

A comparison of tidally influenced salt marshes using a bioenergetics model for Chinook salmon

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Introduction

Estuarine habitats are essential nursery grounds for outmigrating juvenile Pacific salmonids (*Oncorhynchus spp.*), specifically those with an ocean-type life-history strategy (Simenstad et al 1982). The Skagit River system in northern Puget Sound, Washington is unique in that it supports all five species of Pacific salmon, including the largest runs of chum, pink, and chinook salmon in Puget Sound (Brown 2001). These three species (*O. keta*, *O. gorbuscha*, and *O. tshawytscha*, respectively) all share the ocean-type life history strategy, though chinook salmon, in particular, are known to utilize estuarine areas extensively for rearing (Reimers 1973).

Historically, the Skagit River delta was a large estuarine complex of over 29,000 acres. Agriculture and development, mostly during the last century, have eliminated or truncated tidal flows in much of the estuary, causing significant changes in geomorphology, and thus, habitat (Beechie et al 1994). Estuarine emergent marsh habitat alone has been diminished by 68% (of historic levels) to less than 5,000 acres (Beamer 2002). The elimination of functional marsh habitat has meant decreased rearing opportunity for outmigrating juvenile salmonids (Simenstad and Cordell 2000)

Past research has indicated that tidal wetlands are important sources of prey for juvenile salmonids (Congleton 1978, Wolf et al 1983, Shreffler et al 1992, Simenstad and Cordell 2000). Insects from the order Diptera, specifically chironomid larvae, pupae, and adults, and gammarid amphipods are known chinook prey items (Shreffler et al 1992). While

the success of chinook runs (adults returning to spawn) based upon estuarine rearing time is still unknown in the Skagit system, Reimers (1973) showed that chinook utilizing the Sixes River estuary for extended periods made up 90% of the returning spawners, while brief estuary users were absent in adult returns, suggesting that growth while in the estuary may provide some advantage once the fish migrate to sea. Estuarine residence time in the Skagit River estuary is estimated to be from 14 to 35 days (Beamer 2002), though it could be significantly longer.

In 2000, a restoration project aimed at returning a portion of the delta to tidally influenced emergent marsh was undertaken in the Skagit system. This project (Deepwater Slough Restoration Project) removed an upstream agricultural dike and allowed flow to resume to 250 acres of pastureland (Fig. 1). Subsequent beach seine and fyke net sampling has shown adequate fish usage of the restored areas, suggesting that these areas are affording fish the ability to rear. Additionally, fish stomachs were collected for analysis and showed an abundance of chironomid larvae and adults as well as the mysid shrimp, *Neomysis mercedis*. These data, while descriptive in and of itself, was the basis for comparison between study sites using the Wisconsin fish bioenergetics model, as presented here.

Bioenergetics models are mass balance equations often used to predict growth and/or the consumption necessary to achieve an observed growth (Hanson et al 1997). The crux of the model can be summed up in a simple equation:

$$C = G + M + W$$

whereby, G equals growth (both somatic and gonadal), M equals metabolism (including activity costs and specific dynamic action), W equals waste (scaled from consumption), and

C equals the consumption necessary to satisfy the observed growth plus the other costs (Beauchamp 1999, Kitchell 1977). The model can be reversed to solve for growth, if there is a known consumption rate. Since metabolism, and thus consumption, is highly dependent upon thermal experience, water temperatures are used to determine costs and growth, with growth only being attainable once costs have been met. Additionally, it's important to note that both maximum consumption (C_{\max}) and metabolism (M) are functions of body mass in addition to temperature.

By applying the bioenergetics model to catch and fish diet data from the Skagit delta Deepwater Slough restoration research sites, further insight may be gained as to the success of these habitats in terms of fish rearing opportunity. Coupled with further sampling, especially benthic invertebrate samples to determine occurrence and abundance of prey items, the model may quantitatively explain differences between sites and what implications those differences have for fish growth potential. Furthermore, future restoration efforts could be modeled after the types of sites that are deemed most successful from an energetic standpoint.

The questions this project aims to address are the following:

- *What is the energetic difference between restored sites and reference marsh sites?*
- *What is the energetic difference within reference and restored sites and across all sites?*
- *Are emergent marsh sites, especially restored sites, providing the prey resources most valuable to rearing juvenile chinook?*
- *Can a bioenergetics model serve as a tool in evaluating the success of estuarine restoration projects?*
- *What does a bioenergetics model show beyond typical dietary analysis?*

Methods

Data Collection

In the spring of 2001, the Skagit System Cooperative, a research unit operating in the Skagit River watershed, established a number of monitoring sites in the delta, at both the recently restored tidal marsh and adjacent reference areas. Fish were collected in fyke nets on four sampling dates throughout the spring, beginning on 3/15/2001 and ending on 6/8/2001. This period coincided with the outmigration of juvenile chinook salmon from the Skagit River. Fish were identified, counted, lengthed and weighed, and their stomach contents were preserved for analysis. Once in the lab, the stomach contents were identified to the lowest practicable taxa, enumerated, weighed, and recorded in a Microsoft Excel spreadsheet. Attributes such as gut fullness and degree of digestion were also recorded. Plots of prey composition (Fig. 2) show that *N. mercedis* is the dominant prey item (40% of total biomass, across all sites). Dipterans, specifically chironomids, in several life stages were also important prey items.

