TROPHIC ECOLOGY AND BIOENERGETICS MODELING OF SACRAMENTO
PERCH (*ARCHOPLITES INTERRUPTUS)* IN ABBOTTS LAGOON, POINT REYES
NATIONAL SEASHORE

By

Kasey Lauren Bliesner

A Thesis

Presented to

The Faculty of Humboldt State University

In Partial Fulfillment

of the Requirement for the Degree

Master of Science

In Natural Resource Sciences: Fisheries

December, 2005

TROPHIC ECOLOGY AND BIOENERGETICS MODELING OF SACRAMENTO

PERCH (*ARCHOPLITES INTERRUPTUS*) IN ABBOTTS LAGOON, POINT REYES

NATIONAL SEASHORE

by

Kasey Lauren Bliesner

Approved by the Master's Thesis Committee:

_____   12 Oct 05
Walter G. Duffy, Major Professor   Date

_____   21 Oct. 05
Michael K. Saiki, Committee Member   Date

_____   15 Oct. 05
Terry D. Roelofs, Committee Member   Date

_____   17. XI. 05
Coordinator, Natural Resources Graduate Program   Date

05-FI-570-09/06

_____
Natural Resources Graduate Program Number

_____   12/5/05
Donna E. Schafer, Dean for Research and Graduate Studies   Date

ABSTRACT

Trophic Ecology and Bioenergetics Modeling of Sacramento Perch (*Archoplites interruptus*) in Abbotts Lagoon, Point Reyes National Seashore

By Kasey Lauren Bliesner

This study examined the trophic ecology and built a bioenergetics model for Sacramento perch (*Archoplites interruptus*) in Abbotts Lagoon, Point Reyes National Seashore. Objectives of this research were to: 1) document the diet of perch in Abbotts Lagoon; 2) develop a bioenergetics model for perch; and 3) use the model to evaluate energy flow to perch within the lagoon food web.

Sacramento perch were collected from the lower, middle, and upper basins of Abbotts Lagoon using monofilament experimental gill nets during June 2001, November 2001, January 2002, April 2002, and June 2002. Stomach content samples were obtained from 298 perch using gastric lavage and analyzed by frequency of occurrence, percentage wet weight and percentage by number. In July 2001, November 2001, and April 2002, perch were collected and transported to the Humboldt State University hatchery for use in experiments to obtain respiration and consumption parameter values needed for a bioenergetics model. A sensitivity analysis was also performed to evaluate the robustness of the model.

Results showed that smaller perch primarily occupied the upper basin of Abbots Lagoon, while the middle basin was more widely utilized by larger size classes. The

major prey items (by percentage wet weight) consumed were *Hyalella azteca*, *Daphnia*,
Chironomidae pupae and larvae, and Coenagrionidae. As perch in Abbotts Lagoon grew
larger, smaller prey items (such as Daphnia) became more important, an atypical result
for a known piscivore like the Sacramento perch. The bioenergetics model showed a
strong correlation between temperature and respiration rates. Respiration rates increased
during higher temperatures and decreased during lower temperatures. Growth rates of
age 2+ and older declined to near zero $O^2 g \cdot g^{-1} \cdot day^{-1}$ during warmer temperatures. Low
growth rates may reflect the lack of large prey items (such as fish) in diets of larger
perch. Sensitivity analysis of the bioenergetics model showed the model to be sensitive
to optimum temperature for respiration and p-value (a constant proportion of the
maximum specific consumption rate). I recommend replicating consumption and
respiration experiments to better estimate model parameters, and conducting a population
estimate to better understand perch population dynamics.

DEDICATION

This thesis is dedicated to my husband, Aaron, who not only carried my gear through the marsh and poison oak, but with his love and unwavering confidence has carried me through many challenges in the course of this thesis and my life.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The Sacramento perch (*Archoplites interruptus*) is the sole member of the

Centrarchidae family that naturally occurs west of the Rocky Mountains (Moyle 1976).

This geographic isolation, possibly occurring as long ago as the Miocene period, has

resulted in retention of many primitive structural and behavioral characteristics that are

not found in more advanced sunfishes (Moyle 1976). Their primitive characteristics

make perch vulnerable to introduced sunfishes (which are usually more aggressive) and

may have contributed to the "depleted" status of this species within its native range in

central California (Aceituno and Vanicek 1976).

Sacramento perch are described as a euryhaline species because they can survive,

grow, and reproduce in waters of high salinity (up to 17,000 mg/L; McCarraher and

Gregory 1970). The original distribution of perch was wholly within California and

included the Central Valley, Pajaro and Salinas rivers, and Clear Lake (Moyle 2002). In

these environments, they evolved the ability to survive extremes in temperature, salinity,

and alkalinity (Moyle 1976). Their tolerance to salinity and alkalinity have resulted in

the introduction of perch into lakes in a number of western states, including Nevada,

Colorado, Nebraska, and Texas, and into ponds, lakes, and lagoons in California that

normally do not support fish (McCarraher 1971).

1

In their native habitat, Sacramento perch (along with the Sacramento pike minnow, *Ptychocheilus grandis*) were piscivorous and at the top of the food chain (Moyle 1976). Unlike other sunfishes, perch are opportunistic feeders that consume whatever is available (Moyle 1976). Vinyard (1982) described perch as sluggish in movement and, when given a choice, they will attack prey that are the least evasive and least energetically costly to catch. Perch stalk their prey and, when close enough, will expand their buccal cavity to create suction and seize the prey organism with their teeth (Moyle 1976).

Moyle et al. (1974) described the stomach contents of different age classes of Sacramento perch from five different localities. Young-of-the-year fish consumed small crustaceans, small chironomid larvae, trichopteran larvae, and early instars of water boatmen. Older perch fed mostly on chironomid larvae and pupae, and snails in small lakes, and on aquatic insect larvae and fish in larger lakes. Tui chubs (*Siphateles bicolor*), Tahoe suckers (*Catostomus tahoensis*), and smaller perch were reported from the stomachs of large perch in Pyramid Lake, Nevada (Moyle et al. 1974). Sacramento perch were introduced into Abbotts Lagoon, Point Reyes National Seashore, Marin County, California, in the 1950's and noticed again in Abbotts Lagoon in 1971 (Self and Ranlett 1984) (Figure 1). The large and healthy population of perch in Abbotts Lagoon has value to the California Department of Fish and Game as a source for future stockings of perch in other bodies of water (Self and Ranlett 1984). Abbotts Lagoon is a brackish coastal lagoon separated from the Pacific Ocean by a sand spit that can be breached by high water levels and Pacific storms. In the late 1980's, National Park
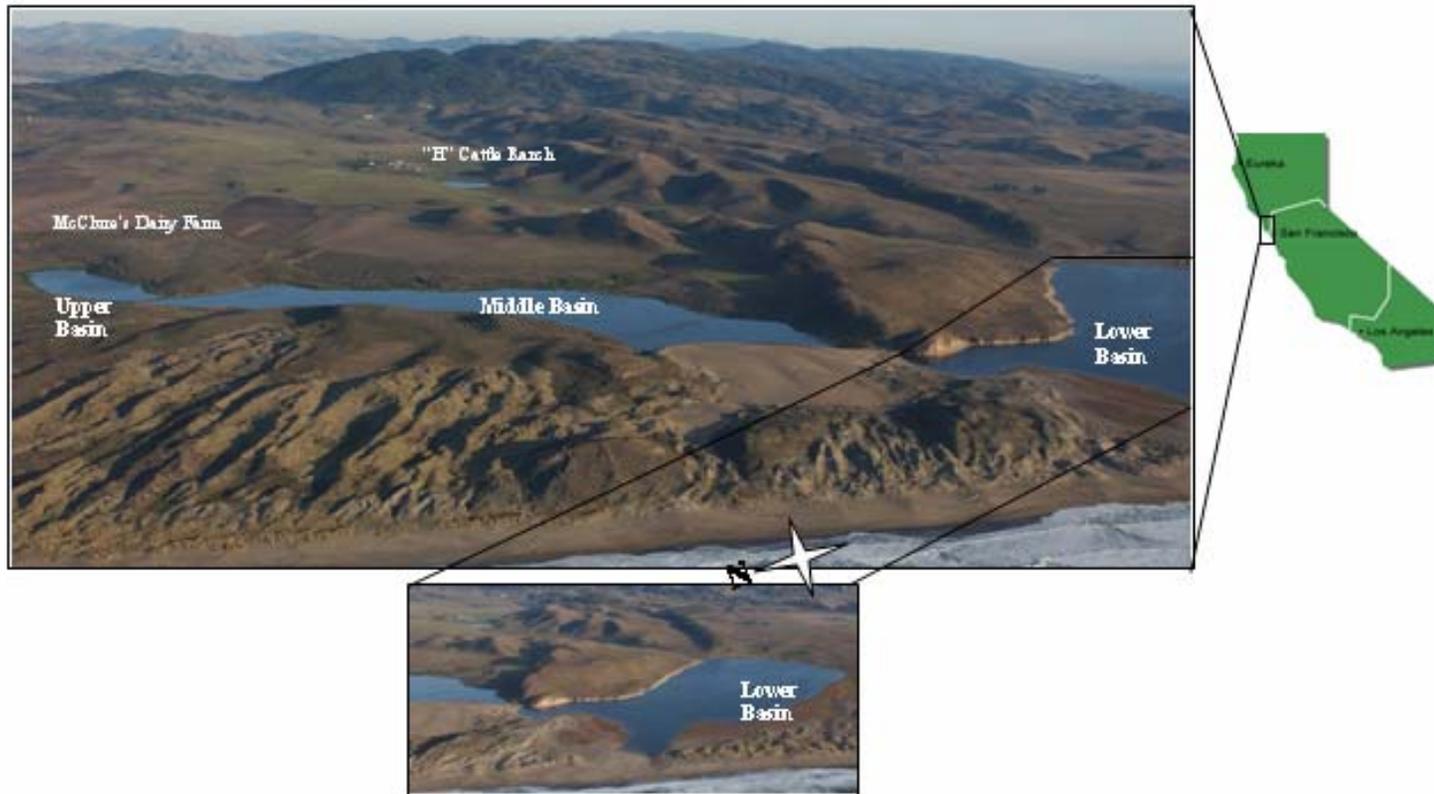
Figure 1. Aerial photographs of Abbotts Lagoon taken in September 2002 showing the upper, middle and lower basins.

Service personnel observed algal blooms in the lagoon. These blooms were thought to be caused by agricultural runoff from nearby dairy farms and cattle ranches (Anima 1990). Potentially degraded water conditions associated with algal blooms could be stressful to fishes inhabiting the lagoon (Saiki and Martin 2001).

Historically, little was known about fishery resources in Abbotts Lagoon. In 1999 Saiki and Martin (2001) investigated fish species occurring in the lagoon, their community ecology and distribution relative to environmental variables. Sacramento perch dominated the species assemblage inhabiting the upper and middle basins of the lagoon, whereas Pacific herring (*Clupea harengeus*) dominated the species assemblage inhabiting the lower basin of the lagoon (Saiki and Martin 2001). Using simple discriminant analysis, Saiki and Martin (2001) differentiated the two species assemblages mostly by salinity, with perch occurring in high abundance at freshwater sites. Species separations along salinity gradients are expected for estuarine habitats such as Abbotts Lagoon, except that several species occurring in Abbotts Lagoon, including perch, are tolerant of a broad range of salinities (Saiki and Martin 2001; McCarraher and Gregory 1970). It appears that other ecological factors (e.g., forage supply, competition, or predator-prey interactions) might be influencing the distribution of fish species in Abbotts Lagoon.

Bioenergetics models have been used to estimate fish growth rates and production, to predict food consumption, and to evaluate the impact of predators on prey populations (Jobling 1994). Bioenergetics models can play important roles in describing trophic interactions.   He et al. (1993) used bioenergetics models of largemouth bass

(*Micropterus salmoides)* and rainbow trout (*Oncorhynchus mykiss)* in an experimental

lake trial to show how changes in fish populations influence lower trophic levels.

Decreased numbers of prey fish and increased consumption of invertebrates by

largemouth bass led to lower but still sufficient growth rates and to shifts in the

composition of benthos (He et al. 1993). Baldwin et al. (2000) used bioenergetics

modeling to determine that elevated consumption of *Daphnia* by higher population

densities of cutthroat trout (*Oncorhynchus clarki clarki*) and rainbow trout in a reservoir

could create seasonal bottlenecks in *Daphnia* supply; possibly leading to reduced growth

and survival of these trout populations. The bioenergetics model of Sacramento perch

may help to identify what the important linkages are in the Abbotts Lagoon food web.

By using wet-weight measurements of prey from diet analysis, bioenergetics

models can be formulated to quantitatively describe the role of fish in the aquatic food

web. The role of prey in the diet can be assessed by inputting the caloric content of the

prey organisms (obtained from the published literature) into Fish Bioenergetics 3.0.

Moreover, the allocation of energy based on what the fish is eating can be estimated from

the model. Output from the model can also estimate the effect of the predator on the prey

species, thereby allowing predictions on how removal or depletion of the predator could

affect the aquatic food web. Output from this model could also help describe how

changes in the environment (e.g., from increased nutrient levels and primary production)

affect the aquatic food web and ultimately the Sacramento perch. Diet and temperature

data collected for different age classes and from different basins of the lagoon can be

used to describe how the energetics of perch in Abbotts Lagoon change across life

histories and locations. Rudstam et al. (1994) used this type of model to better understand production potential and consumption rate of fish such as yellow perch (*Perca flavescens)*.

The purpose of this project was to investigate the trophic ecology of the Sacramento perch in Abbotts Lagoon. Objectives of this research were as follows: 1) to document the diet of perch in Abbotts Lagoon; 2) to develop a bioenergetics model for perch; and 3) to use the model to evaluate energy flow to perch within the lagoon food web.

By documenting the relation between Sacramento perch diet and subsequent growth, and determining how energy consumed is allocated, we can develop a better understanding of the ecological role of perch in the aquatic food web and energy flow in Abbotts Lagoon (Bowen 1996, Duffy 1998).

METHODS

Description of the Study Area

Abbotts Lagoon is part of the Point Reyes National Seashore (Figure 2.) The lagoon is actually three separate, yet usually connected, basins. These basins will be referred to as the upper basin, middle basin, and lower basin (Figure 1). The 3-hectare upper basin is separated from the 20-hectare middle basin by a human enhanced earthen berm. The middle basin is separated from the 60-hectare (and deepest) lower basin by an outcropping of the Monterey Shale Formation, just below a footbridge on the hiking trail. The lower basin is usually separated from the Pacific Ocean by the sandy beach; however, the sand spit occasionally breaches for short periods, allowing direct exchange of seawater with the lagoon. Breaching of the sand spit occurred during January 2002 of this study.

During the 1800's, the Abbotts Lagoon watershed was part of the Berry Spanish Land Grant. The land surrounding Abbotts Lagoon was used for dairy and cattle grazing. Abbotts Lagoon was named for the heroic deeds of one of these early cattle ranchers. In 1962, the National Park Service obtained the land for preservation, leaving four historical dairy and cattle ranches within the 1,373 hectare Abbotts Lagoon watershed (Figure 1). The McClure dairy ranch and Evans beef cattle ranch are located completely within the Abbotts Lagoon watershed, whereas the H Ranch beef cattle ranch and the L Ranch dairy ranch are only partly within the watershed. Land use in the Abbotts Lagoon watershed is

Figure 2. Map of Point Reyes National Seashore, showing location of Abbotts Lagoon.

comprised of approximately 42% grazing, 29% silage, 22% native vegetation and 6% impacted dairy operations. The beach is accessible to hikers all along the western edge (closest to the ocean) of the middle and lower basins. A total of seven freshwater inlets enter Abbotts Lagoon (three in the upper basin, and two each in the middle and lower basins). The largest inlet draining into the upper lagoon is affected by grazing whereas the other two inlets drain the impacted McClure dairy ranch, plus native vegetation, silage and grazing fields. Inlets for the middle lagoon are dominated by grazing. Both inlets for the lower lagoon are dominated by grazing although one inlet drains an impacted area of Evans cattle ranch and is directly accessible to cattle. Dairy and cattle ranching are potential sources of non-point source pollution and sedimentation to Abbotts Lagoon.

The climate at Abbotts Lagoon is typical of coastal California with heavy rains in the winter and drought in the summer. This area has one of the most stable temperature regimes in the world, with an average summer air temperature of 12.8 °C and an average winter temperature of 10 °C. Abbotts Lagoon receives an average of 60.96 cm of rainfall a year.

