus (Harvey, 2010). Biomass estimates for this model group were calculated similarly to the emergent insect's biomass estimates. I used the dry weight biomass documented for Amphipoda, Crustacea and Isopoda, converted it to ton/km^2 and multiplied that result by 300% (Woo et al., 2019). Q/B and P/B estimates were based off estimates for an Ecopath model made for Puget Sound as this data was the most accessible and accurate available at the current time (Harvey, 2010). These estimates are also backed up by other estimates from models used in analyzing other model groups, including juvenile Chinook Salmon (Kenyon, 2005; Watkinson, 2001). Diet composition for this functional group was split evenly between phytoplankton and detritus.



Zooplankton

There are many species within this model group that have been observed to be Chinook salmon prey and the major species chosen for this model were Copepods and Mysids. These two were chosen due to documentation showing that they make up a high percentage of juvenile Chinook salmon prey biomass (Woo et al., 2019). Biomass estimates for copepods and mysids were taken from a study done in the Nisqually Estuary (Woo et al., 2019). There was limited information regarding P/B and Q/B parameters for zooplankton for Puget Sound estuaries. For both P/B and Q/B parameters there were generalized Puget Sound estimates I based my parameters for this model on (Harvey, 2010). Diet composition was also taken from generalized Puget Sound estimates (Harvey, 2010), with additional help provided by my advisor.

Phytoplankton

Phytoplankton is a generalized primary producer group in this model, functioning as a prey group for the emergent insect, benthic invertebrates, and zooplankton groups (Hiltunen et al., 2022). The P/B and biomass estimates are generalized estimates based upon the model for southern Puget Sound (Preikshot & Cheney, 2015). These estimates are supported by research that has shown that estuaries support high rates of metabolism and primary production due to the large inputs of nutrients and organic carbon that they receive from land and oceans (Cloern et al., 2014). Of these phytoplankton there are three groups that characterize estuarine assemblages: diatoms, cryptophytes, and dinoflagellates (Santos et al., 2022). Diatom were the dominant group for this generalized restored estuary model for the Puget Sound (Santos et al., 2022). Diet composition and Q/B estimates are not applicable to for this primary producer model group.

Detritus (Detrital Pools)

The coastal estuarine environments in the Puget Sound inhabit organisms that are supported by detritus-based food webs (Howe, 2012). This means estuarine restoration can increase capacity of this type of food web by increasing the overall area suitable for estuarine primary production in the estuary. This increases the biomass of available organic matter to detritivores. Detritus biomass estimates were estimated based off other estuarine Ecopath models done within the Puget Sound (Harvey, 2010; Kenyon, 2005; Warren et al., 2014)

Results

General Characteristics and Mass Balancing of the Ecopath Model

The Ecopath master equation, Equation 1, contains four core parameters that describe the basic biology of each functional group: biomass, P/B, Q/B, and EE. Usually, all but one of these parameters are input parameters, and the remaining parameter is estimated by the Ecopath mass-balancing algorithm. In my model, the unknown parameter for a particular group was always EE (ecotrophic efficiency which is the proportion of the net annual production consumed by higher trophic levels). The mass balance is achieved within EwE by solving for the unknowns simultaneously for all the groups i . This is possible because all the groups are linked directly or indirectly via consumption (Christensen et al., 2005).

Achieving mass balance involved iterative adjustments to the input values or revisiting data sources, following model-balancing guidelines (Heymans et al., 2016). There was limited data available for many of the basic inputs and diet compositions for these model groups. With these limitations the data collected for this model did not fully meet the requirements before mass balancing adjustments that have been outlined (Heymans et al., 2016). Adjustments were made for both the benthos and

phytoplankton as an error occurred regarding the EE value when running the model. The error that occurred was that the EE value produced pre-adjustments was > 1. An EE value greater than 1 is not possible as more production cannot be passed on to the next trophic level than was originally produced (Heymans et al., 2016). For benthos and phytoplankton model groups, the error resided in the production biomass being too low in comparison to the consumption biomass. Production biomass was balanced at just under 2x the original production for benthos and production biomass was decreased until balanced at 93 t/km² for phytoplankton (Table 4). These adjustments were guided by my advisor who is a more experienced EwE user (K. Sobocinski, WWU, personal communication).

