

UNIVERSITY OF CALIFORNIA

SANTA CRUZ

**The Use of Mathematical Models for Informing Management Strategies:
An Application in Steelhead Trout and Fleet Dynamics**

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of the requirements for the degree of

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by

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Part I

Introduction

Mathematical models can be of tremendous benefit in a multitude of fields. Here I will present the applicability of mathematical models to both behavioral bioeconomics and life history biology. In each section we develop and apply models that provide clear insight into each of the respective fields. In both cases, we opt to sacrifice some fidelity to nature to both obtain more easily interpretable results and to deal with the fact of a data poor system. We will use the setting of an insect parasitoid as gateway to study the use of stochastic dynamic programming in the field of behavioral bioeconomics as it applies to a simple fishery model. We investigate the effects of applying spatial penalties for fishing as a management strategy to reduce by-catch levels. We then turn our attention to the growth potential of the endangered Southern California Steelhead population in the Santa Ynez River basin. Applying an individual based bioenergetics model, we characterize the the growth potential landscape using temperature data gathered from May to October 2012. Since density-dependent food availability has the potential to be the driver of growth within the watershed, we augment the simple model with a model of survival of individuals. Using these techniques we are able to provide a general pattern of growth throughout the watershed. Albeit both of the scenarios that are studied in the following sections utilize simple models which require some biologically justified assumptions, they are able to serve as powerful tools in a management scenario.

Part II

Chapter 1

1 Stochastic Dynamic Programming and Insect Parasitoids

Insect parasitoids deposit their eggs on or in the eggs, larvae or adults of other insects, and their offspring use the resources of those hosts to fuel development. It is helpful to classify the biology of parasitoids using population, behavioral and physiological criteria (Figure 1). First, parasitoids may have one generation (univoltine) or more than one generation (multivoltine) per year. Second, females may lay one egg (solitary) or more than one egg (gregarious) in hosts. Third, females may be born with essentially all of their eggs (pro-ovigenic) or may mature eggs (synovigenic) throughout their lives. When combined, each dichotomous choice leads to a different kind of life history. Here, we consider the univoltine, pro-ovigenic, gregarious parasitoid that lives for one season, of length T (after which the parasitoid dies, for example because the first freeze has come), has all of her eggs upon emergence, but may lay more than one egg in a host.

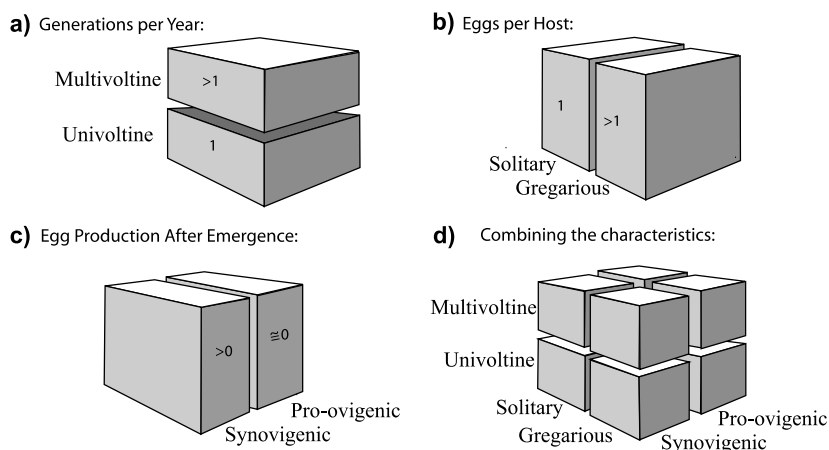


Figure 1: Parasitoid life histories can be classified using population, behavioral, and physiological criteria (from Mangel 2006)

For simplicity, assume that there is only one kind of host, which is encountered in

a single period of search by the parasitoid with probability $\lambda(t)$, which may depend upon time. When a host is encountered and the parasitoid lays y eggs, she receives an increment in her accumulated reproduction $f(y)$, which may also depend upon time but that we treat as constant for simplicity. In general, $f(y)$ (here equated to the number of potential grandchildren) will be a concave function of y , rising at first, then peaking and finally falling as the parasitoid simply overloads the hosts with potential offspring (Figure 2).

We let $F(x, t)$ denote the reproduction that the parasitoid accumulates between the start of period t and the end of season, given that she currently has x eggs. Since she accumulates no reproduction after T , $F(x, T) = 0$. For previous times,

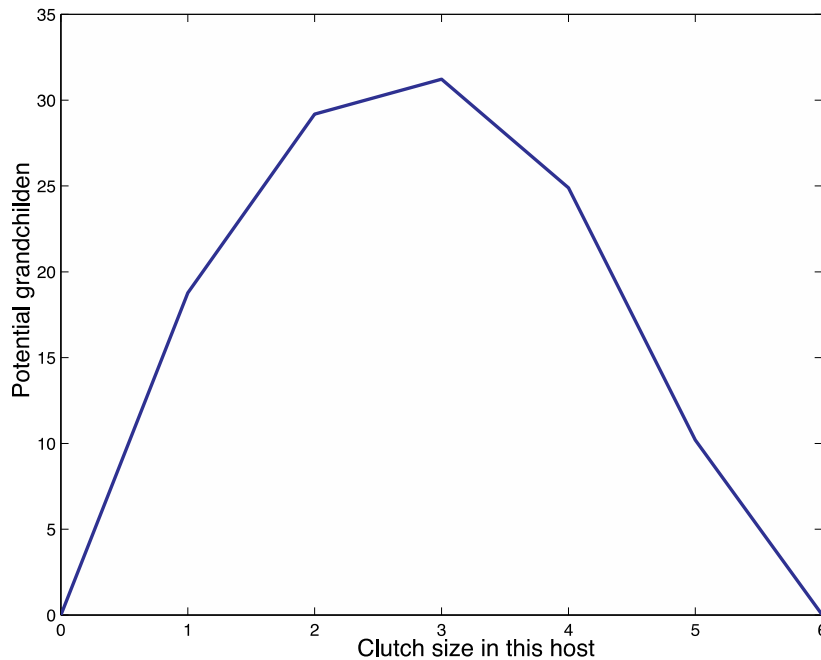


Figure 2: The fitness increment $f(y)$ for an aphytis laying in a single host (from Mangel 2006)

we reason as follows. During period t , the parasitoid may not encounter a host, which occurs with probability $1 - \lambda(t)$, but she still has to survive. If $m(t)$ is the rate of mortality during period t , then the probability of surviving is $e^{-m(t)}$ (Hilborn and Mangel 1997, Mangel 2006) and she begins the next time period with the same number of eggs. If she encounters a host, then she may lay up to x eggs, and if she survives the current period, begins the next one with x decreased by the number of

eggs laid. Thus for $t < T$

$$F(x, t) = (1 - \lambda(t))e^{-m(t)}F(x, t + 1) + \lambda(t)\max_{y \leq x}[f(y) + e^{-m(t)}F(x - y, t + 1)] \quad (1)$$