Water quality of Abbotts lagoon was measured in each lagoon basin during each sampling period. Water quality parameters (water temperature, pH, dissolved oxygen, and salinity) were measured using a DataSonde® 3 multiprobe and Surveyor® 4 (Hydrolab Corporation, Austin, Texas). Parameters recorded were the average of vertical profiles taken at 1.0 meter intervals from surface to bottom. Maximum depth (m) was also recorded. In addition, water temperature was recorded at 4-hour intervals from

October 2001 to November 2002 with temperature data loggers (Hobo, Inc., Pocasset, Mass.). One temperature logger was deployed 120 cm above the bottom in each lagoon basin. Mean daily water temperature in each lagoon basin was calculated from measurements made with the temperature data logger.

Sacramento Perch Collection and Measurements

Sacramento perch were collected with-mesh variable monofilament floating gill nets. Nets consisted of five 7.6m-long by 2.4m-deep panels having square mesh sizes of 12.7, 25.4, 38.1, 50.8 and 63.5 mm. During each sampling period, four nets were set in randomly selected locations within the lower and middle lagoon basins (Figure 1) and fished for 2-hours. Captured fish were placed in buckets of lagoon water. All nets were reset for another 2 hours. Four nets were fished for two hours in the upper lagoon basin on the same periods. All gill nets were set between 0630 and 1130 hours. Time of netting was selected to maximize the likelihood of capturing fish that had recently fed (Moyle 2002) and the short duration of netting was chosen to minimize digestion.

Number and size of Sacramento perch collected were recorded. Size measurements included total length (TL, nearest mm) and weight (nearest 0.1 g). In addition, 10 fish from each of six length classes were selected for scale and stomach samples. Size classes were as follows: less than 100 mm, 100 – 149 mm, 150 – 199 mm, 200 – 249 mm, 250 – 299 mm and 300 mm or longer. When fewer than 10 fish were captured in some size classes, scales and stomach samples were taken from 50 fish

randomly selected from the size range present. When fewer than 50 fish were captured,

scale and stomach samples were taken from all fish collected.

Sacramento perch size data were used to establish a length-frequency distribution

of fish and assign probable ages. Length-frequency distributions were also used to

evaluate the population size structure and estimate survival among ages of fish (Ricker

1975, Anderson and Nueman 1996). Assigning ages from a length-frequency distribution

can, however, lead to bias (DeVries and Frie 1996). Thus ages determined from scale

annuli were used to validate ages assigned from size data.

Scale samples were collected from behind the pectoral fin on the right side of

each fish. Scale samples were placed in coin envelopes. Sample date, fish size, (TL,

weight) and location were recorded on each envelope. Scales from individual fish were

later mounted between glass microscope slides and viewed using a microfiche reader to

identify annuli. Ages were assigned following criteria outlined by Bagenal and Tesch

(1978).

A weight-length relationship was created to determine condition of Sacramento

perch. Weights and lengths collected from each individual perch were plotted and the

power function:

$$W = aL^b \hspace{3cm} \text{(equation 1)}$$

where W = weight (g), L = length (mm), and a and b are constants, was used to describe

the weight-length relationship,. The constants a and b can be determined by

logarithmically transforming weight and length data and performing a regression

analysis. The transformed relationship is reported as:

$$log_{10}(W) = a' + b \cdot log_{10}(L) \qquad \text{(equation 2)}$$

where a' is the intercept of the y-axis and b is the slope of equation 2. The constant a

from equation 1 can be calculated by taking the antilogarithm of a', and b is the same for

both equations.

Condition of Sacramento perch was determined using relative condition factor

(K_n) (Anderson and Nuemann 1996). K_n was calculated for each fish for which length

and weight had been recorded. Relative condition factor is:

$$K_n = \frac{W}{W'} \qquad \text{(equation 3)}$$

where K_n = relative condition factor, W = weight (g) and W' = the length specific mean

weight for each fish as predicted by the length-weight equation calculated for the

population. K_n compensates for allometric growth and gives a condition of one for the

average fish of any length (Anderson and Nuemann 1996).

Diet Collection and Analysis

Stomach contents were collected from Sacramento perch in June, and November

2001 and in January, April, and June 2002. Stomach contents were removed from fish

using gastric lavage (Bowen 1996) so that fish could be released alive. Fish selected for

stomach content sampling were removed from gill nets and placed in a plastic pail

containing lagoon water and an anesthetic (40-60 mg/L clove oil). After fish reached a

state of deep sedation (anesthetic stage 3-4), size measurements were recorded, scale

samples were taken, and stomachs were pumped. Stomach samples were immediately

bottled, labeled, and preserved in 90% ethanol for later measurement and identification. After collecting a stomach sample, fish were placed in a pail of lagoon water and allowed to recover until they appeared active (5-15 minutes).

Prey taxa from all stomach samples were identified to the lowest practical level, counted, and their total length measured to the nearest 0.5 mm. Prey dry biomass was then estimated from published length-mass relationships, (Benke et al. 1999, Kawataba and Urabe 1998). However an unpublished length-mass relationship was used for *Hyalella azteca* (Duffy 2000 unpublished data). Error associated with length-mass estimates is generally less than the error associated with direct weight or biovolume measurements (Benke et al. 1999). Whenever possible, the highest taxonomic level equation was used. Estimates of dry mass for each prey were then converted to wet mass using published conversions (Cummins and Wuyucheck 1971). Wet biomass of unidentifiable fish and gastropods were obtained from direct weight after blotting without correction for preservation in ethanol.

Unidentifiable, digested prey, vegetation and detritus in stomach samples were combined and air dried for 5 minutes, then their weight was recorded to the nearest 0.0001 g wet mass. Proportions of these digested and unidentifiable prey items were assumed to be similar to proportions of identifiable prey items found in the diet. The Fish Bioenergetics III model (Hanson et al. 1997) requires diet data to be entered as the proportion each prey represents in the wet mass of the diet, the mass consumed is determined during modeling. I assumed prey that were digested and unidentifiable represented the same prey that could be identified and that these prey occurred in

stomachs in proportions similar to identifiable prey. Because prey that could not be identified represented only 8.7% prey mass consumed, this assumption should have little effect on model projections.

Stomach contents were analyzed for their contribution to the total diet. Frequency of occurrence, frequency by number, and frequency by weight were calculated following Bowen (1996). Describing the diet with these three methods was intended to reduce bias and problems created when a single method is reported. Mass of each prey was also converted to an energy value (joules per gram wet mass) for use in bioenergetics modeling from data presented by Cummins and Wuyucheck (1971) (Appendix 1).

<center>Bioenergetics</center>

I used a bioenergetics modeling approach to quantify the importance of Sacramento perch in the Abbotts Lagoon food web. Bioenergetics models employ a balanced energy equation of the general form:

$$C = R + SDA + F + U + G \qquad \text{(equation 4)}$$

where C = consumption, R = metabolism, SDA = specific dynamic action, F = egestion, U = excretion and G = growth. Bioenergetics models have been demonstrated to be sensitive to consumption and respiration parameters, but relatively insensitive to parameters for specific dynamic action, egestion, excretion and growth (Bartell et al. 1986, Hewett and Johnson 1992). Criticism of bioenergetics models has focused on the practice of borrowing parameters from one species to use on another and of applying models across broad geographic areas (Hansen et al. 1997). For these reasons, I chose to

conduct laboratory experiments on perch from Abbotts Lagoon to develop model

parameters for consumption and metabolism that would be most appropriate. Parameters

that I chose to borrow from other species were ones which the bioenergetics model has

been shown to be insensitive to, such as egestion and excretion (Hewett and Johnson

1992).

Sacramento perch were collected from Abbotts Lagoon in July 2001, November

2001 and April 2002 for use in bioenergetics modeling lab experiments. Fish were

transported to Humboldt State University and acclimated to tanks at the university

hatchery for 10 days. After initial acclimation, groups of two perch were then acclimated

to water temperatures of 10, 12, 18, 20, and 23°C over a one-week period and held at that

temperature until consumption or respiration experiments were begun.

Consumption was determined for Sacramento perch fed *ad libitum* at each of the

five water temperatures. Perch used in feeding experiments were weighed to the nearest

0.01 gram so that a daily specific consumption rate ($g \cdot g^{-1} \cdot day^{-1}$) could be obtained.

Consumption experiments were initiated by fasting perch for 72 hours, then introducing

goldfish (*Carassius auratus*) (mean wet weight = 0.75 g) in numbers greater than perch

could eat in 24 hours. Goldfish were weighed (nearest 0.01 g) before introduction to the

tank with perch. After 24 hours, uneaten goldfish were collected and again weighed.

The difference between introduced and uneaten goldfish was calculated for each

Sacramento perch to obtain the wet weight (g) eaten during the 24-hour period. Three

replicate feeding trials were conducted with each perch. Mass consumed by individual

perch in each of the three feeding trials was averaged and divided by the weight of that

perch to calculate consumption rates ($g \cdot g^{-1} \cdot day^{-1}$) at each temperature. Water temperature varied ± 2 °C among feeding trials, so consumption rates were calculated for the average temperature during three trials.

The optimum and maximum water temperatures for consumption were identified by fitting specific consumption rates at specific temperatures to a Gaussian Peak regression. This regression was then used to forecast water temperatures at which consumption would be maximum and optimum.

After determining the critical temperatures for consumption, I developed an allometric mass function for consumption at the optimum temperature point. Eleven Sacramento perch ranging in size from 37.5 to 166.35g were acclimated to the optimum temperature for consumption (20 °C). Then feeding trials described above were carried out on 11 perch ranging in size from 41.3g to 153.0g to produce data that could be used to evaluate specific consumption rates at the optimum water temperature as a function of size.

At the conclusion of the consumption experiments, respiration experiments were begun utilizing perch that were already acclimated to hatchery tanks and temperatures. Procedures for measuring respiration followed Jobling (1994). After acclimation to water temperatures, perch were fasted for 72 hours at which point they were introduced to respirometry chambers, one gallon (3.78 L) glass jars fitted with rubber stoppers. I placed two respirometry chambers in tanks at one of the five temperatures for which individual Sacramento perch had been acclimated. Perch were allowed to acclimate for 24 hours in the respirometry chambers before respiration experiments were initiated,

during which time they were shielded from disturbances under low-light conditions, and the oxygen supply was at or slightly above saturation.

Respiration for individual Sacramento perch was determined at each of the five temperatures. One blank bottle (0.05-L glass bottles fitted with rubber stoppers) was placed in each of the tanks containing respirometry chambers. Dissolved oxygen (DO) ($mg \cdot L^{-1}$) was measured in each respiration chamber and blank bottle. After one hour DO ($mg \cdot L^{-1}$) was measured again. Water was flushed from each respirometry chamber and blank bottle and the experiment was repeated twice more, for a total of three replicates. After completion of three trials, individual perch were weighed to the nearest g. DO was measured using an YSI laboratory DO meter, model 5100 (Yellow Springs Instrument Company, Yellow Springs, Ohio).

DO ($mg \cdot L^{-1}$) consumed in each blank bottle was multiplied by the volume of the blank bottle (0.05 L) and DO ($mg \cdot L^{-1}$) consumed by individual Sacramento perch during each of the three trials was multiplied by the volume (3.78 L) of the respirometry chamber to give mg of DO consumed. Milligrams of DO consumed in each blank bottle were subtracted from the Mg of DO consumed in each respirometry chamber. DO consumed by individual perch in each of the three respiration trials was converted to g, multiplied by 24, averaged, and divided by the weight of that perch to calculate respiration rates ($g \cdot g^{-1} \cdot day^{-1}$) at each temperature. Water temperature varied $\pm$ 1 ^{o}C among feeding trials, so respiration rates were calculated for the average temperature.

The optimum and maximum water temperatures for respiration (Table 1) were identified by fitting specific respiration rates at specific temperatures to a Gaussian Peak

Table 1. Sacramento perch bioenergetics model parameters, parameter values, units, their descriptions and sources for parameter values.

Parameter	Value	Units	Description	Source
C		$g \cdot g^{-1} \cdot day^{-1}$	Specific consumption rate, calculated using equation 2 in Hewett and Johnson (1992)	
CA	0.2995	$g \cdot g \cdot day^{-1}$	Intercept of the allometric mass function.	This study.
CB	-0.0582		Slope of the allometric mass function	This study.
CQ	2.86	$^\circ$C	Approximation of a Q_{10} value over low water temperatures	This study.
CTO	20	$^\circ$C	The water temperature at which consumption is highest or optimum.	This study.
CTM	37	$^\circ$C	The maximum temperature at which consumption occurs.	This study.
P			A constant proportion of C_{max}.	
T		$^\circ$C	Ambient water temperature.	This study.
W		g	Wet mass of predator	
R		$gO^2 \cdot g^{-1} \cdot day^{-1}$	Specific respiration rate, calculated using equation 2 in Hewett and Johnson (1992).	
RA	0.005	$gO^2 \cdot g^{-1} \cdot day^{-1}$	Intercept of the allometric mass function for respiration	This study.
RB	-0.0066		Slope of the allometric mass function for respiration.	This study.

Table 1 (continued). Sacramento perch bioenergetics model parameters, parameter values, units, their descriptions and sources for parameter values

Parameter	Value	Units	Description	Source
RQ	3.59	˚C	Approximation of a Q_{10} value over low water temperatures.	This study.
RTO	22.3	˚C	The water temperature at which respiration is highest or optimum.	This study.
RTM	31.8	˚C	The maximum temperature at which respiration occurs.	This study.
ACT	1		The Winberg activity multiplier.	Moyle (2002)
SDA	0172		Specific dynamic action.	Kitchell et al. (1977)
FA	0.158	%	Egestion as a constant proportion of consumption.	Shuter and Post (1990)
UA	0.0253	%	Excretion as a constant proportion of consumption.	Shuter and Post (1990)
PED	4186	$J{\cdot}g^{-1}$	Predator energy density.	Kitchell et al. (1977)
SPAWN	2.5	%	Percentage of weight spawned on one day.	Acetiuno and Vanicek (1976)

regression. This regression was then used to forecast water temperatures at which

consumption would be maximum and optimum (Table 1).

After determining the critical temperatures for respiration, I developed an

allometric mass function for consumption at the optimum temperature point. Eight

Sacramento perch ranging in size from 42.72 to 163.21 g were acclimated to the optimum

temperature for consumption (22 °C). Then respiration trials described above were

carried out on different sized perch to produce data that could be used to evaluate specific

consumption rates at the optimum water temperature as a function of size.

A bioenergetics model for Sacramento perch was constructed by first selecting

equations that mathematically represent energetic processes occurring in perch.

Equations in the bioenergetics model allow one to incorporate influence of water

temperature and fish size on rates of consumption, respiration, egestion and excretion.

Equations I used to build the model for perch are described below.

Predator consumption rates are modeled based on the assumption that an

individual fish cannot consume more than its stomach can contain, digest, and pass. The

equation for specific consumption rate (C) is:

$$C = C_{max} \cdot p \cdot f(T)_C \qquad \qquad \text{(equation 5)}$$

where C_{max} = the maximum specific consumption rate (g·g^{-1}·d^{-1}) and $f(T)_C$ = the

temperature dependence function for consumption. All individual model parameters (e.g.

a_C and b_C) are defined and their values are presented in Table 1. Predator feeding rate is therefore bounded by C_{max}, an allometric function of individual predator weight and ambient water temperature as:

$$C_{max} = a_C W^{b_C} \qquad \text{(equation 6)}$$

The model uses C_{max} to calculate the proportion of maximum ration consumed over the interval modeled, given body size and temperature constraints experienced by the fish.

The temperature dependence function for consumption ($f(T)_C$) used was:

$$f(T)_C = V^X \cdot e^{(X \cdot (1-V))} \qquad \text{(equation 7)}$$

where

$$V = \frac{CTM - T}{CTM - CTO} \quad \text{and} \qquad \text{(equation 8)}$$

$$X = \frac{\left(\ln(CQ) \cdot (CTM - CTO)\right)^2 \cdot \dfrac{\left(1 + (1 + 40)^{0.5}\right)^2}{\ln(CQ) \cdot (CTM - CTO + 2)}}{400} \qquad \text{(equation 9)}$$

The temperature dependence function largely determines the hyperbolic shape of the consumption algorithm.