After following the iterative process of adjusting parameters, the estuary model came into balance. Figure 1 provides a visual representation of the estuary food web's 8 biomass pools, the trophic relationships that link them together, and the sources of production that fuel the system. The core parameters of the mass-balanced food web Ecopath estuary model (including estimated trophic level, TL) are shown in Table 4. The trophic level estimates make ecological sense for the assumed niches of the species represented in the functional groups. All detrital and primary producer functional groups had been assigned TL equals 1, the top predator in the system is GBH (TL = 3.8).

| Table 4. Ecopath parameters for the functional groups post-balance in the generalized restored estuary model. See the Species and functional group descriptions section for description of parameters. Boldfaced values were calculated by the mass-balancing routine in the Ecopath model. | | | | | | | | | |
|---|------------------|---------------|-----------------------|--|------------------------------|------------------------------|-------------------------------|-----------------------|----------------------------------|
| | Group name | Trophic level | Hab area (proportion) | Biomass in habitat area (t/km ²) | Biomass (t/km ²) | Production / biomass (/year) | Consumption / biomass (/year) | Ecotrophic Efficiency | Production / consumption (/year) |
| 1 | Great Blue Heron | 3.789 | 1 | 0.01 | 0.01 | 0.11 | 61.1 | 0.000 | 0.00180033 |
| 2 | Bull Trout | 3.421 | 1 | 0.15 | 0.15 | 0.64 | 1.1 | 0.636 | 0.5818182 |
| 3 | Chinook Salmon | 3.155 | 1 | 0.081 | 0.081 | 4.5 | 14.8 | 0.140 | 0.3040541 |
| 4 | Emergent Insects | 2.364 | 1 | 28.5 | 28.5 | 18 | 32.6 | 0.001 | 0.5521473 |
| 5 | Benthos | 2.000 | 1 | 30.9 | 30.9 | 6.2 | 25 | 0.972 | 0.248 |
| 6 | Zooplankton | 2.000 | 1 | 129.41 | 129.41 | 15 | 75 | 0.000 | 0.2 |
| 7 | Phytoplankton | 1.000 | 1 | 85 | 85 | 93 | | 0.993 | |
| 8 | Detritus | 1.000 | 1 | 10 | 10 | | | 0.616 | |

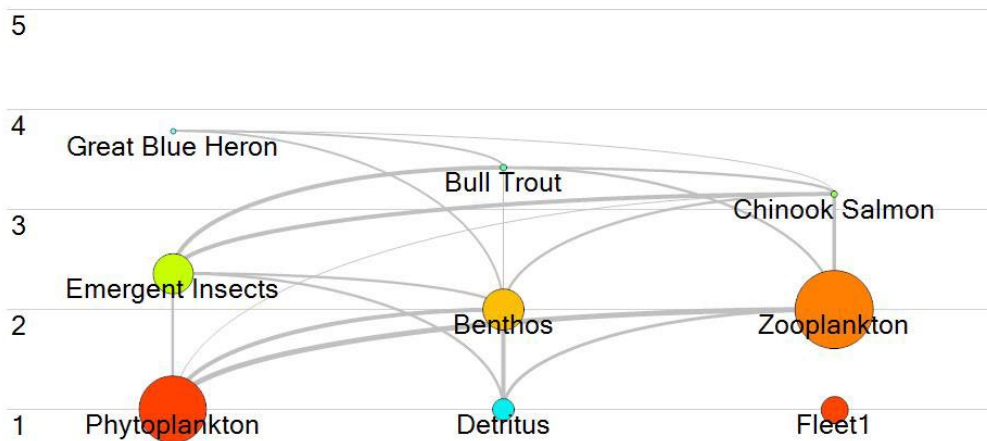


Figure 1. Food web diagram for the generalized restored estuary model, arranged along a vertical axis of trophic level. Sizes of boxes are scaled to the biomass densities of the functional groups. Curved lines link prey sources to predators; line thickness is scaled to the flow of material from prey to predator.