Bioenergetics Model

All modeling was performed in the Windows 95 version of Fish Bioenergetics 3.0, using the chinook salmon model parameterized by Stewart and Ibarra (Stewart and Ibarra 1991). All simulations were run using a cohort model; the cohort was defined as the duration of sampling, or March 1, 2001 (Day 1) to June 8, 2001 (Day 100), which coincided with the period of outmigration and rapid growth in juvenile chinook. The output given is the growth of an individual over the specified time interval.

Inputs for temperature (Fig. 3) and prey energy densities (Table 1) were held constant across all models, as was the population size. Temperature data for simulation days 1-72 were downloaded from *in situ* loggers located in a distributary channel adjacent to the Deepwater Slough sites, while days 73-100 were calculated using regression analysis. The same temperature data was used for all sites since site-specific data were unavailable. Prey items were divided into taxonomic groups and were ascribed energy densities. Prey energy density values were obtained from existing literature (Cummins and Wuychuck 1971, Davis 1993, Davis et al 1998), and values for unreferenced prey items were given an average based upon values for similar prey types. The default chinook salmon predator energy density of 5674 J/g was used in all analyses. The population size was held constant at one, since average values across dates and sites were used. It is likely that the actual population size varied as fish moved into and through the estuary, but it is also likely that this flux resulted in a fairly constant population size during the duration of the simulation, when compared to the population size throughout the rest of the year.

In all cases, diet composition was entered as a proportion. These values were calculated by averaging the proportional values for each prey item in each fish caught at each date/site. These values were then averaged across each date/site for all fish and across reference pairs and treatment pairs (Table 2). All calculations were performed in a spreadsheet and only discreet proportional values were entered into the model.

Several scenarios were simulated using a variety of starting and ending weights and diet inputs, depending upon the desired analysis (Table 3). Because not all sites were sampled on all days (Table 2), a comparison using the same start/end points was not feasible to demonstrate the differences in prey composition and energy values alone. For this reason,

several different analyses were run to illustrate the differences between all four sites, as well as those paired as reference sites and those paired as treatment sites.

Results

The first analysis (file name: All) aimed to establish a baseline and used simulation days 28 and 100 as start and end points respectively (since no treatment sites were sampled on day 15, day 28 was used as the first day). Proportions of prey for each prey type (chironomid, crustacean, neomysis, etc.) were averaged over all sites for days 28, 58, and 100. Average weights were calculated for all fish sampled on day 28 and day 100 and used as start and end points. The p-value, a proportion of maximum consumption, applied in the simulation was 0.52, and the consumption (i.e. the weight of food, in grams, required for a fish to grow from its start weight to its end weight) was 14.56g. In general, while fish growth remained positive, the specific growth rate decreased as the simulation progressed, coinciding with the increase in temperature and thus, the higher metabolic demands, throughout the spring season (Fig. 4).

To compare reference and treatment sites, an analogous simulation was run. In this simulation, average prey proportions from 3/28, 4/27, and 6/8 at both treatment and reference sites were separated, and start/end weights were determined by averaging fish weights at simulation days 28 and 100. This resulted in an “apples to apples” comparison of prey composition (File names: PairWiseRef and PairWiseTreat). This simulation showed that fish surveyed at the treatment site had to consume 27% more food to attain the same weight as fish at the reference site (treatment 16.8g vs. reference 13.2g), suggesting that the quality of prey found at the reference sites was more energy rich.

The third set of analyses broke the sites down further and evaluated each site specifically (four analyses, RE, RW, TE, TW, file names: XYComp). To compare growth over like time-scales, simulations were only run for day 28-58, since site TW lacked data for 3/15 and 6/8. All diet data were calculated from each separate site at these days, however an average start and end weight was entered, again to make a true “apples to apples” comparison. The two reference sites showed similar values, however the two treatment sites differed greatly, with the TE site more closely aligning with the reference condition (Fig. 5). Because of the high p-value (=1.2) and correlated high level of consumption necessary for the stated growth associated with the TW site, it seems that this site is not providing energy-rich prey to fish using the site (in fact TW is dominated by low-energy larvae). In all three of the other sites, p-values were between 60% and 70% of max consumption. Specific growth for all four models is plotted (Fig. 6) and shows a close alignment between geographically similar RE and TE sites. TW shows the sharpest decline in specific growth over time.

Because the playing field was essentially leveled for these comparative analyses, the simulations did not take full advantage of the given data. Further simulations were run, using the best available data (file name: XYBAD) at each site. Simulations for reference sites ran from day 15 to 100, while TE ran from day 28 to 100 and TW ran from 28 to 58. Start and end weights were averaged at the respective dates from fish collected at each site. As with the other models, three of the four sites showed similar results (Fig. 7), with TW showing a much lower level of estimated consumption (due to a shorter simulation period) and p-value.