Respiration (R), the energy loss resulting from fish metabolism was modeled using a species-specific function of predator weight, temperature and activity:

$$R = a_R W^{a_R} \cdot f(T)_R \cdot ACT \qquad \text{(equation 10)}$$

The temperature dependence function for respiration $f(T)_R$ is:

$$f(T)_R = V^X \cdot e^{(X \cdot (1-V))} \quad \text{where} \qquad\qquad \text{(equation 11)}$$

$$V = \frac{RTM - T}{RTM - RTO} \quad \text{and} \qquad\qquad \text{(equation 12)}$$

$$X = \frac{(\ln(RQ) \cdot (RTM - RTO))^2 \cdot \dfrac{\left(1 + (1+40)^{0.5}\right)^2}{\ln(RQ) \cdot (RTM - RTO + 2)}}{400} \quad \text{(equation 13)}$$

An activity multiplier (ACT) is incorporated in bioenergetics models to specify metabolic rates above standard metabolism that result from the activity of fish. The ACT is a constant that is multiplied by the resting metabolism. I chose an ACT multiplier of 1.0. The ACT value selected for Sacramento perch reflects their sluggish nature (Moyle 2002) and has been used for a variety of other cool and warm-water species (Hewett and Johnson 1992).

The metabolic cost of digesting and assimilating ingested food is the energy expenditure for the post-absorptive processes that follows ingestion of food (Beamish and Trippel 1990). The proportion of assimilated energy lost to SDA (S) is defined as:

$$S = SDA \cdot (C - F) \qquad\qquad \text{(equation 14)}$$

I modeled SDA as a constant proportion of assimilated food, and selected a value of 17.2% as the fixed proportion of the total consumption. This value has been used to model a variety of fish species (Stewart et al. 1983, Hanson et al. 1997) and bioenergetics models have been determined to be relatively insensitive to SDA (Bartell et al. 1986).

Egestion and excretion components of energy budgets are commonly incorporated into bioenergetics models to express the loss of energy due to assimilated and non-assimilated waste products. These parameters are often modeled as a constant proportion

of ingested energy. I also modeled waste losses as a proportion of consumption and selected 15.8 % for egestion and 2.53% for excretion. The values I chose for egestion and excretion have been used to model a variety of fish species with ecology similar to Sacramento perch (Shuter and Post 1990).

Predator energy density is the joules per gram wet body mass of Sacramento perch. This parameter is often modeled as a constant throughout the year. I chose to use a value of 4186 joules·g^{-1}. The value I chose for predator energy density has been used in models for a variety Centrarchid species (Hewett and Johnson 1992).

I chose to incorporate the influences of spawning and mortality into the bioenergetics model for Sacramento perch in Abbotts Lagoon. In this bioenergetics model, spawning is treated as occurring on a single day. From visual observations of perch in Abbotts Lagoon, I chose a spawning date June 6. The amount of energy lost during spawning was estimated to be 2.5% based on values used for other closely related Centrarchids and on data collected by Aceituno and Vanicek (1976). In the model, perch of age 0+ and 1+ did not spawn, but all fish greater than and including age 2+ did. Selection of age at maturity was based on visual observation of perch captured in Abbotts Lagoon during the spawning season.

Mortality was incorporated into the bioenergetics model to allow for the evaluation of population level influences on energy flow. Mortality of Sacramento perch in Abbotts Lagoon was estimated using a catch-curve created from perch captured during June and November 2001. Number of perch caught was plotted against age. A curve with ascending and descending legs was created, and cohorts falling on the ascending leg

were considered not yet fully vulnerable to the gear (gill nets). A regression was fit to cohorts of ages 2+ - 5+ to insure that only cohorts fully vulnerable to the gear were considered, and would thus yield a more accurate estimate of the instantaneous rate of mortality (Z). Given that annual survival rate (S) = e^{-z}, the instantaneous rate of mortality (Z) rate can be estimated from the slope of the regression, where S= -ln slope = -ln Z.

Models were created for six different age classes, or cohorts. Individuals were assigned to cohorts based primarily on the length-frequency distribution of individuals captured. However, ages 3+ and older were difficult to distinguish due to reduced growth in length and smaller sample size, relative to younger cohorts. Therefore, weight-frequency distributions were used as a secondary criterion in identifying cohorts. Annuli on scales collected from 50 Sacramento perch were identified and used to assign ages to perch of known size. Scales from individual fish were mounted between glass microscope slides and viewed using a microfiche reader to identify annuli. Ages were assigned following criteria outlined by Bagenal and Tesch (1978).

Size data from Sacramento perch of known ages were then used to corroborate cohort selection based on size frequency data. Distinguishing annuli from perch greater than age 5+ was difficult, thus perch greater than and including age 5+ were combined into one cohort.

Sensitivity analysis was performed to determine how errors in estimated parameters might affect model estimates of total consumption. This analysis identified locally sensitive parameters or those parameters that caused model predictions to deviate

more than 10%. This type of analysis would not indicate the overall precision of the

model (Essington 2003). Sensitivity analyses were performed on all model parameters

using data for the age 2+ cohort of Sacramento perch following methods described by

Kitchell et al. (1977),

$$S_X(p) = \frac{p \cdot \Delta X}{X \cdot \Delta p}$$ (equation 15)

where S_x (p) = sensitivity of output parameter x to deviations in input parameter p, p =

the nominal value of parameter p, Δp = the intput deviation of parameter p, X = nominal

value of output parameter x from model simulation and ΔX = deviation of output

parameter X due to Δp. Model parameter values were adjusted +/- 10% from nominal

values, the model was run, and changes in estimated final consumption (g) were

recorded.

RESULTS

Water quality data were recorded on each sampling date. However, large mats of water lettuce (*Pistia stratiotes)*, an invasive aquatic plant, prevented sampling in the upper lagoon basin in June 2001. Instrument malfunctions also prevented collecting water quality data in the middle and upper lagoon basins in November 2001, and pH at all sites in April 2002. Finally, the water temperature data logger deployed in the upper lagoon basin could not be recovered.

Average water temperature recorded on fish sampling dates ranged from 11.1 °C in the lower basin during January 2002 to 19.1 °C in the upper basin during June 2002. Average water temperatures were consistently highest in the upper basin, intermediate in the middle basin and lowest in the lower basin, although differences among basins only ranged from 0.2-2.2 °C (Table 2). Temperature varied little with depth (standard deviations of means were always ≤ 0.4).

Daily average water temperature in the lower and middle lagoon basins exhibited a similar seasonal pattern (Figure 3). However, during 1 October 2001 – 30 September 2002, daily average water temperatures in the middle lagoon basin (range 9.0 – 21.7 °C, mean = 15.6 °C) were typically warmer than in the lower basin (range 7.8 – 21.5 °C, mean = 14.5 °C).

Salinity varied among lagoon basins and among seasons. Salinity was greatest in the lower lagoon basin on each sampling date (Table 2). Highest (mean 8.0 ppt) and most variable salinity concentrations were recorded in the lower basin during January

Table 2. Summary of water quality, temperature (C), salinity (ppt), dissolved oxygen (mg/L) and maximum depth measured (m) for each basin of Abbotts Lagoon. Numbers in parentheses are standard deviations of the mean.

Lagoon Section	Temperature (C)			Salinity (ppt)			Dissolved Oxygen (mg/L)		
	Lower	Middle	Upper	Lower	Middle	Upper	Lower	Middle	Upper
June 01	16.8 (0.01)	17.8 (0.2)	--a	3.7 (0)	0.3 (0)	--a	8.7 (0.2)	7.6 (2.9)	--a
Nov. 01	13.9 (0.03)	--b	--b	3.9 (0.4)	--b	--b	7.7 (0.3)	--b	--b
Jan. 01	11.1 (0.04)	11.3 (0.3)	11.6 (0.2)	8.0 (6.1)	0.2 (0)	0.1 (0.06)	8.4 (1.0)	6.8 (0.5)	6.7 (1.7)
April 02	13.8 (0.4)	14.2 (0.4)	14.6 (0)	6.0 (2.2)	0.2 (0)	0.1 (0)	7.1 (2.9)	7.9 (1.2)	9.8 (0.2)
June 02	17.1 (0.4)	18.5 (0.4)	19.1 (0.4)	7.4 (0.03)	0.2 (0)	0.2 (0)	7.0 (1.8)	11.0 (1.8)	7.4 (1.3)

Lagoon Section	pH			Maximum Depth Measured (m)		
	Lower	Middle	Upper	Lower	Middle	Upper
June 01	8.2 (0.05)	9.1 (0.5)	--a	3.0	5.0	--a
Nov. 01	8.8 (0.04)	--b	--b	9.5	--b	--b
Jan. 01	8.6 (0.1)	8.4 (0.1)	8.1 (0.1)	6.8	4.4	1.8
April 02	--b	--b	--b	6.9	5.75	1.8
June 02	7.3 (0.1)	8.7 (0.1)	--b	9.7	4.6	1.8

[a] no data
[b] Hydrolab malfunction, no data collected
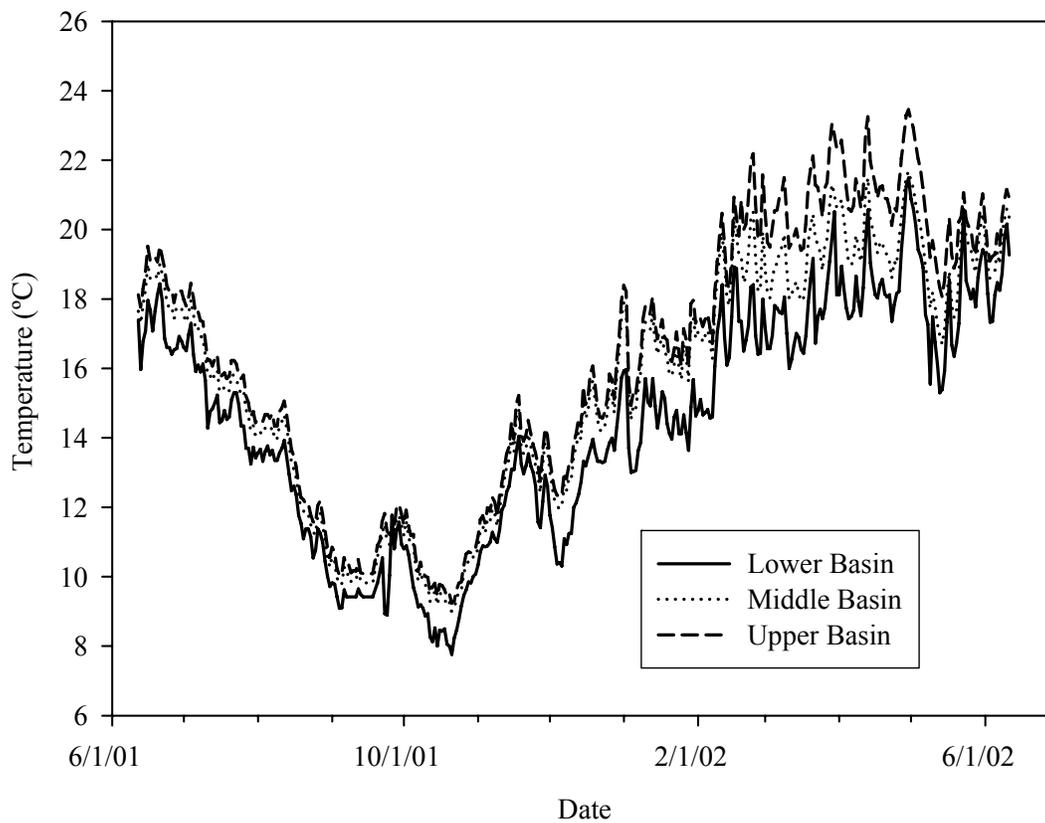
Figure 3. Average daily temperature (ºC) for the lower, middle and upper basins of Abbotts Lagoon used for bioenergetics modeling of Sacramento perch.

2002 and corresponded with a lagoon breach. In the middle and upper lagoon basins, salinity concentrations were consistently lower, relative to the lower basin (Table 2) (Figure 4).

Dissolved oxygen concentration in all three basins was generally adequate for warmwater fish species (Moyle 2002). Over the sampling period, dissolved oxygen concentrations ranged from 3.3 – 11.0 mg·l^{-1} (Table 2). The most variability at depth occurred in the middle lagoon basin during June 2001 (Figure 5). Dissolved oxygen generally decreased as depth increased, dropping as low as 3.3 mg·l^{-1} at a depth of 9.7 m in the lower basin during June 2002.

The hydrogen ion concentration (pH) proved difficult to measure due to instrument malfunctions on three of six sampling trips (Table 2). On the date when pH data were collected, it varied little among lagoon basins or among depths and was always basic.