Since $F(x, T)$ is known, this equation is solved backwards in time (the method of backward induction) and at each time generates both the fitness function $F(x, t)$ and the optimal behavior $y^*(x, t)$ when a host is encountered during period t and $X(t) = x$. This very simple theory is quite testable and lead to a long program linking empirical (laboratory and field) and theoretical work (see Mangel and Clark 1998, Ch 4; Clark and Mangel 2000, Ch 4; or Mangel 2006, Ch 4 for more details and citation to the primary literature).

2 A Connection to Fishing Vessels

Readers will see the connection between a parasitoid searching for hosts, using her eggs when one is encountered, and a fishing vessel searching for schools of fish and using part of its remaining catch quota when fish are encountered. Thus, let us consider a fishing vessel whose quota at the start of the season is $X(0) = R$ and which targets a single species in a spatially distributed fishery. The analogue of fitness for the parasitoid is utility of catch for the fishing vessel. In the simplest case, the utility of catch is catch itself, so we let $F(x, t)$ denote the catch accumulated between time t and the end of the season T when the remaining quota is $X(t)$.

Due to the illustrative goal of this section, we refrain from overcomplicating the model by increasing fidelity to fishing operations and instead make the following simplifying assumptions. We focus on a single vessel type that travels at velocity, v , operating out of a single port. The fisher operates in a region discretized into $I \times J$ regions with distances, $D_{i,j}$ from the port. As explained below, we assume that the fishing region has a spatially uniform but time dependent catchability coefficient

$$q(t) = 0.1 \sin(0.2t) + 1 \quad (2)$$

Following Dowling et al. (2011), we assume that fish abundance is constant and symmetrically distributed according to a centrally located bivariate normal distribution (Figure 3a)

$$N_{i,j} = N_{max} e^{-\left[\frac{(i-i_p)^2}{2\sigma_N^2}\right] - \left[\frac{(j-j_p)^2}{2\sigma_N^2}\right]} \quad (3)$$

where i_p, j_p and σ_N are central locations and the standard deviation. By treating fish abundance as exogenous, we (and Dowling et al. (2011)) are able to focus on economic (price-supply) and by-catch issues, rather than depletion of the target stock.

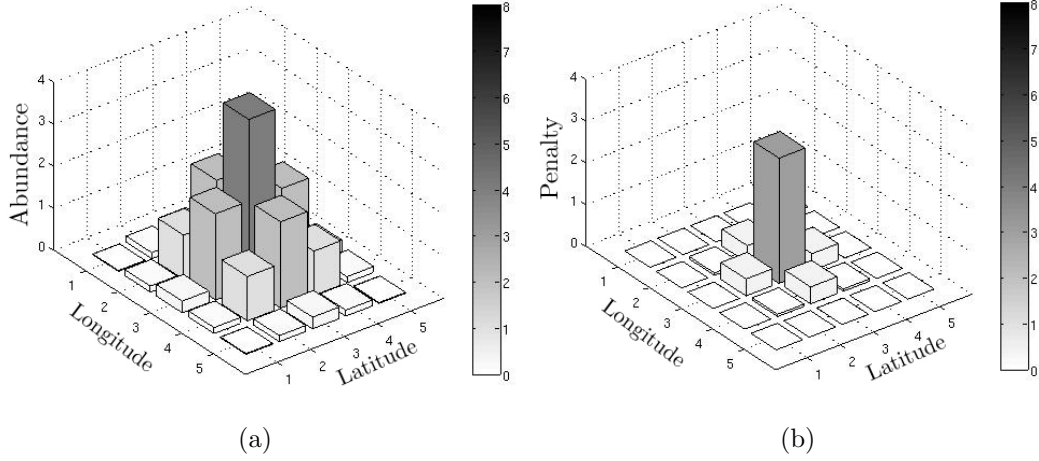


Figure 3: The spatial distribution of the stock (a) and penalty (b) used for the solution of Equation (11)

The fishing season of T days involves multiple fishing trips whose duration, τ , is determined by both travel, τ_t , and handling, τ_h , times, where handling time is directly proportional to catch and travel time is

$$\tau_t = \frac{2D_{i,j}}{v} \quad (4)$$

We model the catch during an individual trip, as a Poisson process $C_{i,j}(t)$ with rate $\lambda_{i,j}(t) = N_{i,j}q(t)$. Thus, from definition of the Poisson process,

$$\Pr(C_{i,j}(t) = c) = \frac{e^{-\lambda_{i,j}(t)} \lambda_{i,j}(t)^c}{c!} \quad (5)$$

We assume that there is by-catch of species for which there are conservation concerns.