Discussion

From diet plots (Fig. 2) and previous analysis (Stomatiou and Cordell 2001), it is clear that chinook diets are similar at 3 of the four sites (RE, RW and TE) and differ at the

fourth site (TW), where *N. mercedis* is not as prevalent in stomach samples (and is absent in samples from 4/27). This bioenergetics analysis further illustrated these differences when the sites were compared using the model. Both diet data analysis and bioenergetics analysis suggest that the absence of an energy rich prey item such as *N. mercedis* in chinook diets, may diminish growth. This result also begs the question of why *N. mercedis* was not in the diets of fish utilizing the TW site. In all likelihood, larger environmental variables are driving occurrence and abundance of prey items. From this study, it is unclear whether or not fish select sites based upon specific prey availability, as consumer mobility is not addressed through this work.

Similar uncertainties remain about other aspects of the model. Since temperature data were derived from the same location for all sites, thermal experience is homogenized and thus simplified. Setting site-specific *in situ* data loggers would be beneficial for further bioenergetics studies at these sites since site-specific data would help evaluate the net energy value of each site (and the trade-off between prey availability, prey quality, and thermal regime). Since thermal tolerance and physical/chemical attributes are regulating factors in the distribution of many species, it is possible that *N. mercedis* was absent from site TW based upon temperature or salinity.

Prey energy densities are another gray area in this bioenergetics analysis. Because many values were ascertained from the literature and not derived from actual samples, the values could be skewed. In general, marine crustaceans showed higher energy densities than insects; however, recent work indicates that the stated values for chironomids may be extremely low (Gray 2002). Early analyses using fewer but wider prey groups with averaged energy density values were not as explicit as those with the prey broken out into more specific groupings (p-values and consumption estimates tended to be muted). Further bomb

calorimetry could more accurately determine prey energy densities for species found in the Pacific Northwest and applying more precise values could change model results.

Because not all sites contained equal data points, comparisons across all sites and between reference/treatment pairs was limited. By collecting data at more frequent intervals and evenly across all sites, further analysis would be possible. In the best available data comparisons (file names: XYBAD), the duration of the simulation affected the outcome, especially since the model for site TW was only run at the point in the season when growth is highest (Fig. 8).

P-value estimates in these simulations, with few exceptions, were quite low. The p-value in the bioenergetics model is a percentage of maximum consumption, iterated from input data and used to run the actual simulation. Values less than 1.00 indicate that fish are feeding below the potential maximum. There are several reasons for this result, but a likely scenario is that the prey items are rich enough that they provide the necessary energy for growth, without requiring high levels of consumption (in weight or count) (Fig. 5). This is especially likely since *N. mercedis*, an energy rich prey, is absent from the TW site, which shows a high p-value and high level of consumption in the comparative model.

Additionally, in the model using best available data for each of the four sites, the consumption levels for RE, RW, and TW are quite high, while that for TE is low, even though the p-values follow the same trend as the comparative model. While these results seemingly contradict the comparative model, when the duration of the simulation is taken into account, the values are consistent with other models. In 30 days, fish at TW ate 6.77g of food; fish at the other three sites ate an average of 14.38 grams of food in 81 days. A simple ratio shows that had the simulation been run for 81 days at TW, fish would have consumed

18.28g (conversely, fish at RE, RW, and TE would have eaten 5.33g in 30 days). These values are consistent with other results.

Another cause of low p-values may be limited prey availability. While this does not appear to be the case in these models, invertebrate sampling for occurrence and abundance would provide additional data about distribution of prey items at these sites. This additional information (especially if prey were found to be in adequate supply) would give credence to the bioenergetics models' results.

While the paired comparison model for reference and treatment sites showed the reference sites to be more energy rich, the true picture of energetics at these sites emerges when the sites are split up. Geographic position and/or localized topography and the associated availability of certain prey types are driving the models. All results (specifically those noted in Fig. 6 and Fig. 8) show the east pair of sites (RE and TE) to have similar results, with RW fitting in closely.

While all of these explanations contribute to the evidence of lower p-values, the most likely factor for p-values considerably less than 1.00 is the inability to track the growth of individuals (this could only be achieved through mark-recapture experiments). Growth data from otoliths (Fig.8) suggest that a pool of individuals cycle through the estuary during outmigration. The growth inferred from group sampling underestimates the growth of individuals, which appear to cycle through more quickly and grow considerably faster than the rate inferred from the average group growth. Larger sample sizes and more frequent sampling may elucidate growth rates more fully.

Conclusion

While standard dietary analyses indicated *N. mercedis* was an important prey item, its nutritional value (outside of raw energy density) was unknown. This bioenergetics model further illustrated differences in prey items and the associated growth response at several sites. If *N. mercedis* is a preferred prey item, and also nutritionally valuable, perhaps efforts should be aimed at restoring areas where this species is likely to persist. By determining what factors are limiting growth at specific sites and which sites provide the best opportunity for growth, future restoration efforts can be directed at sites with the highest growth potential.

Combined with standard dietary analysis, foraging models, and/or data about prey resource availability, fish bioenergetics models are another way of evaluating opportunity for estuarine rearing chinook salmon utilizing emergent marsh sites.

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Figure 1. Map of the Skagit River System. Area within green line was the restoration site where tidal inundation was restored.