Maximum depth measured during water quality measurements varied among lagoon basins and among seasons. Maximum depth was most often greatest in the lower lagoon basin and varied three-fold over the period of sampling. Maximum depth in the middle and lower lagoon basins varied little among seasons (Table 2).
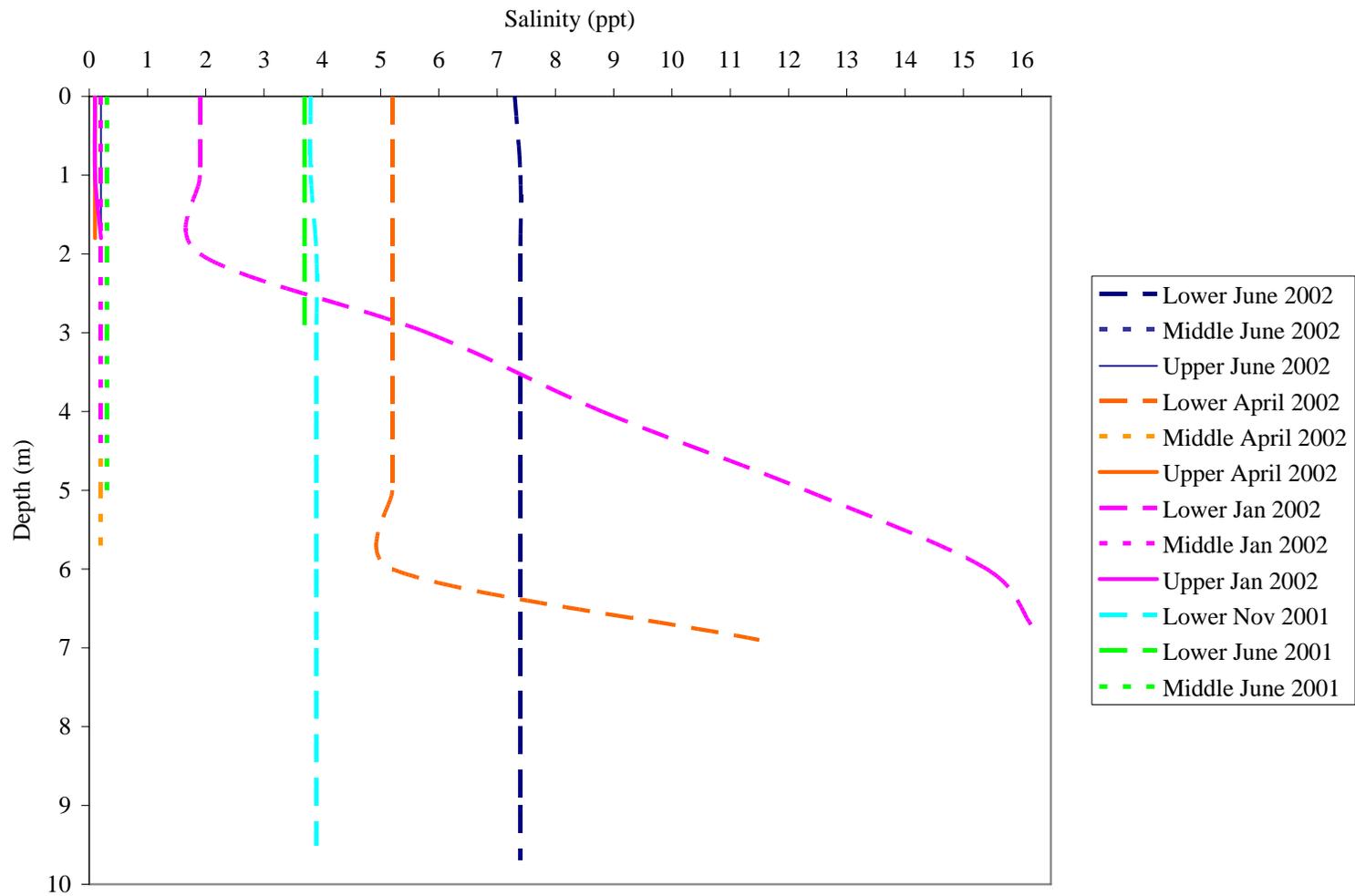
Figure 4. Profile of salinity (ppt) for each basin of Abbotts Lagoon during each sampling session.
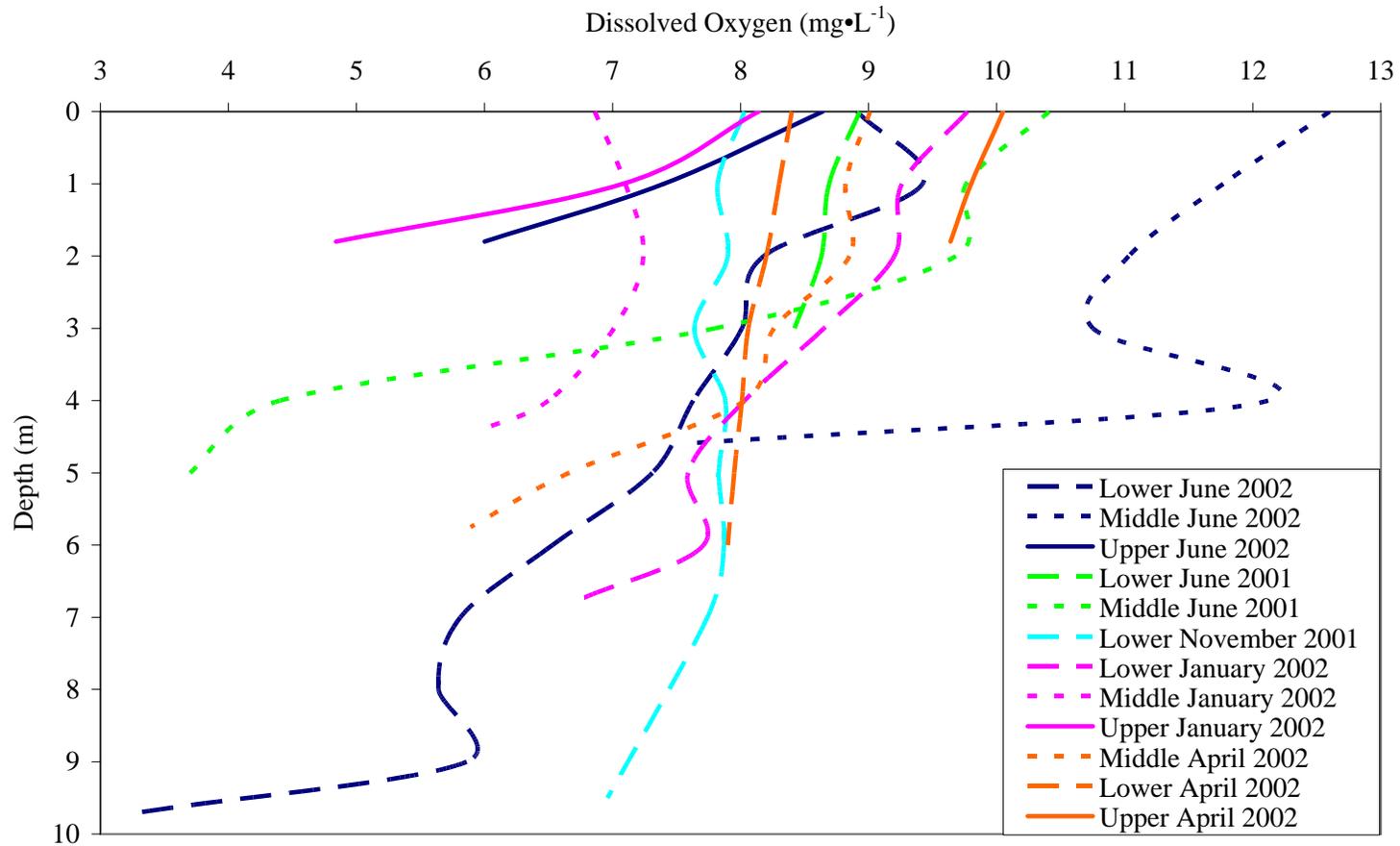
Figure 5. Depth profile of dissolved oxygen (mg·L^{-1}) in Abbotts Lagoon, Point Reyes National Seashore for the upper, middle, and lower lagoon basins.

Fish Abundance and Distribution

A total of 880 fish, consisting of five species, was caught during five sampling trips from June 2001 – June 2002 (Table 3). Sacramento perch represented 55% and Pacific Herring 43% of the total catch. Largemouth bass, threespine stickleback (*Gasterosteus aculaeatus*) and staghorn sculpin (*Leptocottus armatus*) made up the remaining 2% of the total catch. No fish were caught in the lower lagoon basin during June 2002.

Sacramento perch were found in all three lagoon basins. Fifty percent of the Sacramento perch were caught in the middle lagoon basin, 48% in the upper lagoon basin, and 2% in the lower lagoon basin. Largemouth bass were found in the upper and middle lagoon basins, while Pacific herring, staghorn sculpin, and threespine stickleback were only found in the lower lagoon basin (Table 4).

Thirty-seven percent of the Sacramento perch caught were age 2+, 33% were age 1+, while only 3.7% of perch caught were age 0+ (Table 4, Figure 6). Age 1+ Sacramento perch predominated the catch (88%) from the upper lagoon basin, while 69 % of perch caught in the middle lagoon basin were age 2+. Only age 5+ Sacramento perch were caught in the lower lagoon basin.

Seasonal catch of Sacramento perch varied, but with no real trend. Catch was greatest in January 2002 and lowest in June 2002. Most of the age 0+ Sacramento perch were collected in June 2002, while greatest catch of ages 1+ and 2+ was recorded in

Table 3. Species and number of fish other than Sacramento perch collected from Abbotts Lagoon, Point Reyes National Seashore during June 2001 – June 2002.

	Largemouth bass	Pacific herring	Threespine stickleback	Staghorn sculpin
Upper				
21 Nov. 2001	1	0	0	0
9 Jan. 2002	0	0	0	0
3 Apr.2002	0	0	0	0
18 June 2002	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>
Total	1	0	0	0
Middle				
12-13 June 2001	7	0	0	0
21 Nov. 2001	1	0	0	0
8 Jan. 2002	2	0	0	0
1 Apr.2002	2	0	0	0
17 June 2002	<u>1</u>	<u>0</u>	<u>0</u>	<u>0</u>
Total	13	0	0	0
Lower				
11 June 2001	0	25	0	0
19 Nov. 2001	0	53	0	0
1 Jan. 2002	0	244	2	1
2 Apr.2002	0	47	0	0
16 June 2002	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>
Total	0	369	2	1

Table 4. Total catch of Sacramento perch on each sampling date and age distribution of catch in Abbotts Lagoon, Point Reyes National Seashore, as well as fishing effort and catch-per-unit-effort.

	Age 0+	Age 1+	Age 2+	Age 3+	Age 4+	Age 5+[1]	Catch (No.)	Effort (hrs)	CPUE[2]
Upper Lagoon									
21 Nov. 2001	4	3	0	1	1	0	9	10	0.90
9 Jan. 2002	0	85	48	6	0	0	139	13	10.69
3 Apr. 2002	1	15	2	2	0	0	20	8	2.50
18 June 2002	11	41	2	2	5	0	61	8	7.00
Total	16	144	52	11	6	0	229		
Middle Lagoon									
12-13 June 2001	1	2	53	16	11	14	97	47	2.06
21 Nov. 2001	0	0	1	2	6	10	19	16	1.19
8 Jan. 2002	0	3	24	14	0	1	42	20	2.00
1 Apr. 2002	1	5	34	13	3	4	60	16	3.75
17 June 2002	0	7	14	4	0	1	26	10	2.60
Total	2	17	126	49	20	30	244		
Lower Lagoon									
11 June 2001	0	0	0	0	0	1	1	23	0.04
19 Nov. 2001	0	0	0	0	0	5	5	16	0.31
1 Jan. 2002	0	0	0	0	0	0	0	20	0.00
2 Apr. 2002	0	0	0	0	0	2	2	16	0.13
16 June 2002	0	0	0	0	0	0	0	14	0.00
Total	0	0	0	0	0	8	8		

[1] Age 5+ included all fish $\geq$ 5+.
[2] One unit of effort = one experimental gill net fish per one hour.
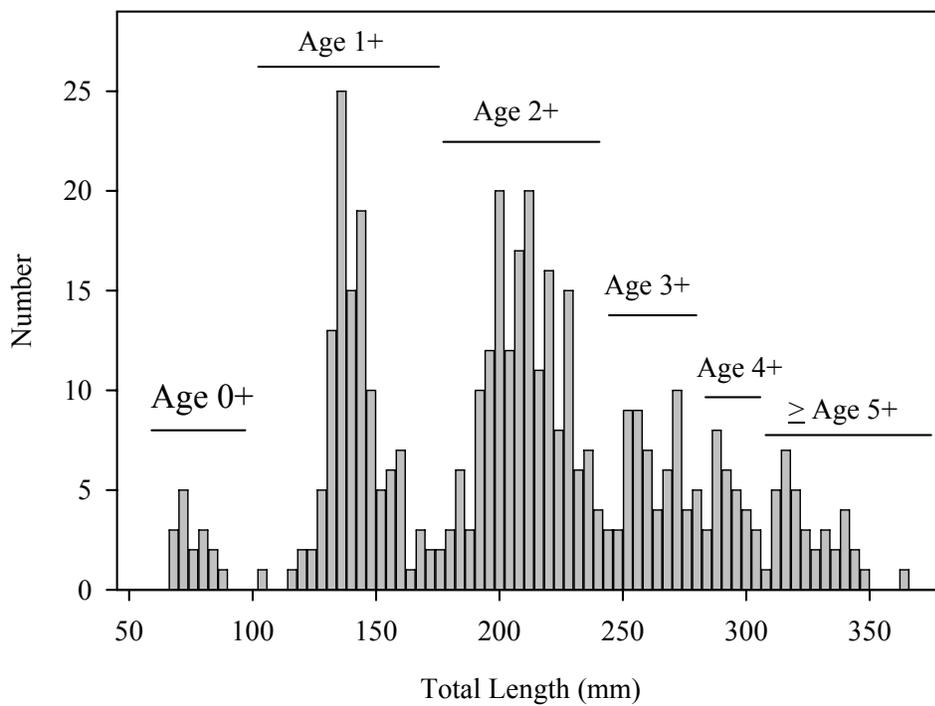
Figure 6. Length frequency histogram for Sacramento perch in Abbotts Lagoon captured
on five occasions between June 2001 and June 2002 with variable mesh gill nets.

January 2002. Apparent seasonal trends in the catch of age 4+ and 5+ were masked by low numbers (Table 4).

Instantaneous mortality (Z) and survival (S) rates for Sacramento perch in Abbotts Lagoon were estimated from a catch curve using perch of ages 2+ to 5+. The regression from the catch curve, ln(Catch) = 5.957 + ln(0.5469 * age), yielded an estimate of Z = 0.547 and an S = 0.6035 (Figure 7).

Catch-per-unit-effort (CPUE) varied from a high of 11.43 in the upper lagoon basin during January 2002 to a low of 0 on two dates in the lower lagoon basin, January and June 2002 (Table 4). Lowest CPUE was consistently recorded in the lower lagoon basin, ranging from 0 to 0.31. CPUE was most consistent in the middle lagoon basin.

Catch at each sample date was too small to create useful length-frequency histograms, so catches from June 2001, November 2001, January 2002, April 2002, and June 2002 were combined (Figure 6). I was able to identify six age groups of Sacramento perch from a length frequency distribution of all data. Ages 0+, 1+, and 2+ were reasonably well separated (Figure 6). However, the length frequency distribution of age 3+ and older fish revealed greater overlap among ages. Therefore, age was assigned to older fish using both length frequency and scale annuli. Age 5+ Sacramento perch includes all fish of age 5+ and older, because more than five scale annuli could not be identified with confidence.

Mean length and weight varied little within age categories of Sacramento perch (Table 5). The greatest variation in total length occurred in age 2+ fish, averaging 208 mm with a standard deviation of the mean of only 17 (Table 5). Weight within age
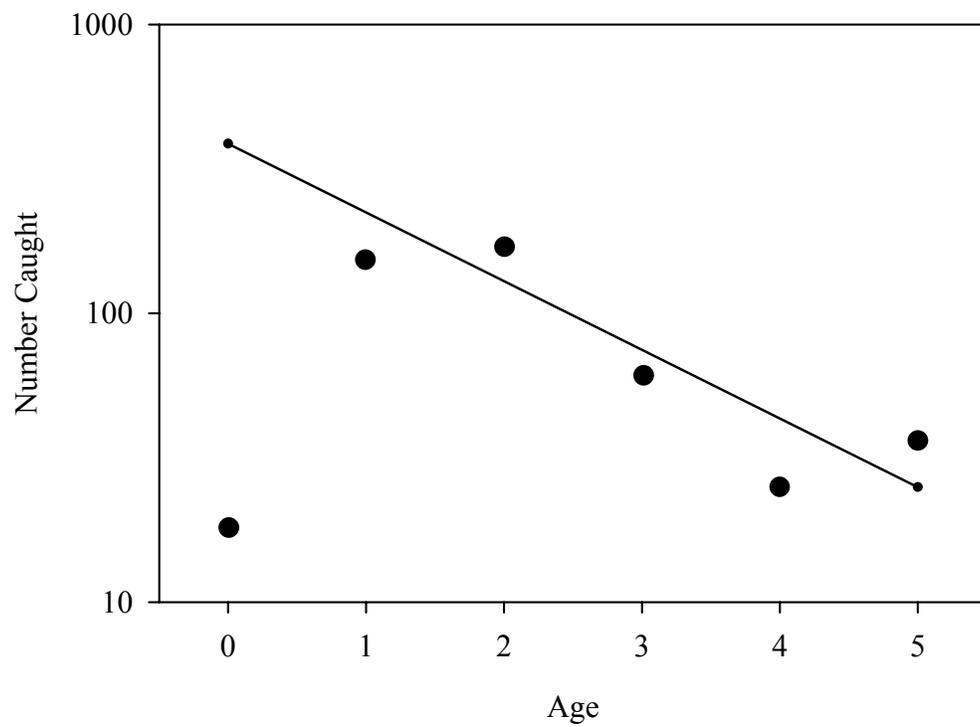
Figure 7. Catch curve for Sacramento perch in Abbotts Lagoon. Age classes 2+, 3+, 4+, and 5+ used for determining instantaneous rate of mortality (Z).

Table 5. Mean total length, weight, and condition (Fulton's K) of Sacramento perch caught in Abbotts Lagoon, Point Reyes National Seashore. Numbers in parentheses are standard deviations of the mean.

	Age 0+	Age 1+	Age 2+	Age 3+	Age 4+	Age 5+[1]
Mean Length (mm)						
11-13 June 2001	68	152 (10)	218 (15)	260 (11)	293 (5)	318 (10)
19-21 Nov. 2001	79 (6)	128 (10)	222	275 (16)	294 (5)	327 (14)
7-9 Jan. 2002		140 (11)	205 (14)	263 (11)	292 (7)	347
1-3 Apr.2002	73 (1)	133 (7)	205 (15)	265 (9)	289 (6)	323 (14)
16-18 June 2002	73 (6)	139 (9)	198 (23)	263 (6)		321
Mean Weight (g)						
11-13 June 2001	9.8	67.4 (8.1)	202.3 (54.8)	345.5 (57.3)	469.7 (61.1)	636.4 (65.2)
19-21 Nov. 2001	16.2 (8.3)	55.1 (6.1)	192.9	348.2 (37.5)	481.5 (95.2)	627.9 (74.2)
7-9 Jan. 2002		63.8 (18.9)	167 (33.2)	328.4 (51.2)	413.8 (55.7)	730.0
1-3 Apr.2002	5.5 (0.4)	45.8 (7.4)	169.7 (35)	353.4 (50.5)	413.8 (55.7)	644 (87.1)
16-18 June 2002	6.6 (1.9)	56.4 (11.29.5)	143.8 (39.6)	347.9 (28.7)		681.3
Condition (K_n)						
11-13 June 2001	1.63	1.17 (0.16)	1.14 (0.20)	1.18 (0.11)	1.17 (0.14)	1.19 (0.06)
19-21 Nov. 2001	1.46 (0.38)	1.54 (0.53)	1.04	1.02 (0.14)	1.16 (0.20)	1.11 (0.12)
7-9 Jan. 2002	0.96	1.25 (0.16)	1.14 (0.12)	1.08 (0.10)	1.03 (0.10)	1.08
1-3 Apr.2002	0.75 (0.07)	1.09 (0.08)	1.14 (0.17)	1.14 (0.10)	1.23 (0.10)	1.23 (0.05)
16-18 June 2002	0.87 (0.18)	1.18 (0.11)	1.05 (0.09)	1.16 (0.04)		1.27

[1] Age 5+ included all fish $\geq$ 5+.

categories was more variable than length and greatest in age 4+ fish, where mean weight

was 469.9 g with a standard deviation of 83.1. Sacramento perch do not display isometric

growth, as shown by the weight-length relationship (Figure 8). A slope of 2.89

demonstrates that perch become slightly lighter as they get older.