A possible management technique to mitigate these effects is a system of spatial incentives to deter effort allocation in certain regions through the introduction of a penalty associated with fishing in a given area. We impose the base spatial incentive $\delta_{i,j}$, in a given region (i,j) , as a net detriment from the quota, and consider two possibilities for the penalty function, $\epsilon_{i,j}$, that represent two different conservation scenarios. First, the fisher may be penalized for fishing in an area in proportion to the abundance of the target species as in

$$\epsilon_{i,j} = \lambda_{i,j}(t)\delta_{i,j} \quad (6)$$

i.e., a higher overall penalty for a more attractive (i.e. higher abundance) area. Alternatively, the fisher may be penalized for actual catch as in

$$\epsilon_{i,j} = c_{i,j}(t)(1 + \delta_{i,j}) \quad (7)$$

For computations presented here, we used Equation (7), with the penalty modeled as a bivariate normal distribution:

$$\delta_{i,j} = \delta_{max} N_{max} e^{-\left[\frac{(i-ip)^2}{2\sigma_\delta} + \frac{(j-jp)^2}{2\sigma_\delta}\right]} \quad (8)$$

For the baseline computations we set $\delta_{max} = 3/4$. For a fishing trip that lasts time τ , the dynamics of the quota are

$$X(t + \tau) = X(t) - \epsilon_{i,j} \quad (9)$$

During the last trip of the season, if there is any quota remaining, the fishing vessel will presumably maximize catch, without regards to penalties or travel time, so that if $X(T) > 0$

$$F(x, t) = \max_{i,j} (\lambda_{i,j}(T)) \text{ if } X(T) \neq 0 \quad (10)$$

For each trip prior to the end of the season, the fisher will decide where to fish by selecting the the region that maximizes the combination of current and all future

catch. In analogy to Equation (1) we have

$$F(x, t) = \max_{i,j} \left(\sum_{c=0}^{\infty} \frac{e^{-\lambda_{i,j}(t)} \lambda_{i,j}(t)^c}{c!} (c + F(x - \epsilon_{i,j}, t + \tau_{i,j})) \right) \quad (11)$$

Note that since $\epsilon_{i,j}$ depends upon catch in the current period, future fitness must be included in the summation in Equation (11), unlike Equation (1). Using the end condition Equation (10), we solve Equation (11) by backward iteration yielding the decision matrix for the fishing regions that optimize the total catch accounting for the penalties and remaining effort. (There are some technical issues here: We must account for the fact that catch and time are continuous, since solutions to the DPE are given for discrete state values. We approximated between two integer values using a two dimensional linear interpolation as described in detail in Clark and Mangel Ch 2, 2000).

Once Equation (11) is solved, we can create stochastic forward projections under the scenarios where penalties are present and for when they are not. During these forward iterations we introduce by-catch, which we assumed to be proportional to abundance so that the by catch in cell (i,j) is $b_{i,j} = 0.4N_{i,j}$, which will allow us to illustrate the effectiveness of the spatial incentives.

Results

Due to the simplicity of the model, in the scenario where there was no penalty present, the optimal location for the vessel to utilize its effort was generally in the location which the abundance was at its maximum. When the penalty was enforced (in the regions of maximum abundance), the optimal strategy was to fish in adjacent regions of lower abundance, penalties and distances (Figure 4a, 4b). In the baseline case, introduction of the penalty in specific regions significantly reduced the levels of by-catch by an average of 40% by a shift in the location of fishing effort. More importantly, the introduction of the penalties had a less significant effect on catch, only reducing it by 19%. Other values of δ_{max} (ranging from 0 to 1) show that relative catch is always higher than relative by-catch (Figure 5) and that the values are relatively stable to variation in δ_{max} . Under our assumptions, an argument can

be made that it is possible to mitigate the effects of the fishing vessels with low impact on catch levels (see Dowling et al. 2011 for more detail).

Here we echo the assertion that simple models may not be completely realistic, but no model is. We don't assume to explain the exact dynamics of the fishery but rather illuminate general patterns and motivate models with more fidelity to operational and biological detail; which has been analyzed in detail by Dowling et al. (2011)

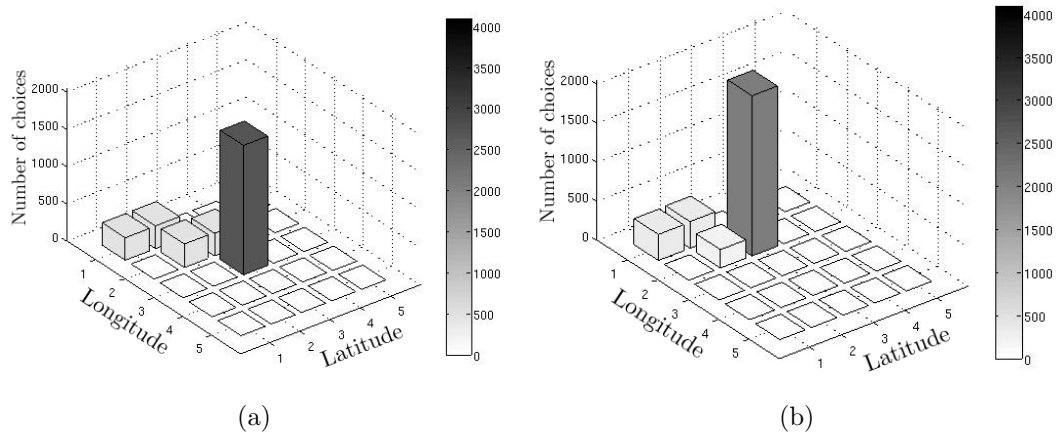


Figure 4: The spatial distribution of effort in the absence of a targeting penalty (a) or in the presence of one (b).

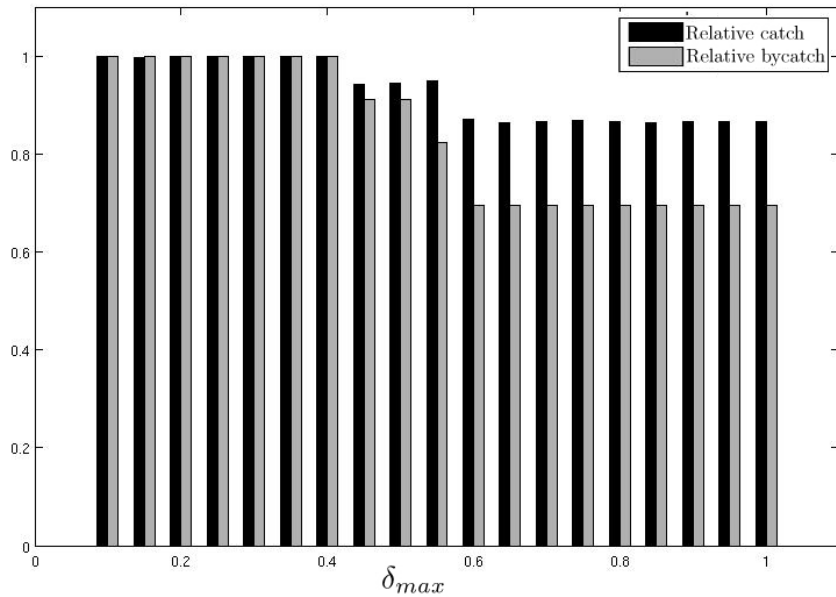


Figure 5: The relative catch and relative by catch as a function of δ_{max} in Equation (7)