TW=Treatment, West
RW=Restoration, West
TE=Treatment, East
RE=Restoration, East

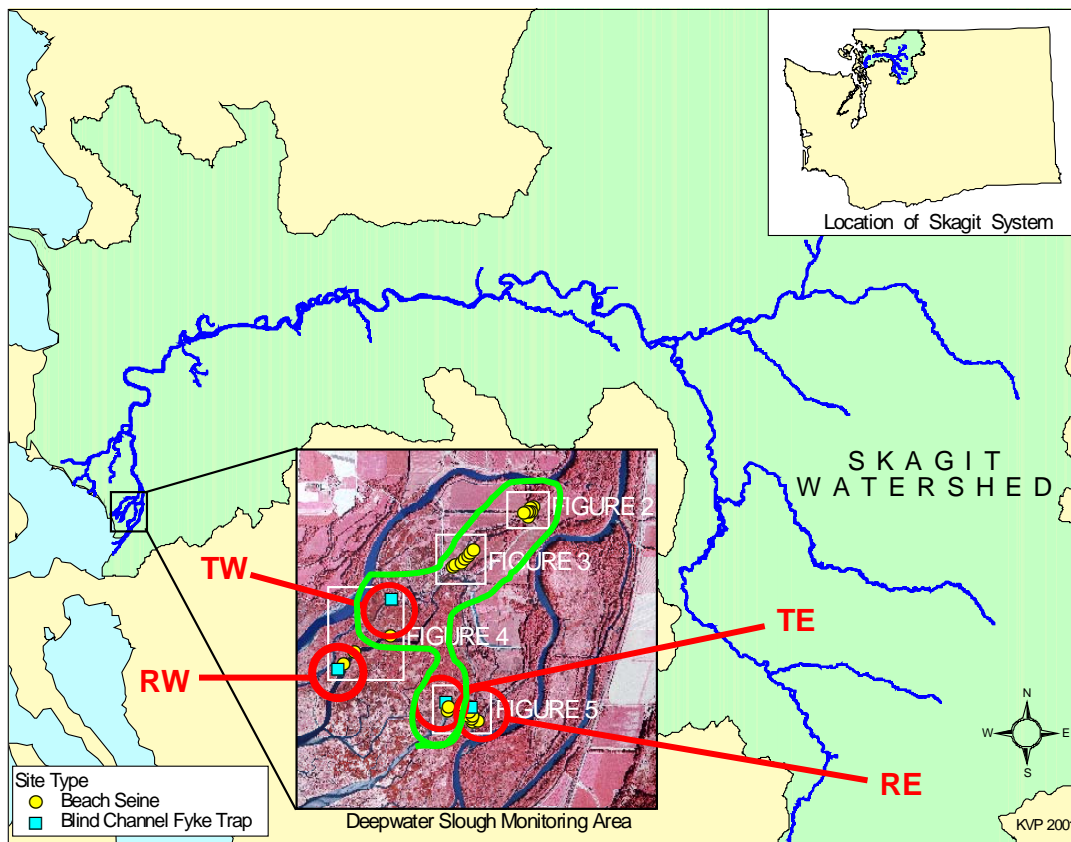


Figure 2. Prey composition by weight averaged across all fish caught at each site on each sampling day.

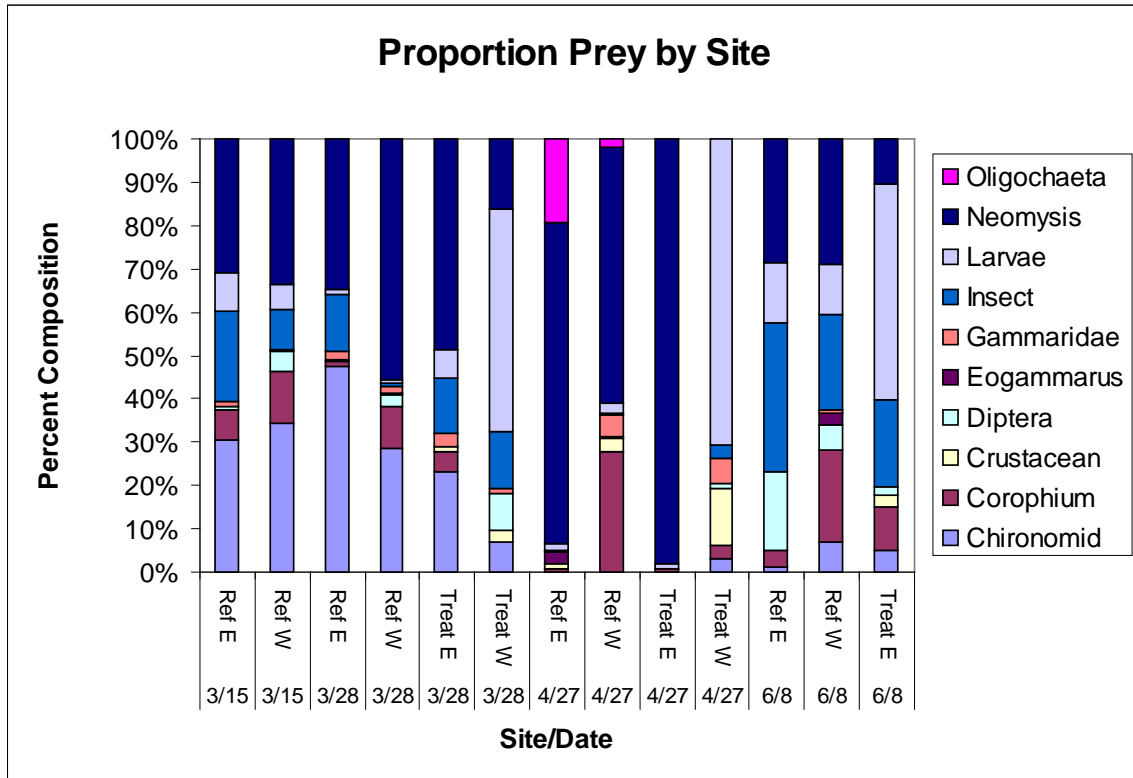


Figure 3. Average daily temperatures for distributary channel adjacent to Deepwater Slough sites.