Condition varied among age categories, but not consistently across all dates. The

condition factor for age 0+ Sacramento perch was less than for older fish in January,

April and June 2002 (Table 5). Mean condition factor for age 0+ Sacramento perch

during these dates ranged from 0.75 to 0.96. Average condition factors for age 0+ on

other dates, and for older fish on all dates tended to be slightly more than 1.0 (Table 5,

Figure 9).

Diet Analysis.

Stomachs from 299 Sacramento perch were analyzed. All stomachs examined

contained some food, even if only detritus.

A total of 29 different prey taxa were identified in stomach samples. These

included 15 families of aquatic insects, five families of crustaceans, two families of

leeches, snails, freshwater clams, two species of fish, and detritus (Appendix A). Each of

the three methods of diet analysis used illustrated the importance of different prey items.

Analysis of frequency of occurrence revealed several identifiable prey taxa as common in

the diet of Sacramento perch. The most frequently encountered prey taxa found in

stomachs of Sacramento perch from Abbotts Lagoon was the amphipod *Hyalella azteca*.
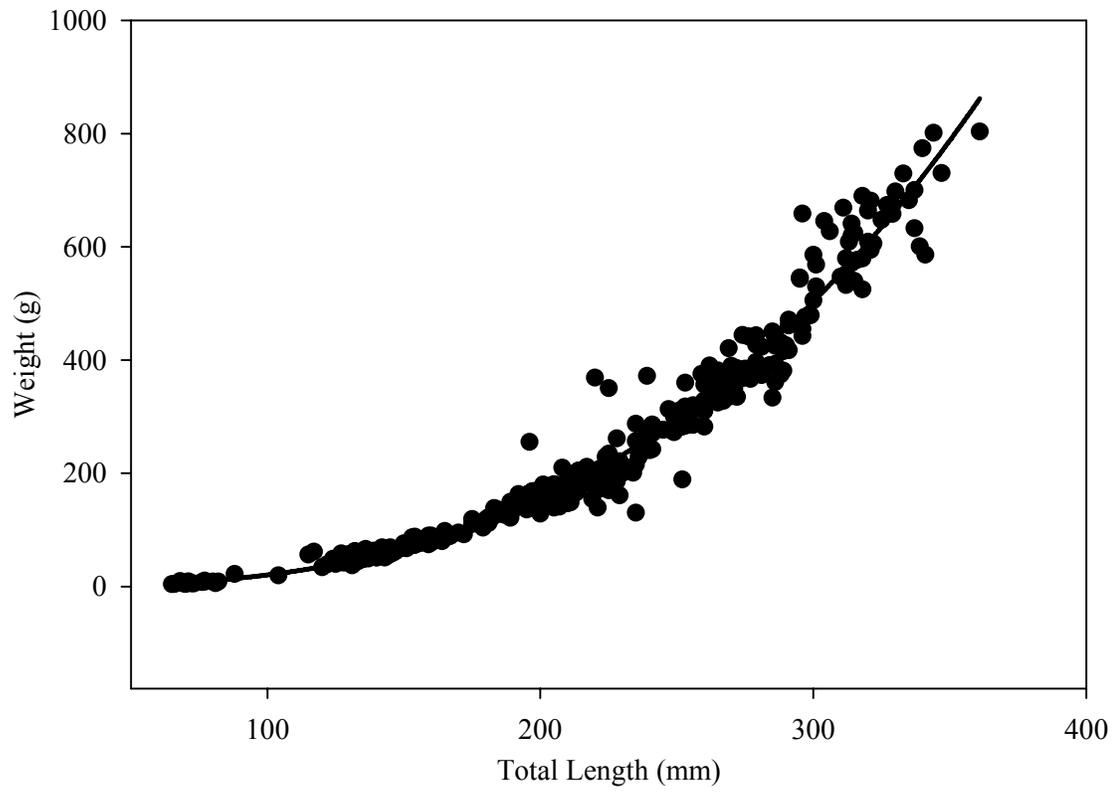
Figure 8. Weight-length relationship (W=0.00003$L^{2.0}$, r^2=0.97) for Sacramento perch in Abbotts Lagoon collected from June 2001 to June 2002 using gill nets.
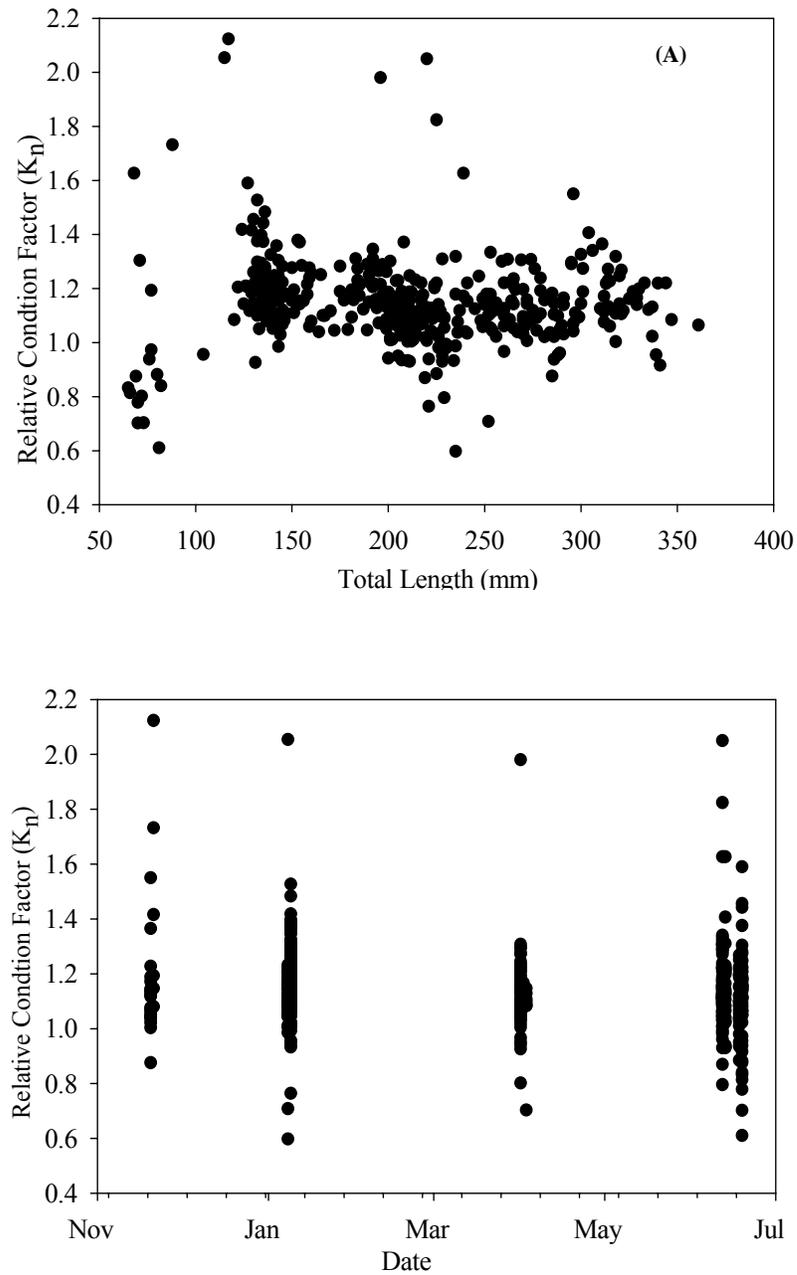
Figure 9. Relative condition factor (K_n) for Sacramento perch collected in Abbotts Lagoon collected by gill netting, (A) K_n plotted per total length (mm); K_n plotted by sample date.

Other common prey items included *Daphnia*, Chironomidae larvae and pupae, and another amphipod, *Corophium* (Table 6).

Analysis by percentage number and biomass of prey suggested that prey occurring less frequently were also important. Among the five prey taxa consumed by most Sacramento perch, *Daphnia* was consumed in the greatest numbers. Relatively large numbers of *Hyalella azteca* and Chironomidae larvae were also consumed. When percentage contribution by biomass was analyzed, Coenagrionidae was the most important prey even though they were not particularily common in stomachs and were consumed in very low numbers. *Daphnia*, *Hyallela azteca*, Erpobdellidae and Chironomidae larvae and pupae also contributed important amounts to the percent biomass consumed (Table 6).

Diet of Sacramento perch varied among lagoon basins (Table 6). Diversity of prey consumed was lowest in the lower lagoon basin, but few samples were available to analyze. Of the six prey items identified in stomachs from the lower lagoon basin, Mysidae occurred most frequently in stomachs and were the most important prey by number. However, three prey (fish, *Corophium*, and Sphaeromatidae) made up 84.5% of the biomass.

The diet of Sacramento perch was more diverse in the middle lagoon basin than in other basins. Six prey species occurred in more than 49.5% of the stomachs examined (Table 7). *Daphnia* and *Hyalella azteca* were consumed by the majority of perch in the middle lagoon basin. Other common prey included Coenagrionidae, *Corophium*, and

Table 6. Major prey of Sacramento perch in Abbotts Lagoon, Point Reyes National Seashore. Prey items were collected in June, November 2001, and January, April, and June 2002.

Prey Item	Lower Lagoon Basin			Middle Lagoon Basin			Upper Lagoon Basin		
	% Occurrence	% Number	% Weight	% Occurrence	% Number	% Weight	% Occurrence	% Number	% Weight
Hyallela azteca	25.0	0.6	5.0	73.2	18.3	18.2	49.6	29.3	15.6
Chironomidae larvae	0.0	0.0	0.0	52.5	5.2	5.9	74.0	20.6	9.0
Chironomidae pupae	0.0	0.0	0.0	49.5	5.5	6.2	57.0	6.2	6.1
Mysidae	87.5	82.1	4.7	22.2	1.2	0.0	5.4	0.5	0.0
Daphnia	0.0	0.0	0.0	78.3	57.0	25.1	28.0	19.6	7.9
Coenagrionidae	0.0	0.0	0.0	66.3	1.5	25.0	25.8	1.4	17.5
Corophium	25.0	0.7	28.4	53.0	5.5	5.5	2.2	0.2	0.0
Copepoda	0.0	0.0	0.0	19.2	1.6	0.1	34.4	7.3	0.9
Erpobdellidae	0.0	0.0	0.0	8.6	1.5	2.9	37.6	8.8	16.3
Fish	37.5	--	31.3	1.0	--	0.5	1.1	--	0.0
Sphaeromatidae	12.5	12.5	24.8	10.6	0.2	0.2	1.1	0.0	0.0
Asellidae	0.0	0.0	0.0	1.5	0.0	0.1	19.4	3.7	2.4
Other	0.0	<u>4.1</u>	<u>5.8</u>	0.0	<u>2.5</u>	<u>10.3</u>	0.0	<u>2.4</u>	<u>24.3</u>
Total		100.0	100.0		100.0	100.0		100.0	100.0

Table 7. Percentage by weight (g) of prey consumed by six age classes of Sacramento perch in Abbotts Lagoon, Point Reyes National Seashore.

	Age					
Prey Item	0+	1+	2+	3+	4+	5+[1]
Hyalella azteca	27.6	18.8	23.9	19.1	16.9	6.5
Chironomidae larvae	18.9	9.6	5.1	3.2	4.4	11.1
Chironomidae pupae	13.6	11.8	4.3	1.2	7.9	7.0
Daphnia	15.4	6.3	21.8	27.8	24.9	29.4
Coenagrionidae	7.2	14.4	25.9	26.8	22.6	30.2
Corophium	0.0	6.1	4.8	5.4	0.0	3.6
Hirudinea	11.3	28.3	10.9	7.6	14.4	1.5
Other	6.0	4.7	3.3	8.9	8.9	10.7
Total	100.0	100.0	100.0	100.0	100.0	100.0

[1]Age 5+ included all fish ≥ 5+.

Chironomidae larvae. *Daphnia* made up over half of the individual prey consumed in this basin, with *Hyalella azteca* also consumed in relatively large numbers. Three prey *Hyalella azteca*, *Daphnia*, and Coenagrionidae) contributed 68.3% of the biomass consumed by Sacramento perch in the middle lagoon basin (Table 6).

Diet of Sacramento perch in the upper lagoon basin was also relatively diverse. *Hyalella azteca*, Chironomidae larvae and pupae occurred in over half of the stomachs examined. Numerically, *Hyalella azteca,* Chironomidae larvae and *Daphnia* were consumed in greater numbers than other prey. Three prey *(Hyalella azteca,* Coenagrionidae, and Erpobdellidae) along with other prey, made up most of the biomass consumed by fish in the upper lagoon basin (Table 6).Composition of diet varied little among age classes. Three prey, *Hyalella azteca*, *Daphnia*, and Coenagrionidae, together contributed at least 60% of the biomass consumed by four of the six age categories (Table 7). Sacramento perch did not appear to select larger prey with increasing age. Coenagrionidae, a relatively large prey, contributed most to the diet of age 2+ - 5+ Sacramento perch. However, *Daphnia*, one of the small prey, also represented more of the biomass consumed in age 2+ - 5+ Sacramento perch. In contrast Hirudinea, another large prey, contributed most to the diet of age 1+ perch.

The diet of Sacramento perch did vary with season. Seasonally, five prey were consumed most consistently, Coenagrionidae, *Daphnia, Hyalella azteca*, Chironomidae larvae and pupae (Table 7). *Daphnia* represented a greater proportion of the biomass consumed in June and November 2001 than later, while *Hyalella azteca* represented a greater proportion of the biomass consumed during January – June 2002 than earlier.

Hirudinea appeared in stomach samples in November 2001 and represented almost 25%

of the biomass consumed in January 2002.

Bioenergetics

Parameters used in the bioenergetics model were either estimated from laboratory

experiments or taken from the literature. Eleven of 17 parameter values were derived

from laboratory experiments (Table 1).   Values for specific dynamic action (SDA),

activity (ACT), proportion of consumed food egested (FA), proportion of consumed food

excreted (UA), and predator energy density were taken from literature values for bluegill

(*Lepomis macrochirus*) and smallmouth bass (*Micropterus doliemue*) (Table 1).

Consumption of goldfish (*Carassus auratus*) by Sacramento perch was estimated

as functions of water temperature and body mass, as suggested by Kitchell et al. (1977).