Part III

Chapter 2:

3 The General Life History of Steelhead Trout

(*Oncorhynchus mykiss*)

In California, steelhead trout are distributed throughout the entire coast and divided into five Distinct Population Segments (DPSs), which are anadromous components of Evolutionarily Significant Units (ESUs) as defined by the Endangered Species Act (ESA). These are: Northern California Coast Steelhead, Central California Coast Steelhead, CA Central Valley Steelhead, South-Central California Coast Steelhead, and Southern California Steelhead. Due to a both natural and anthropogenic factors, four of these DPS are listed as threatened (Northern California Coast, Central California Coast, CA Central Valley, South-Central California Coast) and one is listed as endangered (Southern California). Difficulty in the recovery efforts of these populations in increased due to the complexity and variability of steelhead life histories (Figure 6); (Boughton et al. 2006, Thorpe et al. 1998). Individuals are iteroparous and can either be anadromous and migrate from fresh water to the ocean and return to fresh water to spawn in fluvial gravel deposits; or resident, and stay in fresh water. Like all salmonids, steelhead begin as eggs then develop into alevins, where they consume the egg yolk and begin to move up the gravel. An individual will enter the stream as a fry and remain in the stream for growth. After a given amount of time, which can vary from months to years, an individual will “decide” whether to smolt or remain a resident. Although evidence exists for genetic control of the life history of an individual, there is also considerable evidence for plasticity, with a resident trout spawning anadromous offspring and anadromous trout spawning resident offspring (Pascual et al. 2001; Thrower et al. 2004; Olsen et al. 2006; Ciancio et al. 2008). The level of variation among life histories in salmonids, defined in terms of age at smolting, age at maturity, and semelparity vs iterparity, is extensive, with 32 possible trajectories having been identified (Thorpe 1998). Different life history

trajectories are determined, at least in part, by an individual’s size and growth at a specific decision window (Mangel 1994, Thorpe et al. 1998, Satterthwaite et al. 2010), in which the response to these conditions are genetically controlled.

As with most ectotherms, temperature is a main driver of many biochemical processes and affects many physiological factors such as rates of development and growth. Therefore, the range size of steelhead is highly affected through temperature due to the thermal tolerance of individuals and these physiological requirements. Since temperature influences achievable growth rates, and growth influences the likelihood of smolting, it is common and logical to use temperature dependent growth models for individuals to gain biological insights for potential life history strategies. In the following sections, we will utilize a temperature dependent bioenergetic growth model to characterize the growth potential of individuals within multiple locations of the Santa Ynez River basin of Southern California, with a specific emphasis on highlighting the heterogeneity of growth conditions due to the environment.

4 Methods

4.1 Growth Model:

We utilize a bioenergetics model, which balances tradeoffs in energy intakes against energy expenditures, to characterize the growth of individuals (Railsback and Rose 1999, Rand et al. 1993, Satterthwaite et al. 2010). Assuming the relationship for growth developed by Satterthwaite et al. (2010), energy intakes and expenditures are modeled as weight- and temperature-dependent functions for food consumption and respiration respectively:

$$\frac{dW}{dt} = \Psi(T(t))fcW(t)^{0.86} \frac{a(t)}{\kappa(t) + a(t)} - (1 + a(t))\alpha e^{0.071T(t)}W(t) \quad (12)$$

In this equation, growth of an individual is a balance between maximum consumption ($\Psi(T(t))fcW(t)^{0.86}$) and catabolic costs ($(\alpha e^{0.071T}W(t))$) at a specific time (Figure 7). Anabolism is composed of four terms: relative energy density of food to fish tissue, f , the daily maximum weight of food that can be consumed by a 1g fish

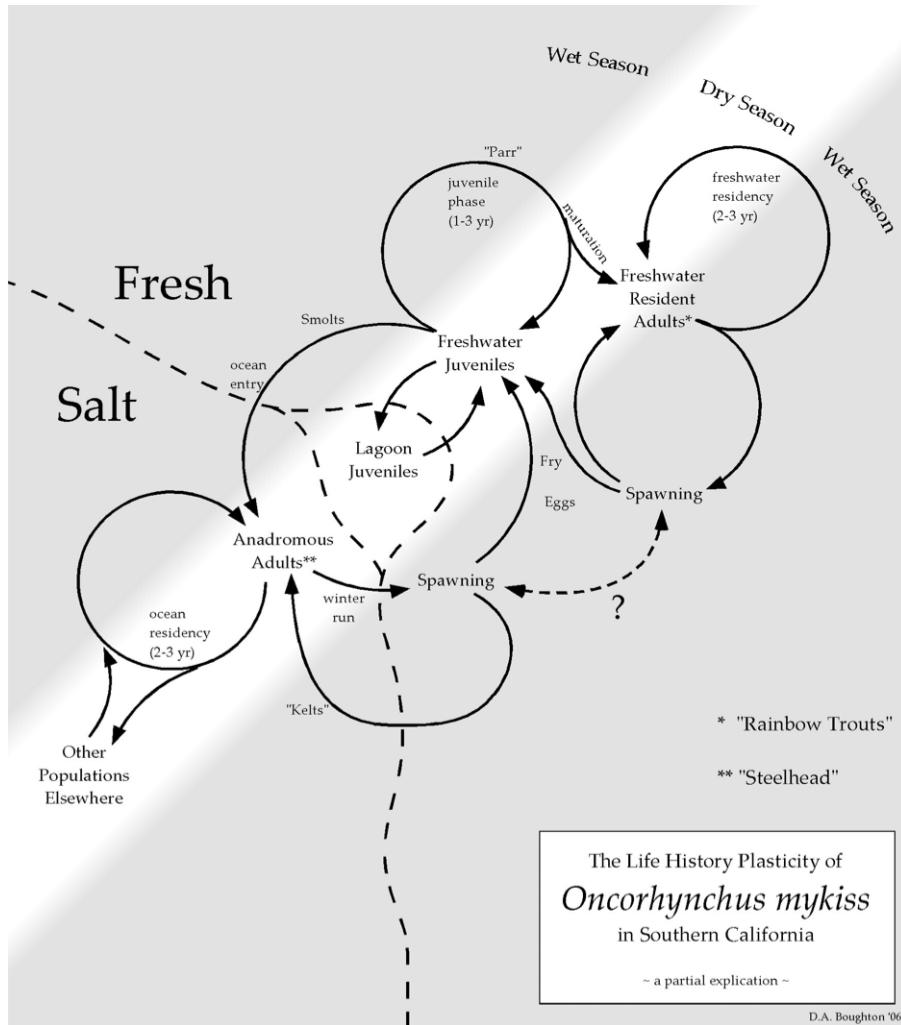


Figure 6: Illustration of complexity of life history trajectories of Southern California Steelhead