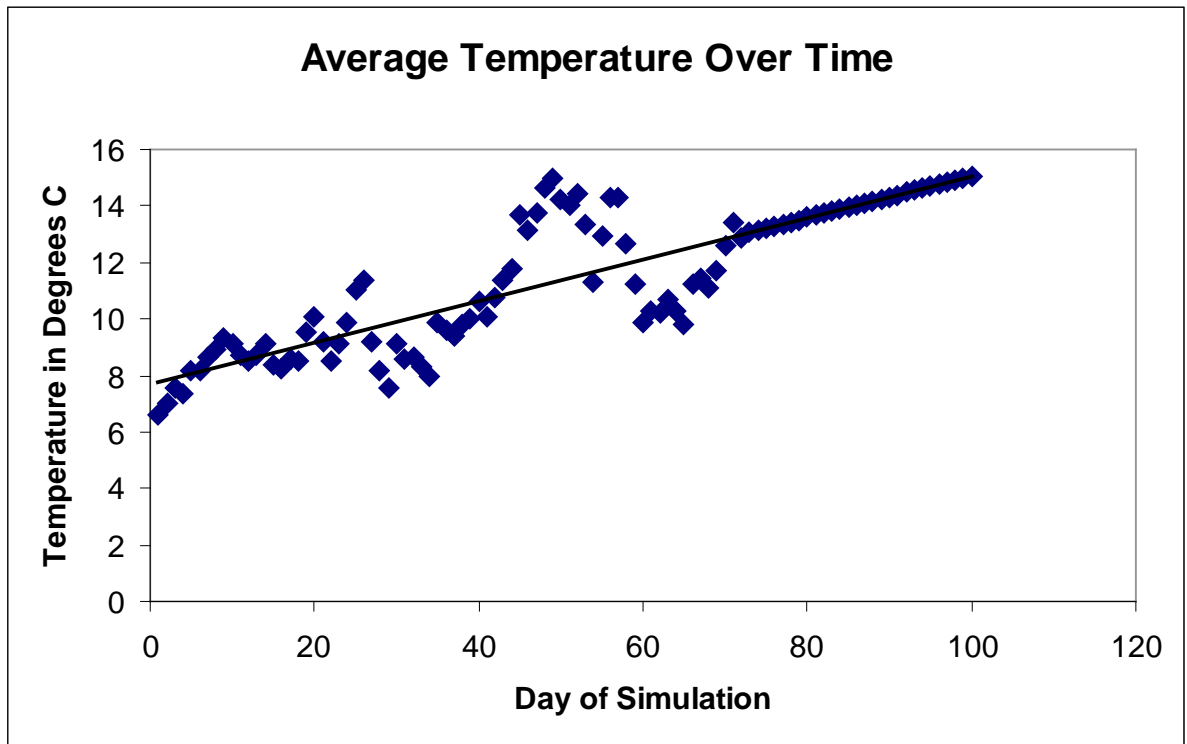


Figure 4. Simulation outputs for average fish growth over time.

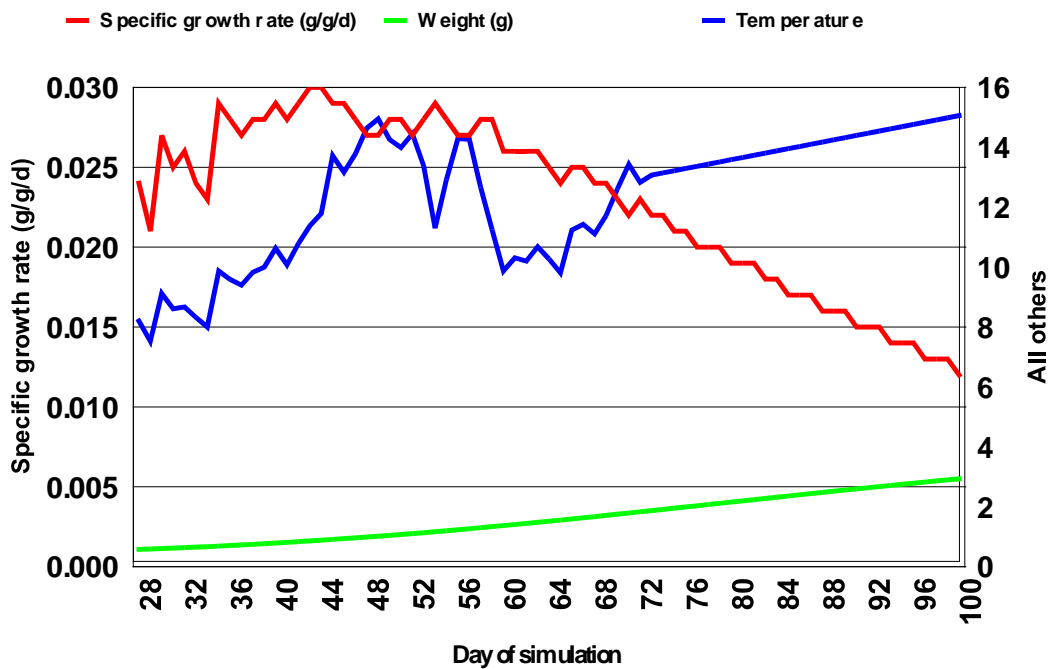


Figure 5. Simulations comparing four sites, using constant variables, with the exception of diet data, which varied per site (file name: XYComp).