Data from specific consumption rate experiments at water temperatures ranging from

10^oC to 24 ^oC were fit using a three-parameter Gausian regression model:

$$\text{Specific consumption} = 0.0913^{-0.5*\left(\frac{T-19.76}{5.611}\right)^2}$$

where T = water temperature at time t and T_0 = water temperature at time 0. The

relationship between water temperature and specific consumption weight was significant

(P = 0.0005) and model r^2 was 0.778 (Figure (P = 0.0005) and model r^2 was 0.778 The

peak of this curve (20 ^oC) was interpreted as the optimum water temperature for

consumption (Figure 10). The curve was also used to select 37 ^oC as the maximum water

temperature at which consumption could occur (Figure 10).
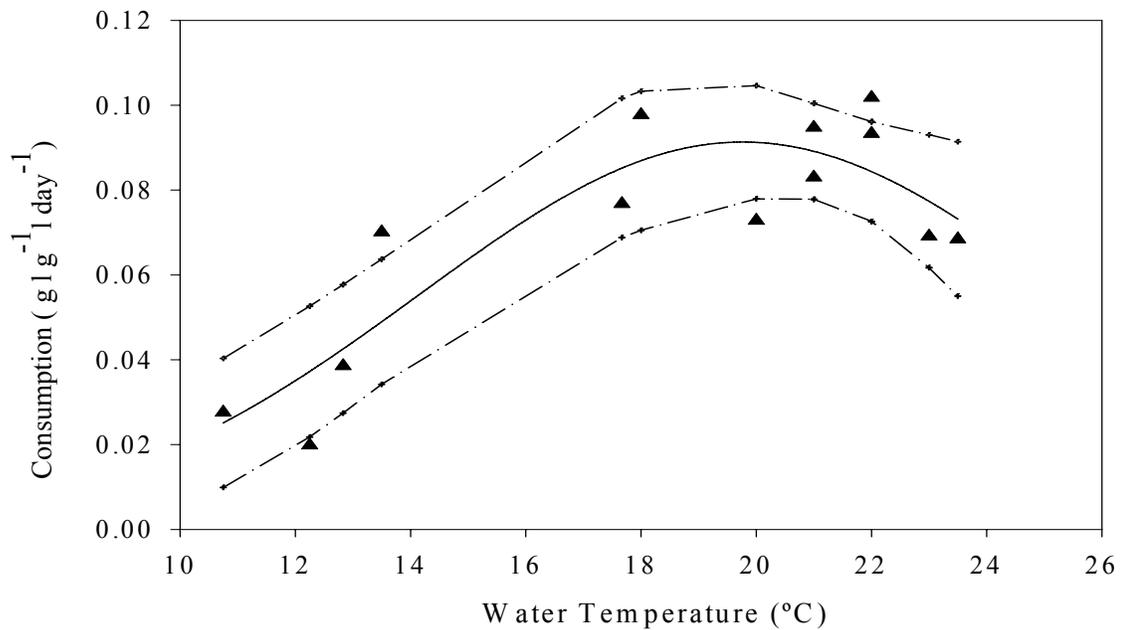
Figure 10. Relationship, with 95% confidence intervals, between consumption rate (g·g^{-1}·day^{-1}) and wet weight of Sacramento perch in Abbotts Lagoon. Optimum temperature for consumption (CTO) = 20 ºC, maximum temperature for consumption (CTM) = 37 ºC.

The peak of this curve (20 $^{\circ}$C) was interpreted as the optimum water temperature for consumption. The curve was also used to select 37 $^{\circ}$C as the maximum water temperature at which consumption could occur. The allometric equation for specific consumption rate at the optimum water temperature was:

Specific consumption $= -0.0582W^{0.2995}$

where W = wet weight (g), the r^2 for this model was 0.57. The intercept from this equation provided the CA value, while the slope provided the CB value (Table 1) for calculating a maximum consumption rate (C_{max}) following Kitchell et al. (1977) (Figure 11).

Metabolism by Sacramento perch was also estimated as functions of water temperature and body mass, as suggested by Kitchell et al. (1977).   Data from metabolism rate experiments at water temperatures ranging from 11.26 $^{\circ}$C to 24.4 $^{\circ}$C were fit using a three-parameter Gausian regression model:

Oxygen consumption rate $= 42.40^{\,-0.5*\left(\frac{T-22.25}{6.85}\right)^{2}}$

where T = water temperature at time t and T_0 = water temperature at time 0. The relationship between water temperature and specific respiration weight was not significant (P = 0.20) and model r^2 was 0.25 (Figure 12). The peak of this curve (22.3 $^{\circ}$C) was interpreted as the optimum water temperature for respiration. The curve was also used to select 31.8 $^{\circ}$C as the maximum water temperature at which respiration could occur.
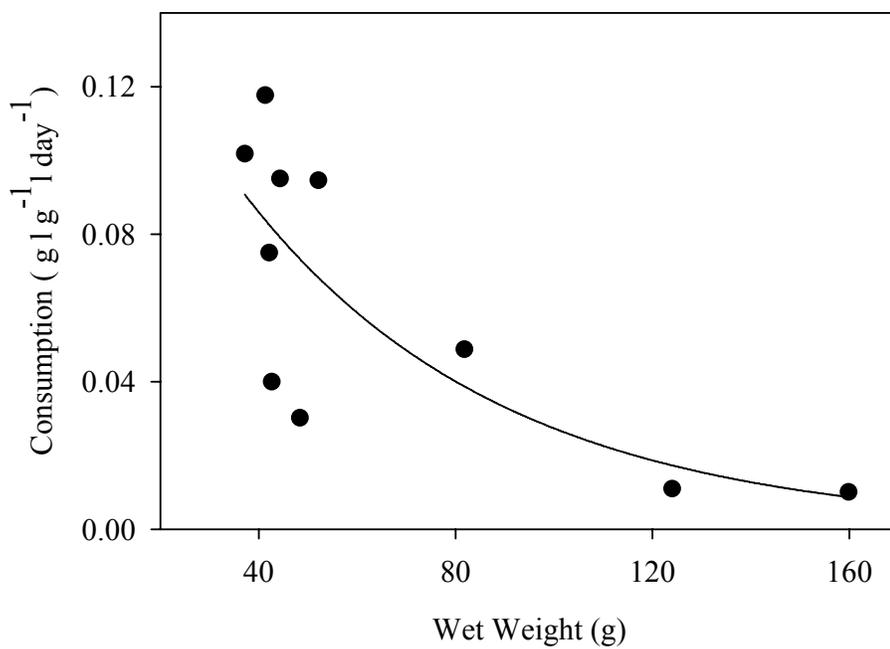
Figure 11. Relationship between consumption rate (g·g⁻¹·day⁻¹) and wet weight (g) of
Sacramento perch in Abbotts Lagoon at 20 ºC. (slope = -0.0582, intercept =
0.2995)
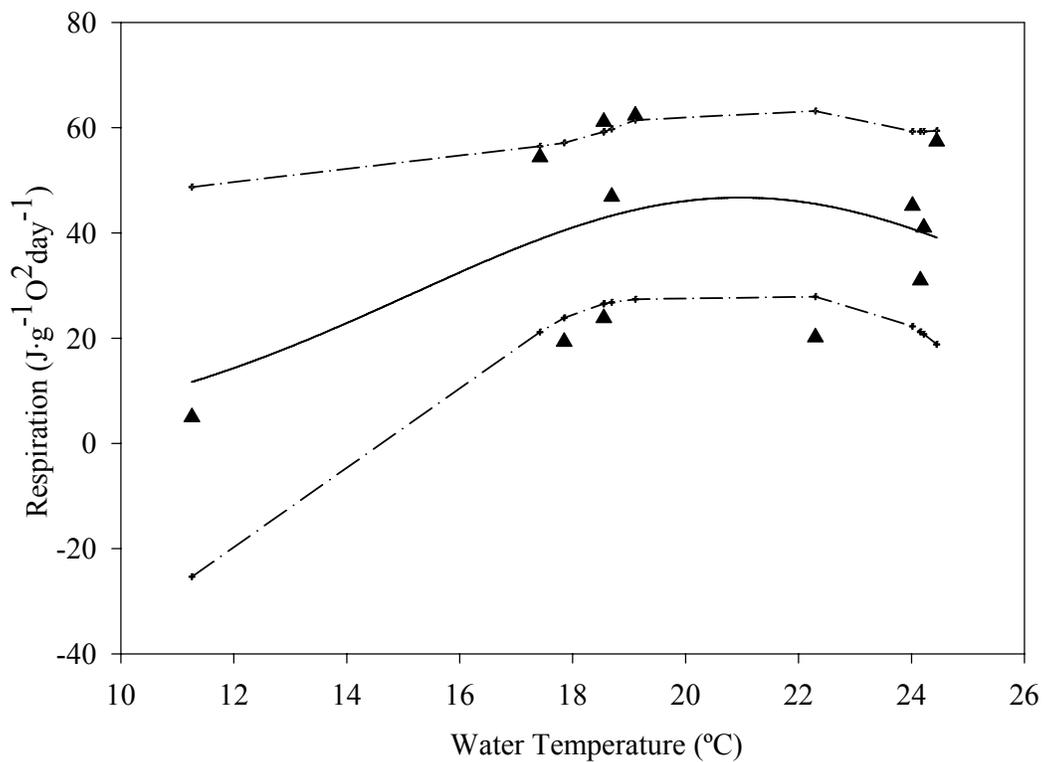
Figure 12. Relationship, with 95% confidence intervals, between respiration
        $(J \cdot g^{-1} O^2 \cdot day^{-1})$ and average water temperature (ºC) for Sacramento perch in
        Abbotts Lagoon. Optimum temperature for respiration (RTO) = 22.3 ºC;
        maximum temperature for respiration (RTM) = 31.8 ºC.

The allometric equation for metabolic rate at the optimum water temperature was:

Oxygen consumption rate $= -0.0066W^{0.005}$

where W = wet weight (g), the r^2 for this model was 0.961. The intercept from this

equation provided the RA value, while the slope provided the RB value (Table 8) for

calculating a maximum metabolic rate (R_{max}) following Kitchell et al. (1977) (Figure 13).

Model sensitivity was evaluated using individual parameter perturbation and

evaluating change in consumption resulting from changes in parameters. Model

sensitivity was less than 3% for all parameters (Table 9) The model was most sensitive

to the parameters for proportion of maximum feeding (P-value) and the optimum

temperature of the respiration equation (RTO). Sensitivity for all other parameters was

less than 1.0% (Table 9).

Specific energy consumption by Sacramento perch varied with season and age

(Figure 14). Seasonally, specific energy consumption by age 0+ fish was relatively

constant, ranging from 55 to 115 $J \cdot g^{-1} \cdot d^{-1}$ and declining only during early spring. In

older age fish, specific energy consumption declined during winter and was higher during

summer and spring. Greatest range in specific energy consumption, 40 to 140 $J \cdot g^{-1} \cdot d^{-1}$,

was observed in age 2+ fish (Figure 14). When averaged over the year, average daily

specific energy consumption declined from 91 $J \cdot g^{-1} \cdot d^{-1}$ by age 0+ fish to 81 $J \cdot g^{-1} \cdot d^{-1}$

by age 2+ fish.   Average specific energy consumption for fish aged 3+ - 5+ ranged from

65 to 67 $J \cdot g^{-1} \cdot d^{-1}$ (Figure 14).

Specific growth rates ($J \cdot g^{-1} \cdot d^{-1}$) also varied with season and age of fish.

Specific growth rates of age 0+ and 1+ were generally less variable seasonally than in

Table 8. Percentage by weight of prey consumed by Sacramento perch in Abbotts Lagoon, Point Reyes National Seashore.

	Date				
Prey Item	11-13 June 2001	19-21 Nov. 2001	7-9 Jan. 2002	1-3 Apr. 2002	16-18 June 2002
Hyalella azteca	6.5	5.0	23.2	11.6	20.3
Chironomidae larvae	8.4	9.9	4.5	1.9	6.7
Chironomidae pupae	12.8	1.2	0.7	2.1	11.9
Daphnia	29.8	34.4	5.2	16.3	9.9
Coenagrionidae	20.6	11.1	19.3	26.7	3.5
Corophium	0.2	0.8	2.1	6.4	6.9
Hirudinea	0.0	4.0	23.8	8.8	0.3
Other	21.7	33.6	21.2	26.2	40.5
Total	100.0	100.0	100.0	100.0	100.0
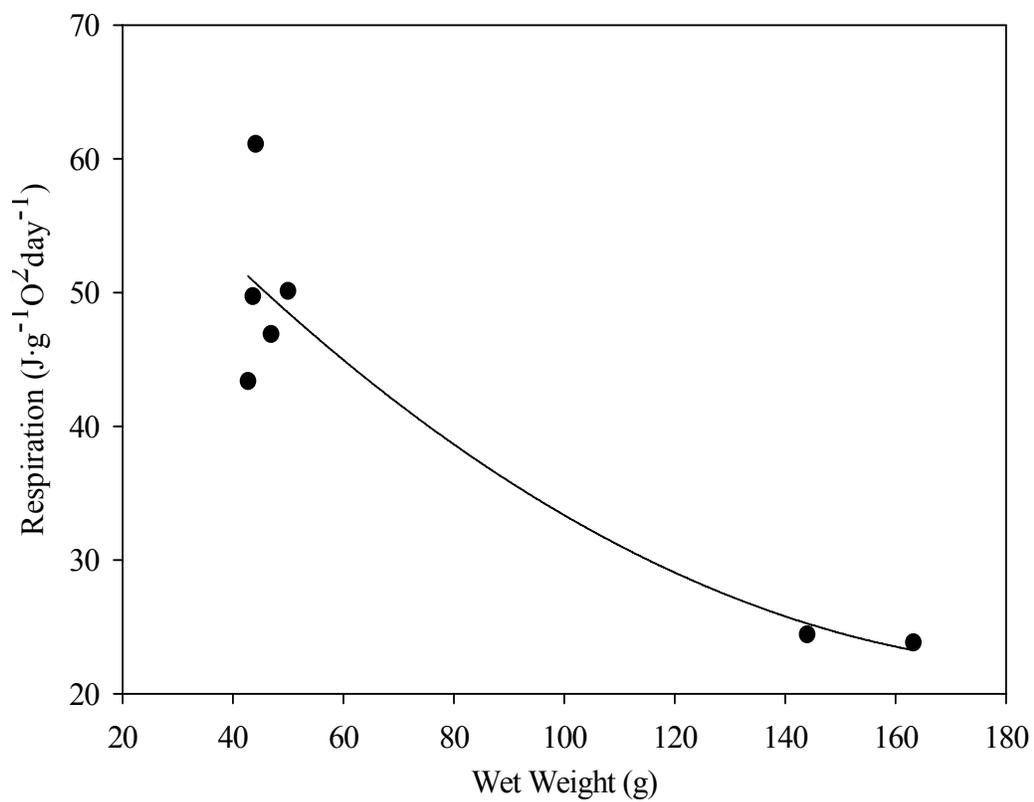
Figure 13. Relationship between respiration (J·g⁻¹O²·day⁻¹) and wet weight (g) of Sacramento perch in Abbotts Lagoon at 20ºC. (slope = -0.0066, intercept = 0.005).

Table 9. Sensitivity analysis of age 2+ Sacramento perch bioenergetics model parameter estimates of final consumption (g). Values shown are percent change from nominal values after perturbations of +/- 10%.

	Consumption (g)	
Parameter	+10%	-10%
Consumption		
CA	0	0
CB	0.0215	0.0215
CQ	0.0828	0.0826
CTO	0.2601	0.2659
CTM	-0.0168	-0.0201
Respiration		
RA	0.4835	0.5068
RB	-0.0175	-0.0176
RQ	-0.3190	-0.3691
RTO	-1.4332	-1.5061
RTM	0.0649	0.0341
ACT	0.3984	0.5585
SDA	0.2188	0.2099
Egestion/ Excretion		
FA	0.1912	0.1842
UA	0.0315	0.0315
Start Weight	0.1936	0.1994
End Weight	0.7906	0.8037
P-Value	3.446	2.5816
Spawning	0.0194	0.0193
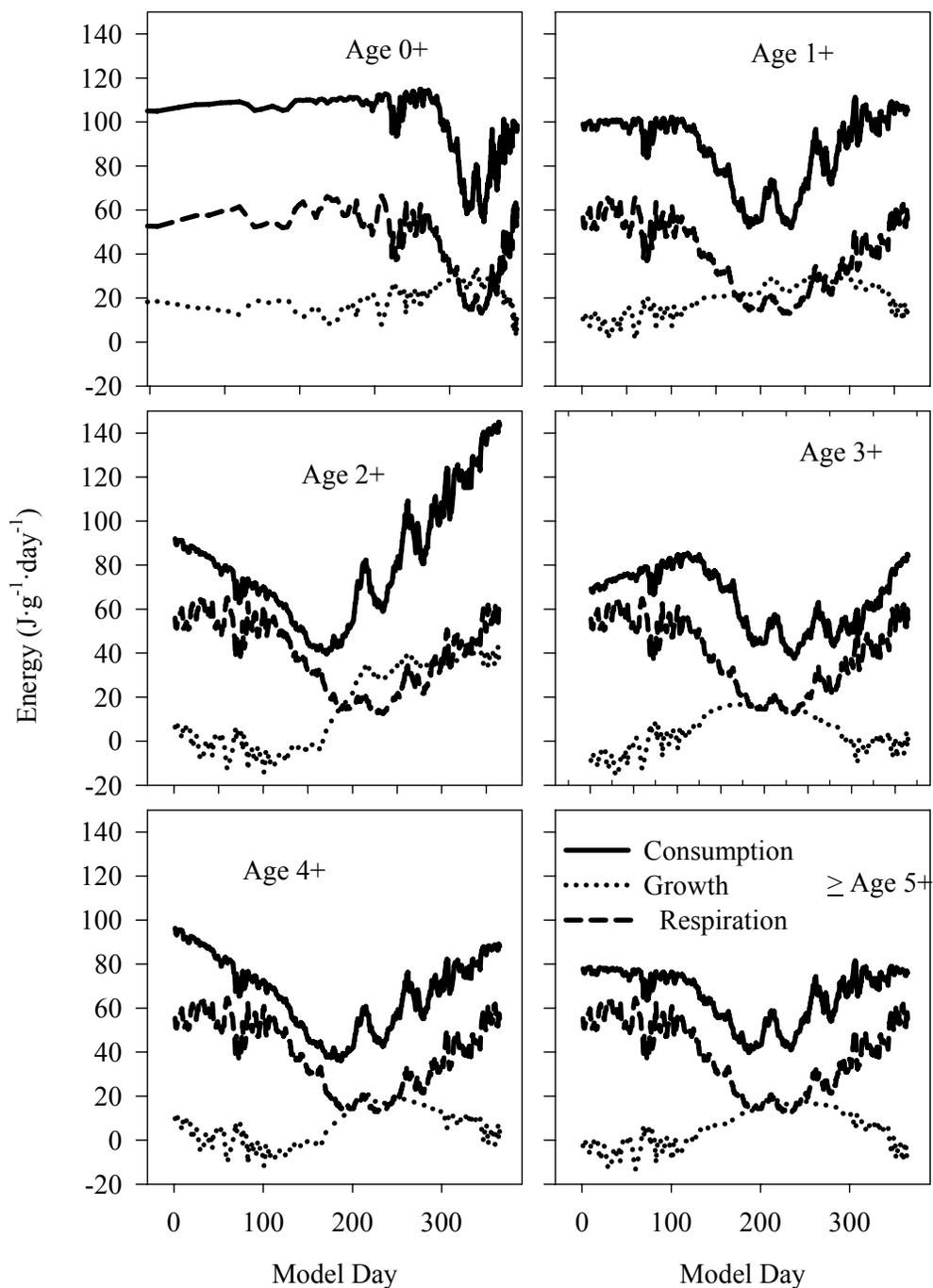
Figure 14. Division of the major components of the energy budget to consumption, growth and respiration produced from bioenergetics modeling for each age class of Sacramento perch in Abbotts Lagoon. Model days are from 12 June 2001 to 11 June 2002.