Another useful mass balance diagnostic matrix is the P/Q ratio (Table 4), which is the P/B ratio divided by the Q/B ratio and approximates growth efficiency. The functional groups for trout and emergent insects did not have P/Q ratios within the range of 0.05 and 0.3 for consumers, which would not be reasonable as it would assume that prey biomass is being consumed than is being produced (Heymans et al., 2016). The functional group that would be the longer-lived, slower-growing species, GBH, had a low P/Q (<0.05) would be considered reasonable. One prey category of note in the import category. This is a nondynamic pool comprised of all prey resources that are not themselves modeled functional groups.

Discussion

The EwE model presented here is a first attempt at meeting the objectives described in the introduction of this report. It remains a simplification, as it is missing a considerable amount of the species diversity, total production, and ecological linkages in a generalized restored estuary model. This model also reflects many assumptions and known bias inherent in this type of model. Nevertheless, it is a step forward in developing an ecosystem-scale restored estuary model in Puget Sound with which meaningful ecological and management-related questions can be asked. This model can be improved with additional information on biomass and abundance estimates, and diet composition percentages.

Objectives 1 and 2: Model Development and Data Gap Identification.

Objectives 1 and 2 of this project were to build a simplified model that represents the current understanding of a generalized restored estuary food web, which would enable us to ask basic ecological questions about estuarine restoration practices based on the best available information. It also enables

us to make broad assessments about how those restoration practices might be expected to influence the community via direct effects on ecologically important species and indirect effects created through the food web interactions and feedbacks. I addressed objectives 1 & 2 throughout the iterative mass-balancing phase of model development. The mass-balancing phase of model development involved identifying the most important functional groups and compiling relevant quantitative data. There are significant data gaps for the higher trophic level consumer diet matrices, and the P/B and Q/B estimates for most functional groups. Further research into the production biomass and consumption biomass could be beneficial to this project. This model is also a vast simplification of the functional groups and species that reside in Puget Sound estuaries, which include more migratory birds, shorebirds, and fish species among others. Incorporating additional groups, given available data, would allow for more accurate understanding of the trophic and food web dynamics of a restored estuary.

Objective 3: Juvenile Chinook Salmon Prey Evaluation

In terms of objective 3, the estimates used for this model were also taken from an estuary, where they found that the biomass for terrestrial invertebrates increased 3-fold between 1 and 3 years (Woo et al., 2018). With this knowledge this model could potentially be used to compare a natural or undisturbed estuary in the Puget Sound. This comparison between mass-balanced models could potentially give insight into the changes in diet matrices and juvenile Chinook salmon biomass through the lens of salmon prey sources. As a proof of concept, an Ecosim model for the Delaware Bay ecosystem ran simulations to assess gains from marsh restoration (Frisk et al., 2010). The results from this model comparison indicated that restoration increased total ecosystem biomass by $47.7 \text{ t km}^{-2} \text{ year}^{-1}$, with increased biomasses across a wide range of species including important forage species (Frisk et al., 2010). The Delaware Bay model also created an Ecosim model representing the period of 1966-2003 to show potential temporal changes in restoration efforts (Frisk et al., 2010). This similar process could be applied to a restored estuary model in Puget Sound, to account for the time outside of the out-migration period for salmon. Additionally, this would account for potential disturbances such as drought or flood conditions (Sinnickson et al., 2021).

There are environmental variations that influence salmon prey biomass fluctuations during the out-migration period for salmon such as water temperature, salinity, sediment, and vegetation transport (Woo et al., 2018). There is literature that discusses using Ecosim with Ecosim to build comprehensive ecosystem models to provide a thorough understanding of resilience to changes such as salinity (Smith et al., 2020). This could be a potential use for restored estuaries in Puget Sound, as an increased understanding of effects of changes in environmental variations such as salinity and sediment transport on salmon prey biomass would increase the parameters that could be used to help document the estuary restoration process.

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