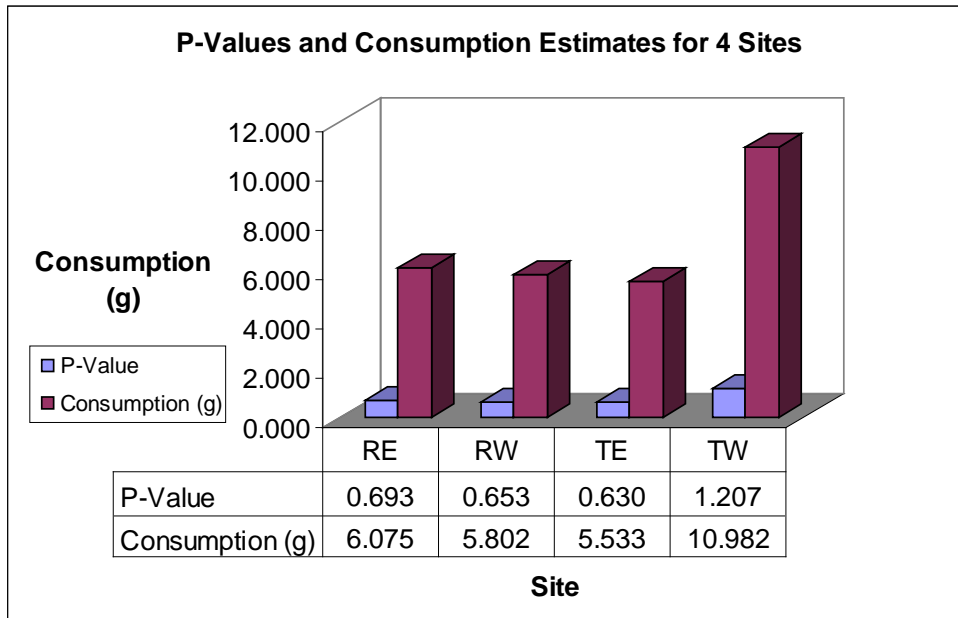


Figure 6. Specific growth rates at 4 sites using comparative data, plotted with temperature.