under optimal temperature conditions, c , the allometric relationship of consumption and fish weight, $W(t)^{0.86}$, and the functional relationship of maximum consumption and temperature, $\Psi(T(t))$. The functional form of the temperature, $\Psi(T(t))$, is that of Thornton and Lessem (1978) for cold-water species, which was re-parametrized for steelhead by Railsback and Rose (1999). Basal catabolism is composed of two terms: weight-specific catabolic costs, α , and the effect of temperature in catabolism, $e^{0.071T(t)}$ (Brett and Groves 1979).

Both the anabolic and the catabolic terms are scaled by expressions involving energy expenditures for activity, $a(t)$, and the difficulty of finding food, $\kappa(t)$. Including such terms can be advantageous by providing higher fidelity to nature and has

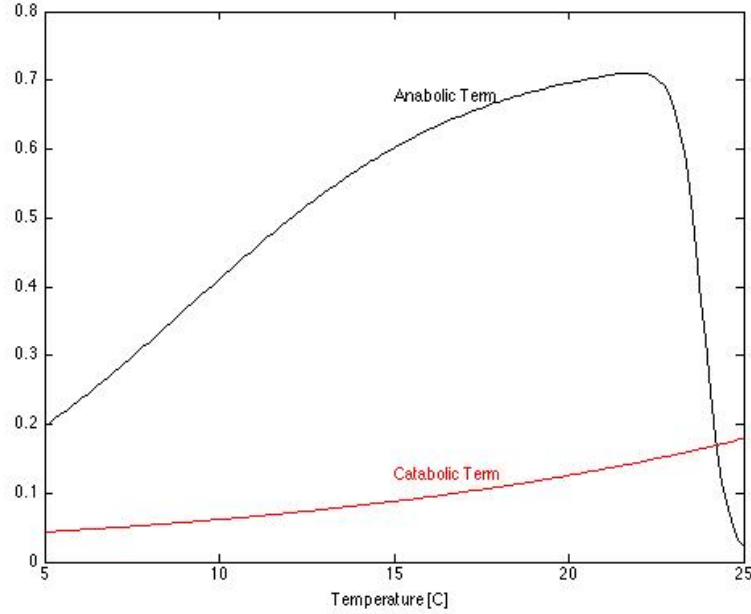
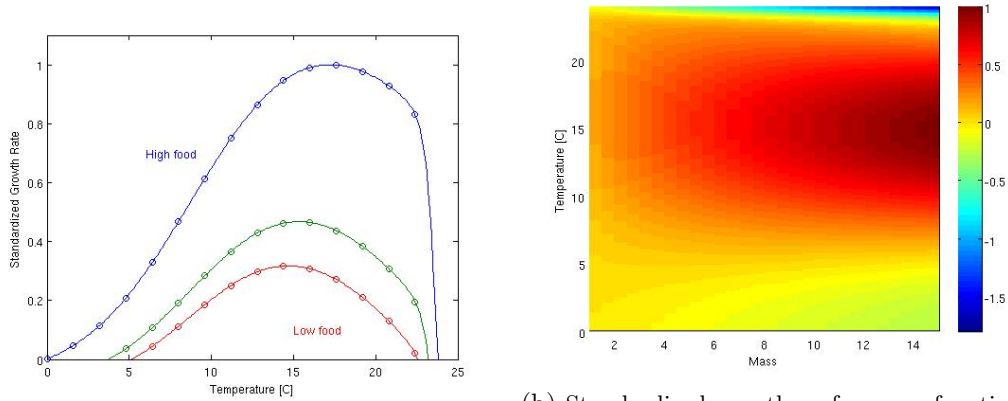


Figure 7: Comparison of anabolic and catabolic terms in Equation (12) for a 1-gram fish under difficulty of finding food $\kappa = 1$. Catabolism is a constantly increasing while anabolism peaks and begins to decrease.

been encouraged by Andersen and Riis-Vestergaard (2004) and Bajer et al. (2004). While increased activity increases consumption, total catabolic cost is also increased. Here we assume that given all the parameters for growth, except activity levels, fish choose the activity level, $a^*(t)$, that optimizes growth. To determine this level we differentiate (12) with respect to $a(t)$ and solve for the the point which optimized growth:

$$a^*(t) = \sqrt{\frac{\kappa(t)\Psi(T(t))fcW^{0.86}}{\alpha e^{0.071T(t)}W(t)}} - \kappa(t) \quad (13)$$

The model described in (12) allows large fish to lose weight due to the fact that the mass dependent consumption term, $W(t)^{0.86}$, specifies maximum consumption that must decrease as fish grown larger whereas total consumption is allowed to increase. The model parameters, c, f, α , have all been previously estimated for Pacific steelhead (Central Valley) on the basis of laboratory studies (Satterthwaite 2010, Railsback and Rose 1999, Myrick 1998, Rao 1968,1971).