older fish, ranging from 4 to 33 $J \cdot g^{-1} \cdot d^{-1}$ in age 0+ and from 1 to 31 $J \cdot g^{-1} \cdot d^{-1}$ in age

1+ . Sacramento perch age 2+ – 5+ exhibited a period of negative specific growth during

summer. Seasonal, specific growth of age 2+ Sacramento was most variable, ranging

from -14 – 43 $J \cdot g^{-1} \cdot d^{-1}$ (Figure 14). Specific growth of age 3+ fish ranged from -15 to

18 $J \cdot g^{-1} \cdot d^{-1}$, while in age 4+ fish it ranged from -12 to 21 $J \cdot g^{-1} \cdot d^{-1}$ and in age 5+ it

ranged from -13 to 20 $J \cdot g^{-1} \cdot d^{-1}$. When averaged over the year, specific growth was

relatively high in Sacramento perch aged 0+ (22 $J \cdot g^{-1} \cdot d^{-1}$), aged 1+ (20 $J \cdot g^{-1} \cdot d^{-1}$) and

aged 2+ (16 $J \cdot g^{-1} \cdot d^{-1}$). Annual average specific growth in older Sacramento perch

ranged from 5 – 7 $J \cdot g^{-1} \cdot d^{-1}$.

Respiration rates varied seasonally, but were more consistent among age classes

of Sacramento perch than either specific consumption or specific growth. Seasonally,

respiration rates were highest in July and August 2001 and lowest in late December 2001

and late January 2002, ranging from 12 – 66 $J \cdot g^{-1} \cdot d^{-1}$ among all ages. The annual

average respiration rate was 16 $J \cdot g^{-1} \cdot d^{-1}$ in each age class of Sacramento perch (Figure

15).

Food Web Influence

I used the bioenergetics model to simulate consumption by and growth of

Sacramento perch in Abbotts Lagoon. The model simulation began on 8 June 2001 and

ended on 7 June 2002. Numbers of fish in each age cohort were estimated by multiplying

numbers predicted from the catch curve by 10.
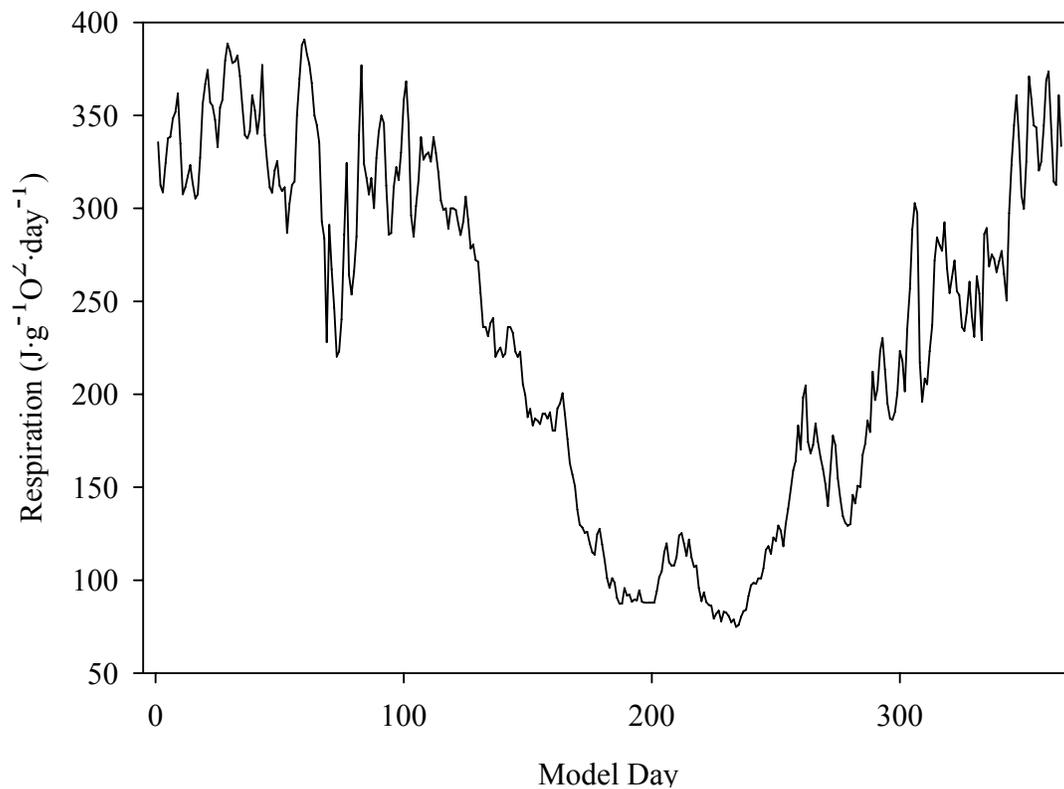
Figure 15. Respiration (J·g^{-1}O^{2}·day^{-1}) for all age classes of Sacramento perch in Abbotts
Lagoon. Model days are from 12 June 2001 to 11 June 2002.

Therefore, population numbers used in the model are theoretical and intended only to provide a relative forecast of consumption by Sacramento perch.

Six prey taxa or categories contributed most of the biomass to the diets of each age class. These taxa included Chironomidae larvae and pupae combined, *Hyalella azteca*, *Daphnia*, Coenagrionidae, Hirudinia and Copepoda. All other prey taxa were combined into an "other prey" category. Modeled prey consumption varied among age classes of Sacramento perch and among seasons. Copepoda were consumed only by age 0+ fish and were the most important prey of age 0+ fish, particularly during spring (Figure 16). Copepoda made up 38% of the prey mass ingested by age 0+ fish throughout the year. Chironomidae were the most important prey of age 1+ fish making up 42% of the prey mass ingested during the year (Figure 16). Hirudinea, Coenagrionidae and *Hyalella azteca* made up an increasing proportion of the mass consumed by age 1+ fish during winter, while *H. azteca* continued to be an important prey during spring.

Prey mass consumed by fish older than 1+ consisted primarily of *Daphnia* and Coenagrionidae. Together, these taxa represented more than half of the prey mass consumed by fish aged 2+ to 5+ (Figures 17, 18). Age 2+ and 3+ fish consumed increased amounts of *H. azteca* during spring, while *H. azteca* was important in the diet of age 4+ fish during summer (Figure 18). Chironomidae were an important prey for age 2+ 4+ and 5+ fish during spring, but were not as commonly eaten by age 3+ fish (Figures 17, 18). Hirudinea were consumed by age 3+ fish throughout the year, but less so in
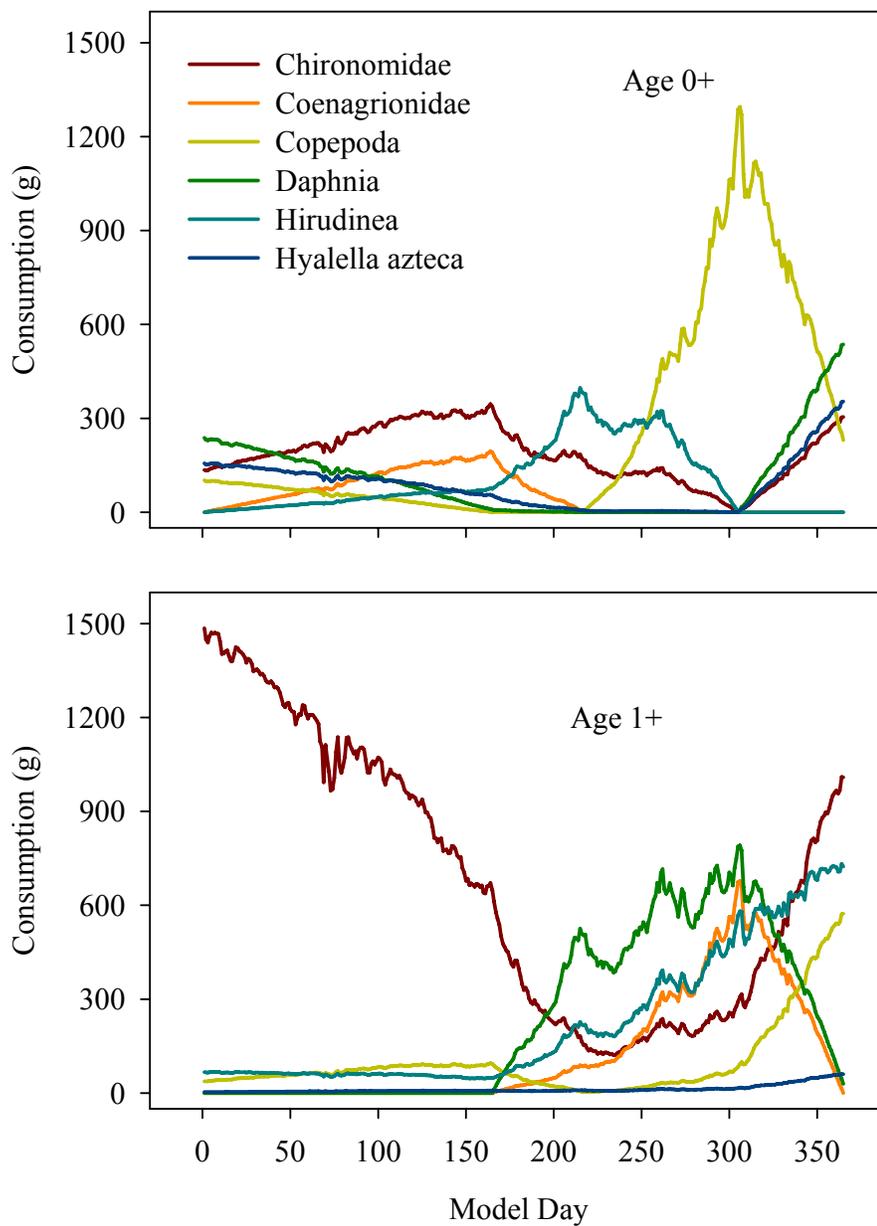
Figure 16. Bioenergetics model output of prey consumption by ages 0+ and 1+ Sacramento perch in Abbotts Lagoon. Model days are from 12 June 2001 to 11 June 2002.

Figure 17. Bioenergetics model output of prey consumption by ages 2+ and 3+ Sacramento perch in Abbotts Lagoon. Model days are from 12 June 2001 to 11 June 2002.
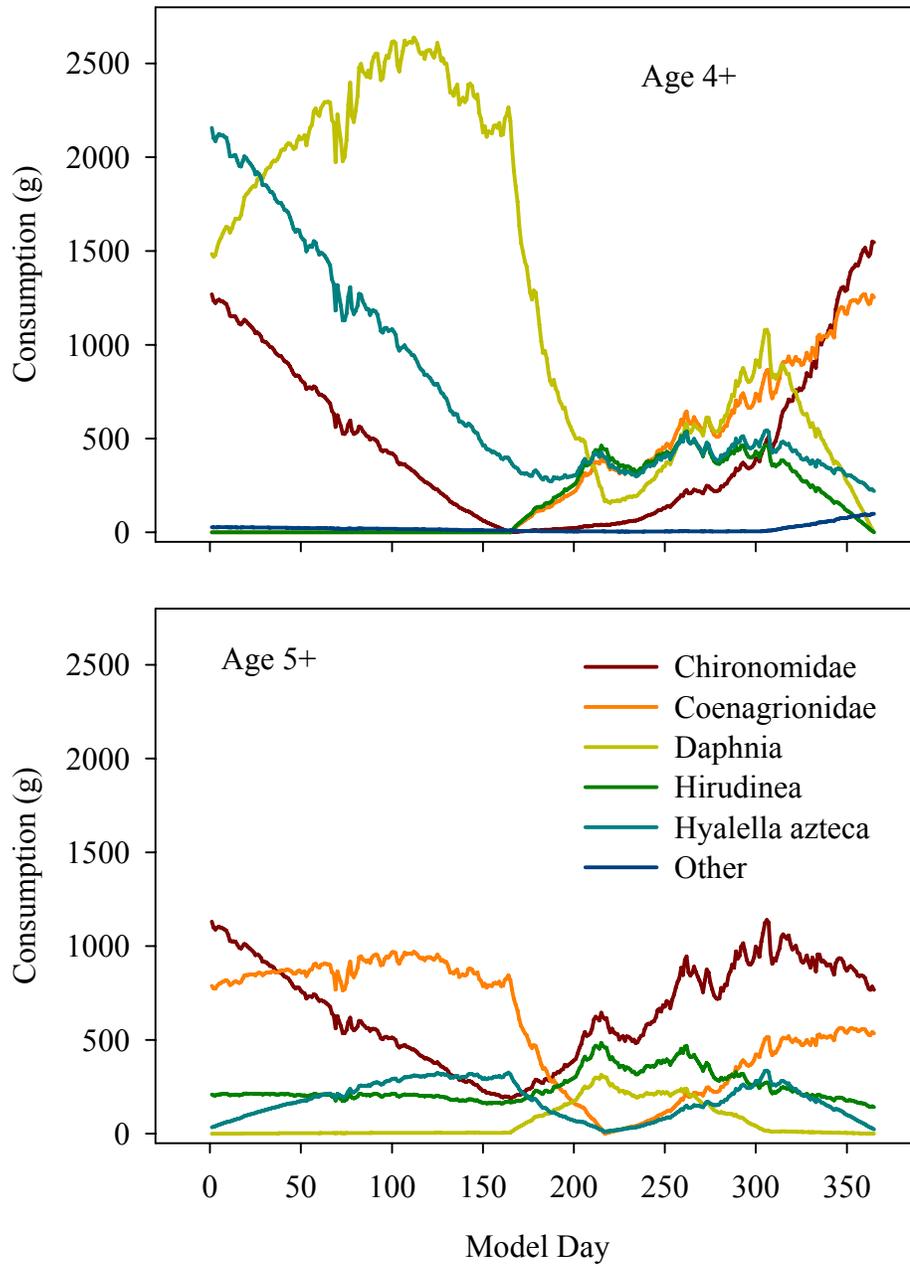
Figure 18. Bioenergetic model output of prey consumption (g) by ages 4+ and 5+ Sacramento perch in Abbots Lagoon. Model days are from 12 June 2001 to 11 June 2002.

spring. In contrast, age 4+ and 5+ fish consumed more Hirudinea in spring than during other seasons (Figures 17, 18).