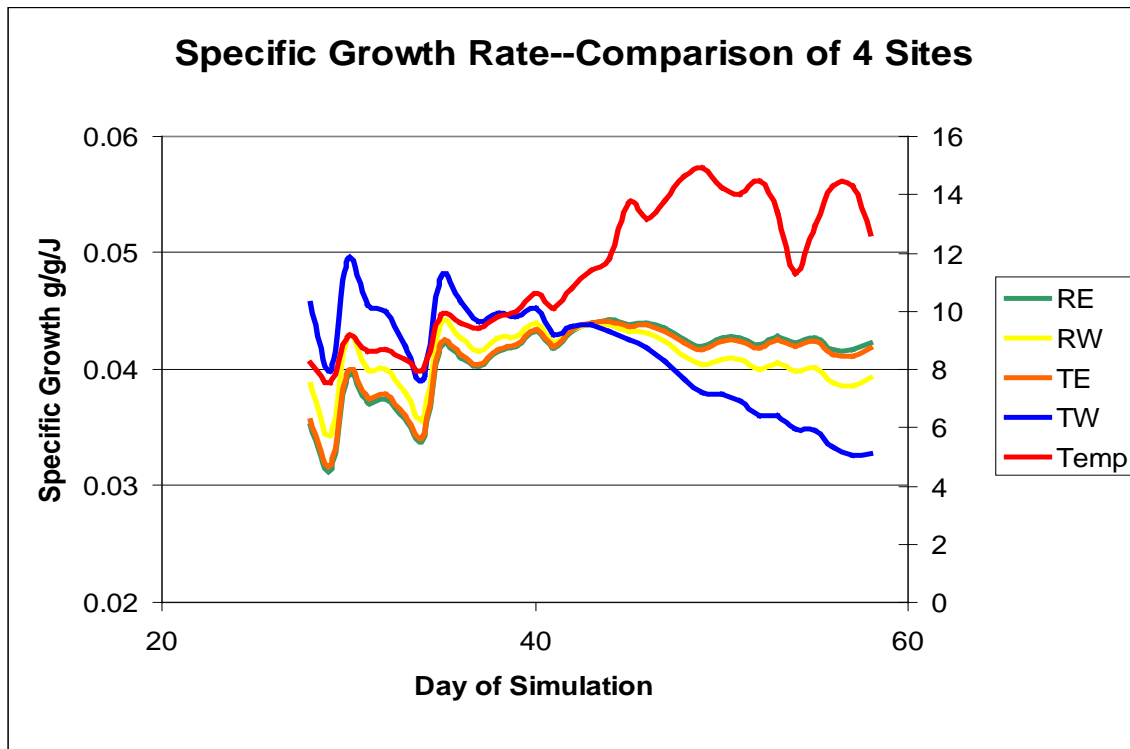


Figure 7. P-Values and Consumption outputs from simulations

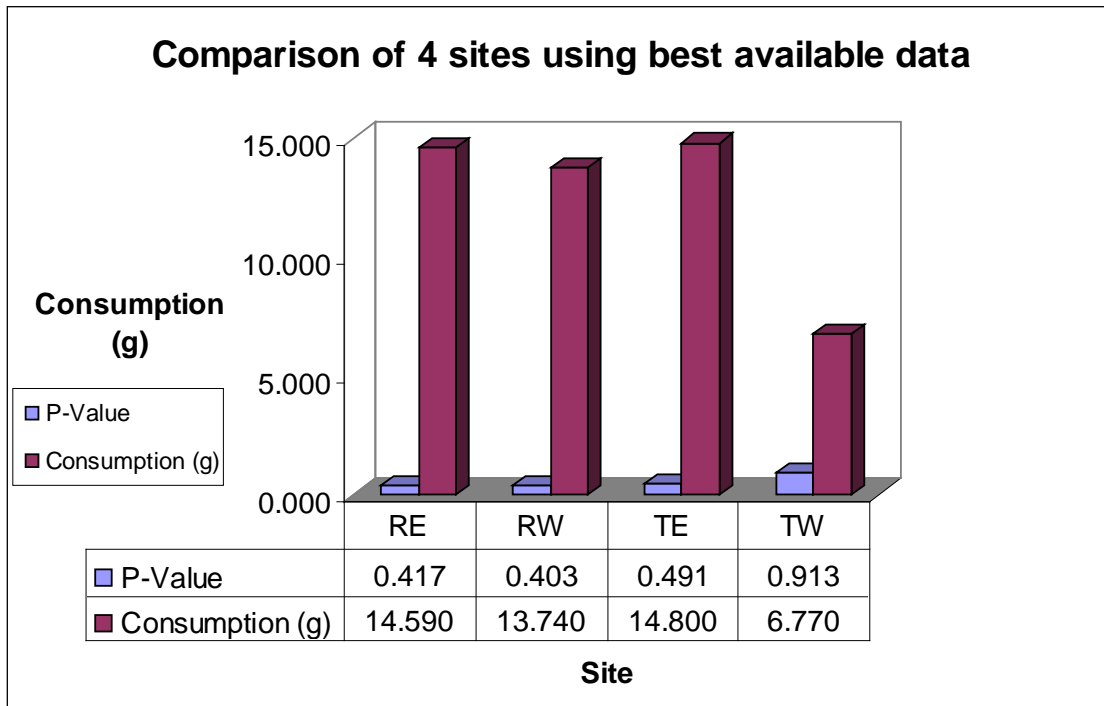


Figure 8. Growth across time using data from fish collected in 2001 at Deepwater Slough Sites and an average of otolith values from estuarine fish from 1995 and 1996.

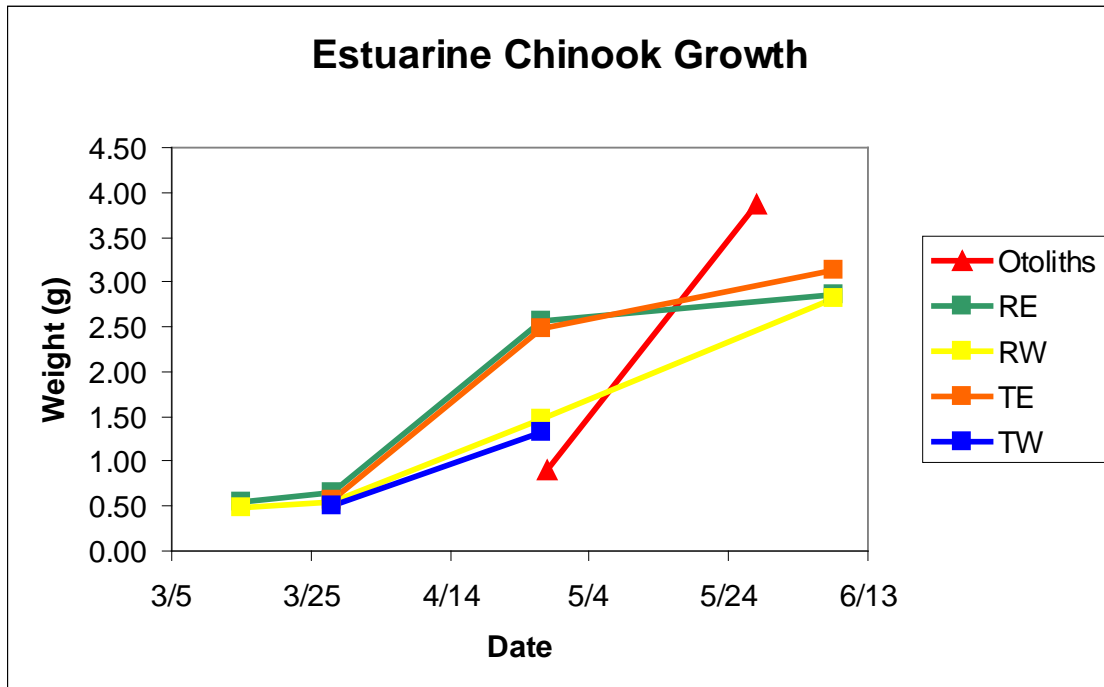


Table 1. Prey energy densities used in model. Note that specific values were used when available in the literature (asterisked values), otherwise an average of stated values was applied.