(a) Standardized growth curve for a 1-gram fish mass and temperature for a single level of difficulty under different levels of food availability

(b) Standardized growth surface as a function of multiple temperatures and mass for a single level of difficulty of finding food, $\kappa = 1$

Figure 8: Visualization of Equation (12) as for different food availability levels (a) and for multiple temperatures (b)

4.2 Study System

The Santa Ynez River is a 92-mile river flowing east to west located in central Santa Barbara County. It drains into the Pacific Ocean just north of Point Conception. The 900-square mile drainage basin for the Santa Ynez river watershed is composed the Purisima Hills and San Rafael Mountains to the north and the Santa Ynez Mountains to the south. Within these mountain ranges, the Santa Ynez River gradient varies from 25 to 75 feet per mile in the upper watershed to a gently sloping coastal plain in the lower watershed. Due to these gradient changes, the Santa Ynez River is composed of both narrow channels and broad alluvial floodplains. The river basin experiences a Mediterranean climate with hot, dry summers and cool, wet winters. The basin-wide climate is highly variable with high amounts of heterogeneity occurring within the basin itself. Temperature can vary from $-5\text{ }^{\circ}\text{C}$ to $46\text{ }^{\circ}\text{C}$ with an average of $15\text{ }^{\circ}\text{C}$. The region experiences highly variable yearly precipitation that occurs mainly between November and April. Within the basin, average rainfall varies between 14 inches near the Pacific Ocean to 30 inches at Juncal Dam, and perhaps higher on mountain tops. The vegetation in the drainage basin is primarily native chaparral and oak woodlands with areas of savannas. Historically the Santa Ynez watershed maintained the largest population of steelhead in southern California with an estimated 10,000 to 30,000 adult spawners annually. (Shapovalov

1944, 1945; McEwan 2001; Moyle et al. 2008; Titus et al. 2010). Beginning in 1920 the Gibraltar, Juncal and Bradbury dams were erected to supply water and power to Santa Barbara County. The dams blocked passage to a majority of the highest quality steelhead rearing habitat in the basin; as a consequence, in recent years there have been reports of fewer than ten migrating adults reaching Bradbury dam (the most downstream dam) (Alagona et al. 2012). While increased agricultural and residential activity and development have played a factor in the decline of steelhead numbers, several studies have attributed the decline to the construction of the dams (CDFG 1975, 1993; NMFS 2000b; Cachuma Operations and Maintenance Board 2008, 2009; Hunt et al. 2008; Santa Ynez River Adaptive Management Committee 2009; SYRTAC 2009).

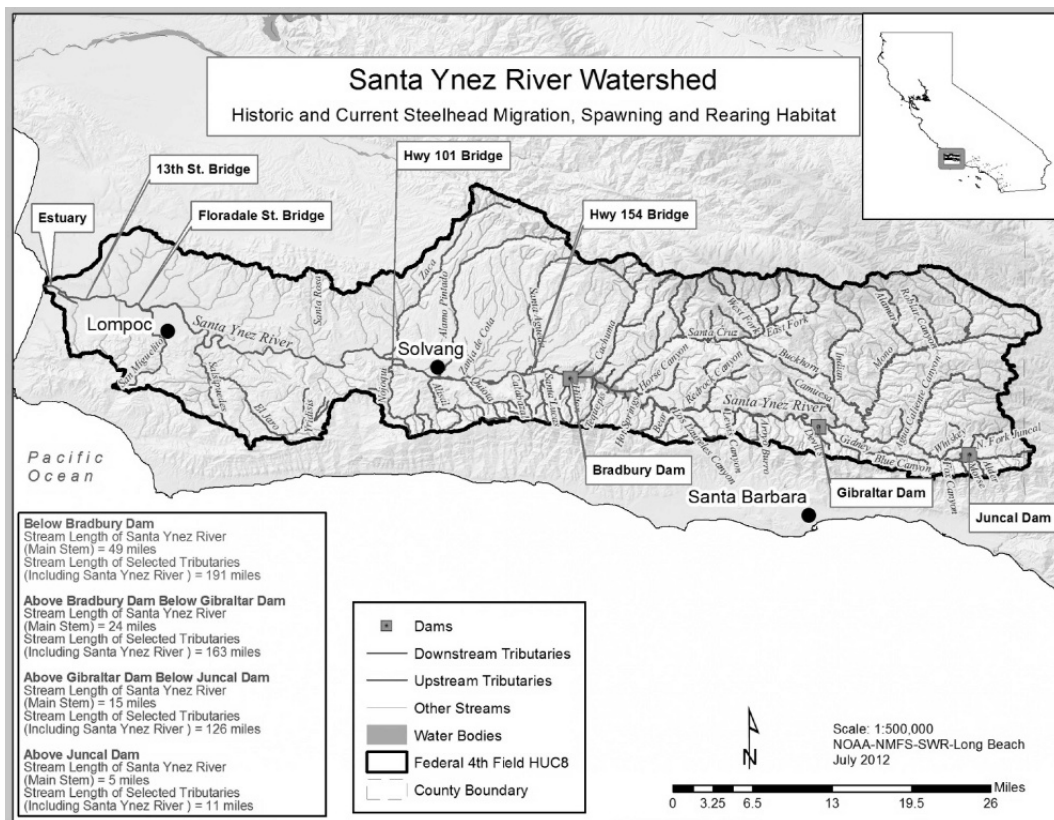


Figure 9: Historic and current steelhead migration, spawning and rearing habitat within the Santa Ynez River watershed. Designations based on the evidence developed by the National Marine Fisheries Services designation of critical habitat and steelhead recovery planning and Alagona et al. (2012) historical evidence (Capelli et al. 2004; Boughton and Goslin 2006; Boughton et al. 2006; NMFS 2012). (Map from Alagona et al. (2012))

To characterize the thermal suitability of steelhead habitat upstream of the Bradbury dam, members of the Fisheries Ecology Division, NOAA Fisheries, Santa Cruz deployed 86 temperature loggers throughout the mainstem and tributaries above the dam. Loggers recorded temperature in ten-minute intervals from May to October 2012. They selected deployment sites as tributaries and locations on the main stem with a historical record of steelhead presence and where access was possible for deployment. The sites were also selected to provide informative contrasts on the structural heterogeneity present in elevation, gradient, tree cover, and habitat types (Boughton et al. 2012). Using these temperature time series, we used the model described previously, to explore the growth potential of the watershed for constant and density dependent environmental conditions, and the effects of variable vs. constant daily temperature regime.