Prey Item	Energy Density (J/g)
Chironomid*	2742
Corophium*	4429
Crustacean	3086
Diptera	2562
Eogammarus	3368
Gammaridae*	4638
Insect	3926
Larvae*	1711
Neomysis*	4868
Oligochaeta*	3176

Table 2. Diet proportions for each prey group, per sampling site/day

	Date	Chironomid	Corophium	Crustacean	Diptera	Eogammarus	Gammaridae	Insect	Larvae	Neomysis	Oligochaeta
Reference E	3/15	0.307	0.068	0.000	0.008	0.000	0.010	0.211	0.088	0.308	0.000
	3/28	0.474	0.014	0.000	0.000	0.000	0.019	0.135	0.009	0.348	0.000
	4/27	0.000	0.004	0.002	0.000	0.028	0.000	0.000	0.013	0.742	0.211
	6/8	0.011	0.038	0.001	0.181	0.000	0.000	0.343	0.142	0.284	0.000
Reference W	3/15	0.3455	0.1161	0.0000	0.0465	0.0000	0.0041	0.0932	0.0579	0.3367	0.0000
	3/28	0.2858	0.0947	0.0007	0.0263	0.0053	0.0167	0.0079	0.0060	0.5566	0.0000
	4/27	0.0000	0.0059	0.0143	0.0000	0.0276	0.0010	0.0028	0.0136	0.7421	0.1927
	6/8	0.0681	0.2125	0.0000	0.0602	0.0259	0.0063	0.2224	0.1152	0.2894	0.0000
Treatment E	3/28	0.2317	0.0461	0.0105	0.0000	0.0000	0.0316	0.1288	0.0646	0.4866	0.0000
	4/27	0.0000	0.0075	0.0000	0.0016	0.0000	0.0005	0.0000	0.0079	0.9825	0.0000
	6/8	0.0510	0.1000	0.0267	0.0208	0.0000	0.0000	0.1973	0.4995	0.1046	0.0000
Treatment W	3/28	0.0686	0.0000	0.0298	0.0841	0.0000	0.0125	0.1292	0.5142	0.1616	0.0000
	4/27	0.0308	0.0294	0.1324	0.0121	0.0000	0.0560	0.0317	0.7075	0.0000	0.0000

Table 3. Iterations of the bioenergetics model and the parameters/data used in the simulations.

File Name	Day Start	Day End	Start (g)	End (g)	Source	Prey Proportion
All	28	100	0.564	2.933	Average weight for all fish caught on 3/28 and 6/8	Averages for all sites on 3/28, 4/27, and 6/8
PairWiseRef	28	100	0.564	2.933	Average weight for all fish caught on 3/28 and 6/8	Averages for all reference sites on 3/28, 4/27, and 6/8
PairWiseTreat	28	100	0.564	2.933	Average weight for all fish caught on 3/28 and 6/8	Averages for all treatment sites on 3/28, 4/27, and 6/8
RefEastComp	28	58	0.564	1.959	Average weight for all fish caught on 3/28 and 4/27	Averages for RE on 3/28 and 4/27
RefWestComp	28	58	0.564	1.959	Average weight for all fish caught on 3/28 and 4/27	Averages for RW on 3/28 and 4/27
TreatEastComp	28	58	0.564	1.959	Average weight for all fish caught on 3/28 and 4/27	Averages for TE on 3/28 and 4/27
TreatWestComp	28	58	0.564	1.959	Average weight for all fish caught on 3/28 and 4/27	Averages for TW on 3/28 and 4/27
RefEastBAD	15	100	0.538	2.86	Average weight, fish caught on 3/15 and 6/8, E reference sites	Averages for RE on 3/15, 3/28, 4/27, and 6/8
RefWestBAD	15	100	0.486	2.81	Average weight, fish caught on 3/15 and 6/8, W reference sites	Averages for RW on 3/15, 3/28, 4/27, and 6/8
TreatEastBAD	28	100	0.57	3.13	Average weight, fish caught on 3/28 and 6/8, E treatment sites	Averages for TE on 3/28, 4/27, and 6/8
TreatWestBAD	28	58	0.5	1.33	Average weight, fish caught on 3/28 and 4/27, W treatment sites	Averages for TW on 3/28 and 4/27

File Name	P-Value	Consumption (g)
All	0.52	14.563
PairWiseRef	0.472	13.180
PairWiseTreat	0.593	16.820
RefEastComp	0.693	6.075
RefWestComp	0.653	5.802
TreatEastComp	0.630	5.533
TreatWestComp	1.207	10.982
RefEastBAD	0.417	14.590
RefWestBAD	0.403	13.740
TreatEastBAD	0.491	14.800
TreatWestBAD	0.913	6.770