Variance in mean temperature among sites	1.94 °Celcius
Mean variance in diel temperature across all sites	1.04 °Celcius
Mean variance in between-day temperature across sites	1.53 °Celcius
Mean stream persistence time	63.52 Days

Table 1: Summary of basin wide stream characteristics

4.3 Modeling Approach

4.3.1 Constant Food Availability

Using the stream temperature data, we characterize the growth potential of the sites throughout the upper watershed using the previously described growth model. We examine the growth potential of individual streams under constant food availability for both a single fish with an initial mass of 1.9 grams and a cohort of 100 fishes whose initial mass is normally distributed based on empirical data collected in other watersheds. Since the difficulty of finding food is unknown in the Santa Ynez river watershed, we analyze the growth trajectories for a range of parameter values that have been observed in the American and Mokelumne rivers with the understanding that our results should be interpreted with caution due to the differences between these three river systems (Satterthwaite et al. 2010).

4.3.2 Density Dependent Food Availability

The difficulty of finding food for an individual fish is presumably density dependent; therefore, we extend the analysis of the cohort of fish by modeling individual survival (Elliot 2002). We model mortality as being composed of both mass-dependent and mass-independent factors:

$$m(t) = m_0 + m_1 W(t)^{-\frac{1}{3}} \quad (14)$$

where m_0 accounts for mass-independent mortality and m_1 accounts for mass dependence. The temporal evolution of survival is then described by:

$$\frac{dS}{dt} = -(m_0 + m_1 W(t)^{-\frac{1}{3}})S(t) \quad (15)$$

Since $S(0) = 1$, the survival of an individual to time t , $S(t)$, is :

$$S(t) = e^{-m_0 t - m_1 \int_0^t W(\hat{t})^{-\frac{1}{3}} d\hat{t}} \quad (16)$$

Given a specific survival level through a season of length T , \hat{S} , and growth trajectory, $\hat{W}(t)$, we can develop a relationship between mass-dependent and mass-independent mortality. That is, when mortality is completely mass independent ($m_1 = 0$), the mass independent mortality term is given by:

$$m_0^* = -\frac{\log(\hat{S})}{T} \quad (17)$$

It is then clear the relationship between mass-dependent and mass-independent mortality is linear for a given season.

$$m_0 = -\frac{\log(\hat{S})}{T} - \frac{m_1}{T} \int_0^T \hat{W}(t)^{-\frac{1}{3}} dt \quad (18)$$

Having established a relationship for mass dependent, and mass-independent mortality rates, we consider the difficulty of finding food for an individual fish as a

density dependent value:

$$\kappa(t) = \frac{\kappa_0}{1 - \frac{\gamma}{n} \sum_{i=1}^n S_i(t)} - \gamma\kappa_0 \quad (19)$$

Where n is the total number of individuals and in the limiting case we consider a large enough time, t_∞ , such that $S_i(t_\infty) \approx 0$, implying:

$$\kappa(t_\infty) = \kappa_0(1 - \gamma) \quad (20)$$

which is representative to the amount of food available to a single individual. From the analysis under no density dependence, we chose to model the growth trajectory as $\hat{W}(t) = 1.9e^{0.0157t}$. We see high variability of survival rates in the literature, but set the survival level at 1.8% after Snover et al. 2006, whose survival estimates came from Shapovalov and Taft (1954). Under these assumptions, we can analyze the growth potential of individual streams under density dependent food availability.

4.3.3 Effects of Constant and Fluctuating Temperatures

Studies suggest salmonid growth and survival levels in constant thermal regimes can greatly differ from those in fluctuating thermal regimes. (Boughton et al. 2007, Geist et al. 2010, Hokanson et al. 1977). Since the growth potential curve for our model is strictly concave, it implies that the mean growth at fluctuating temperatures will always be less than growth at the mean temperature (Figure 10);(Casella and Berger 2001).

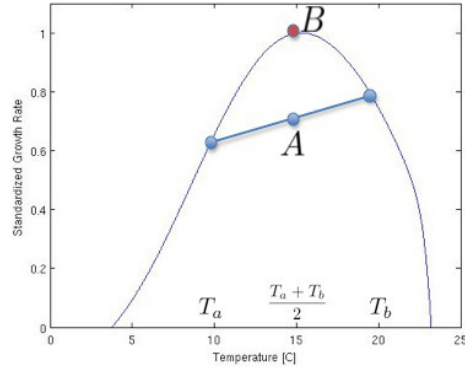


Figure 10: Pictorial representation of Jensen's inequality. The mean growth rate of T_a and T_b (A) is less than the growth rate at the mean of T_a and T_b (B)

To determine to what extent daily fluctuations affect the growth potential of individuals, the growth model is applied to a distribution of 100 fish under the conditions of fluctuating daily temperature and

mean daily temperature.

5 Results

5.1 Constant Food Availability

Our model is able to capture the expected heterogeneity in growth conditions within the watershed due to both temperature regimes and stream persistence. Food availability plays a dominant role in determining the overall growth potential of a majority of streams.

For both the individual and the distribution of fish, varying food availability levels from $\kappa = 1$ to 4 yields dramatically different results for growth potential within streams; with a positive relationship to growth. Although food availability is the driving factor for growth in a majority of streams, our model predicts that many streams experience temperature limited growth. Growth in these streams was particularly low and nearly identical regardless of food availability

Smolting time is a crucial life history choice for an individual. Although there is strong evidence for smolting to be dependent on size, there is a wide range of values reported for length at smolting varying from 125mm to 185mm (Peven et al. 2011, Hayes et al. 2008).

Using an intermediate value for smolting length of 150 mm which corresponds to roughly 13 grams (using allometric length-weight relationship), based on the model,

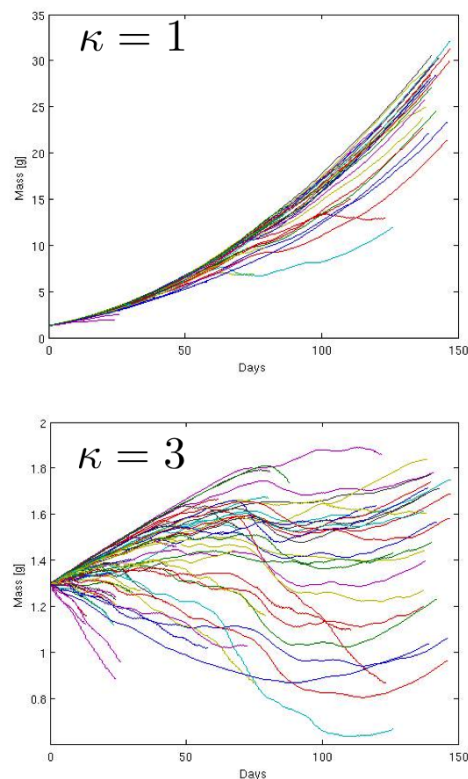


Figure 11: Seasonal simulated growth trajectories across all streams for an individual with an initial mass of 1.3 grams in two different food availability regimes.

we predict that even for high food availability levels, only about $\frac{1}{3}$ of the sites would have conditions for the level of growth needed to reach this size by the end of summer.

5.2 Density Dependent Food Availability

Taking into account density dependent effects of food availability influences the final mass of fish across streams through a feedback loop in which if growth conditions are poor, food availability will increase due to the mortality of poorly growing fish. The level of mass-dependent mortality present is highly influential in determining the strength of the feedback. Although different combinations for m_1 and m_0 yield final masses which vary as much as 20% in the extremes of mass dependent and independent mortality, the change is consistent across sites.

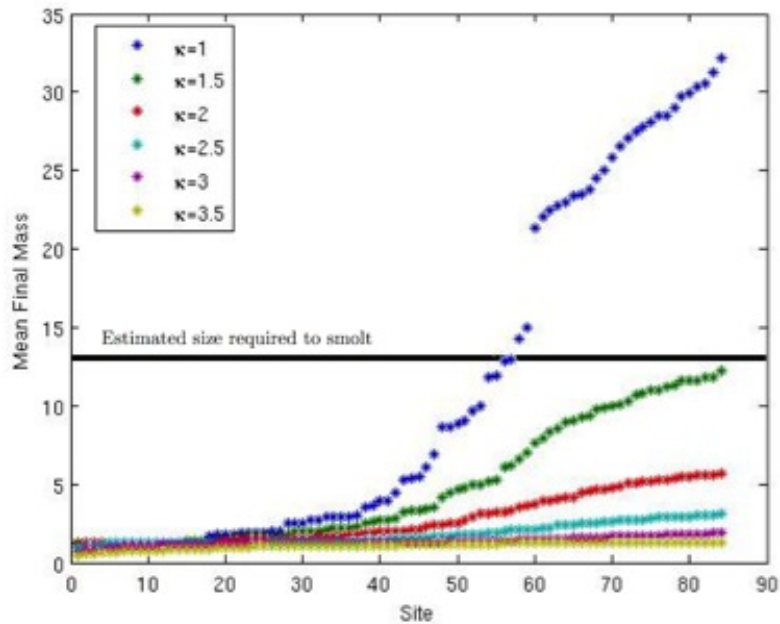


Figure 12: Mean final mass for 100 simulated individuals within sites for multiple levels of finding food. Growth is essentially independent of difficulty of finding food, therefore temperature limited, for many of the streams.

5.3 Effects of Constant and Fluctuating Temperatures

While previous experimental studies have reported significant differences in growth for individuals exposed to constant and fluctuating temperature regimes, our model

predicts the effects of daily fluctuations to be minimal in most streams. While our model coincides with the theory that growth at a constant temperature would be higher than growth at variable temperatures, empirical results from previous laboratory and field studies disagree. The results of both Hokanson et al. (1977) and Boughton et al. (2007) suggest that variable temperatures produced higher growth than constant temperatures, at least while the mean temperature was below the optimal temperature. The discrepancy between theory and data is an opportunity for further study.

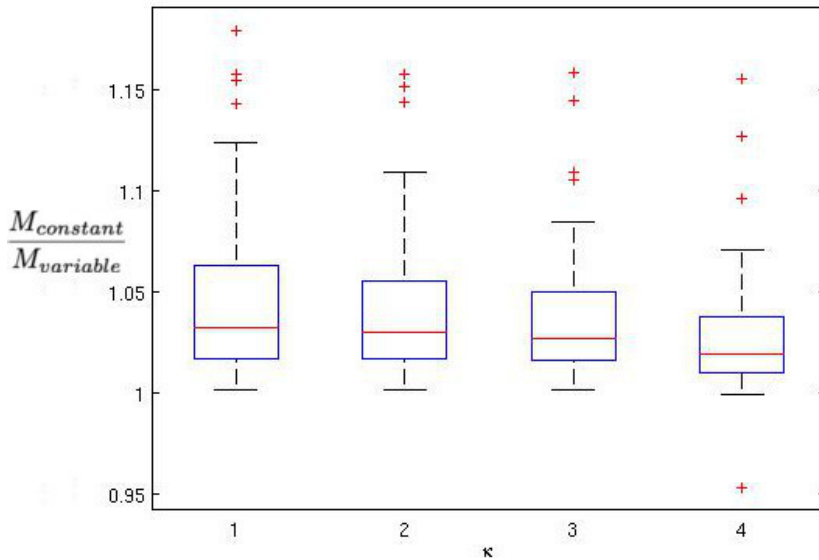


Figure 13: Ratio of final masses under constant vs. fluctuating temperatures. Constant temperatures yield final masses that are up to 18% larger than those achieved under fluctuating temperatures.

6 Discussion

Although the Santa Ynez river watershed is a data poor system, with the use of bioenergetics models we are able to provide some insight into the general growth potential landscape. The approach taken for this analysis illustrates both the utility and limitations of using a modeling approach in a data poor system. With only the knowledge of temperature regimes and some well-justified biological assumptions we

are able to provide insight into which locations in the watershed may play key roles in biological processes. While analysis suggests that it is likely that some sites are temperature limited, others have the potential of being food-limited. Determining whether food limitation would indeed occur requires further data collection, but this could be focused on sites that are not temperature-limited. Furthermore, food limited streams would be subject to higher density dependence which would result in further heterogeneity of growth conditions within the watershed. The primary analysis of growth potential within the Santa Ynez River basin using individual based growth models acts a powerful tool for allowing management to develop more targeted studies for those streams which have environmental conditions that are conducive to growth. Although it has been shown in the literature that steelhead in the southern limit of their range often make use of thermal refuges, the aim of this analysis to illustrated the growth potential of individual streams and not to account for any behavioral choices that would allow steelhead to optimize the landscape.

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