Specific consumption rates expanded to the population by age structure illustrate how different age classes of Sarcamento perch might influence the food webs of the three lagoon sub-basins. Age 1+ Sacramento perch consumed more prey than any other age class (Figure 19). Throughout the year, average biomass of prey consumed by age 1+ Sacramento perch among all basins was predominantly Chironomidae (Figure 20).

In the middle lagoon basin, age 0+ and 1+ Sacramento perch consumed less than all other age classes, while age 2+ and 3+ fish consumed more prey than other ages, particularly in spring 2002 (Figure 19). Among prey taxa, age 2+ Sacramento perch consumed more *Daphnia* than any other prey, while age 3+ fish consumed more Coenagrionidae and *Daphnia* (Figure 20). Only age 5+ Sacramento perch were found in the lower lagoon sub-basin (Figure 19). Age 5+ Sacramento perch consumed far more Coenagrionidae than other prey taxa (Figure 20).
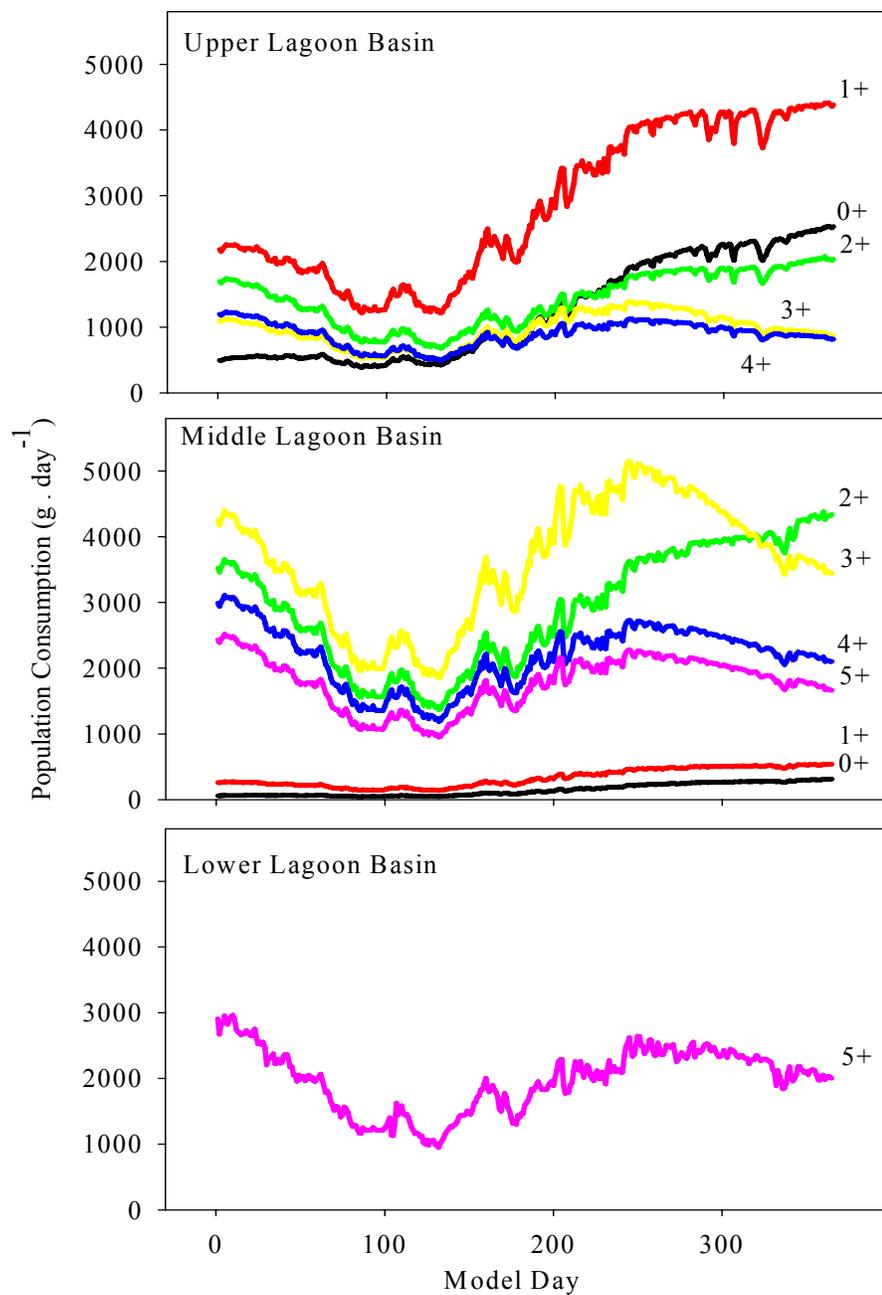
Figure 19. Bioenergetic model output of population consumption (g·day^{-1}) for each age class of Sacramento perch in each basin of Abbotts Lagoon. Model days are from 12 June 2001 to 11 June 2002.
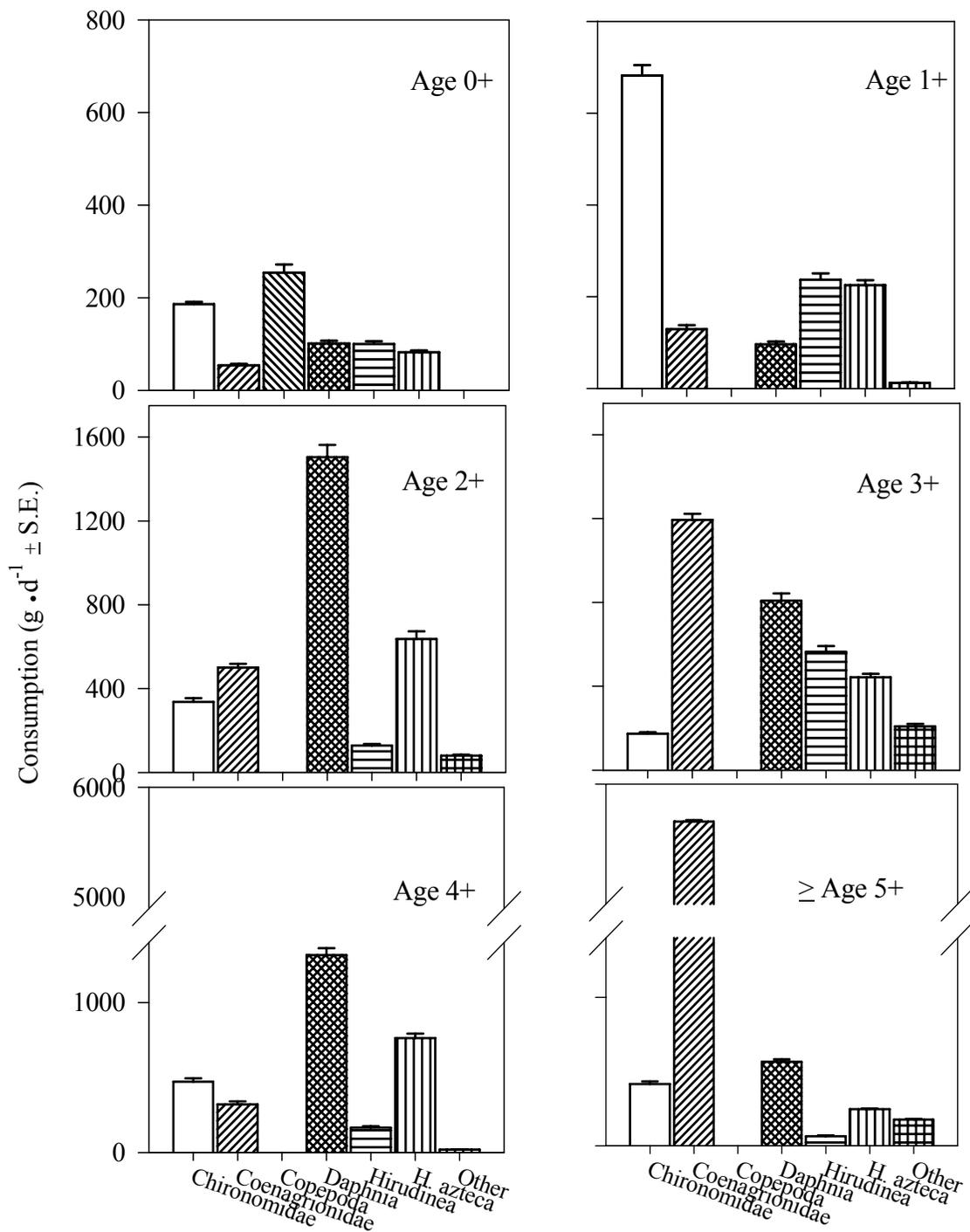
Figure 20. Bioenergetics model output of average population consumption (g·day^{-1}) by each age class of Sacramento perch in Abbotts Lagoon.

DISCUSSION

Findings from this study improve our understanding of the bioenergetics and trophic ecology of the Sacramento perch in Abbotts Lagoon. Since little is known about the ecology and population status of perch in California, this study also contributes information that may prove useful in maintaining the current status of the species.

I found that Sacramento perch and Pacific herring were the predominant species in the fish community of Abbotts Lagoon. This corroborates the work of Saiki and Martin (2001). The relative abundance of other species collected in this study differ from relative abundances reported by Saiki and Martin (2001) Whereas, I caught very few three-spine stickleback, Saiki and Martin (2001) found an abundance of three-spine stickleback in the lower basin. I also encountered no Pacific herring in the middle basin or during June 2002, Saiki and Martin (2001) found Pacific herring common at two sites in the middle basin and during every sampling event using the same gill nets. I also did not encounter silver surfperch (*Hyperprosopon ellipticum*), striped bass (*Morone saxatilis*), or longfin smelt (*Spirinchus thaleichthys*) during my sampling. A number of factors may be responsible for differences in the catch of less abundant fish species in this study with catches reported by Saiki and Martin (2001). Foremost among these is gear. Saiki and Martin (2001) sampled with both gill nets and minnow traps while I

employed only gill nets. Other factors affecting the differences in catch between my sampling and Saiki and Martin (2001) may include the lagoon breach, gillnet set site selection, and the selective nature of gill nets.

While Saiki and Martin (2001) encountered 35 largemouth bass in gillnets during sampling, I collected only 14 largemouth bass during sampling. None were young-of-the-year and only one was a juvenile. Saiki and Martin (2001) collected 35 largemouth bass during their studies. Low numbers collected and rarity of juvenile largemouth bass in my study suggests population size is low and recruitment is inconsistent or often fails. Largemouth bass are not as adaptable to high salinity and alkalinity as Sacramento perch (Moyle 2002) and may not have the ability to exploit Abbotts Lagoon, as they have in lakes and impoundments. This is likely to be an important factor in the continued success of the perch population in Abbotts Lagoon. Sacramento perch have been shown to do quite poorly when introduced to habitats occupied by other Centrarchids (Moyle 2002). Thus, the relative success of the perch population in Abbotts Lagoon appears to be related to the simple fish community. The introduction of another Centrarchid species, or an increase in the largemouth bass population could lead to a decline in perch (Aceituno and Nicola 1976, Moyle 2002).

Distribution of Sacramento perch among the lagoon basins appears to be related to habitat choice, as well as prey availability. Perch primarily occupied the middle and upper basins of Abbotts Lagoon, (Saiki and Martin 2001). A lagoon breach in the lower basin during January 2002 caused a steep increase in salinity and conductivity in the lower basin, and also led to a drop in water level. The following April, this influx of salt

water led to a salinity chemocline with high salinities at depths above 3 m in the lower

basin. Although perch are a euryhaline species, fluctuating and increased salinity in the

lower basin may limit their ability to occupy this portion of the lagoon. The primary

reason for the lack of perch in the lower basin, however, was likely the prey base.

Salinity in the lower basin was probably high enough to exclude the majority of

important prey items to perch, such as *Hyalella azteca, Daphnia,* and Coenagrionidae,

which are freshwater invertebrates (Merrit and Cummins 1996). Food resources in the

lower basin consisted mainly of *Mysis* shrimp, *Corophium*, and fish. Although these prey

resources were observed in high density during parts of the year, they may have limited

the age and size of perch that could successfully occupy this basin to older and larger

individuals.

The lagoon breach also resulted in a drop in water level that created a cascade

between the lower and middle basins, effectively creating a barrier to fish movement and

offering another explanation for distribution of Sacramento perch among the three lagoon

basins. Depth of the upper lagoon was the shallowest and most uniform of the three

basins. Depth of the upper basin also appears to have decreased somewhat in recent

years, from an average of 2.0 m reported by Saiki and Martin (2001) to 1.8 m in this

study. Filling of this basin as a result of agricultural runoff has been a concern of the

National Park Service.

Moyle (2002) found that in moderately clear water, such as the conditions found

in Abbotts Lagoon, perch often associated themselves with patches of aquatic vegetation.

Habitat of the lower basin was nearly devoid of vegetation except near the connection to

the middle basin. In addition, the west side of the lower basin was a shallow mud flat, with steep and rocky walls along the east side. In contrast, the upper basin of the lagoon had dense growths of aquatic vegetation, including large mats of water lettuce (*Pistia stratiotes*) floating on the surface (personal observation). The middle basin contained patches of aquatic vegetation near shore and in shallow areas, and mats of water lettuce also covered part of the basin.

Size groups of Sacramento perch in Abbotts Lagoon were segregated among the three basins. Generally, smaller perch were found in the upper basin, mid-sized perch in the middle basin, and only larger age 5+ perch were captured in the lower basin. The middle basin may not offer enough cover to smaller perch to facilitate rearing because it contains areas of deep water and has less vegetation than the upper basin. However, I did observe spawning in the shallower, weedier sections of the middle basin during June 2001, which may indicate this basin contains important spawning habitat. It appears that perch rear in the upper basin, move into the middle basin when older, perhaps for food or spawning habitat, and will occasionally occupy the lower basin then they are energetically able to exploit the prey base occurring there.

Eight prey were identified as being most important in the diet of Sacramento perch. Three, *Hyalella azteca, Daphnia*, and Coenagrionidae (a damselfly nymph) were important across all age classes and throughout the year. A decrease in consumption of *Daphnia* during January 2002 is not a surprising result, as *Daphnia* populations are well know to exhibit seasonal shifts in population size. What is less clear is whether increased consumption of other prey at this time, including Hirudinea and *Hyalella azteca*, is the

result of an increase in the population size of these prey, or a shift in diet to another prey because *Daphnia* populations are low. Consumption of zooplankton should reflect seasonal shifts in zooplankton populations (Boldt and Haldorson 200), but these shifts were not distinct in this study.

Results of the diet analysis are not typical of a known piscivorous species like Sacramento perch. Diet of young-of-the-year perch consisted mainly of the amphipod *Hyalella azteca* and Chironomid larvae and pupae. Although *Daphnia* occurred in a large number of young-of-the-year stomach samples, *Daphnia* did not make up a large part of the biomass they consumed. Conversely, *Daphnia* became a more important prey in the diet of larger and older perch. This was also true of the damselfly nymph Coenagrionidae. Moyle (1974) described perch as a top predator in their native habitat. Larger perch moved away from feeding on small crustaceans like *Daphnia*, to feeding on larger aquatic insects and fish (Moyle 1974).

The lack of piscivory in Abbotts Lagoon is unusual. There appears to be plenty of opportunity for piscivory. Large schools of Pacific herring were encountered in both this study and in the survey conducted by Saiki and Martin (2001). Saiki and Martin (2001) captured sizeable numbers of threespine stickleback, and I observed large numbers of young-of-the-year Sacramento perch and possibly largemouth bass in the middle and lower basins during July 2001. Perhaps foraging on smaller prey is an opportunistic feeding behavior. In laboratory experiments Sacramento perch have been shown to eat the least energetically costly prey (Vinyard 1982). Fish may be more energetically costly

for large perch to catch than are the smaller, more abundant, prey like *Daphnia* and

Hyallela azteca.

Algal blooms observed in Abbotts Lagoon during recent years are thought to be

caused by agricultural runoff. The highly zooplanktivorous population of Sacramento

perch in Abbotts Lagoon may also be a contributing factor to these algal blooms.

Biomanipulation studies have shown a top-down effect in food webs caused by

planktivorous fish. When planktivorous fish are removed or depleted from the food web,

the composition of zooplankton will shift from smaller sized individuals to larger ones,

which are more efficient grazers (Tolonen et. al. 2000) and could lead to a decrease in

algal biomass.

Age 2+ Sacramento perch in the upper basin consumed the most, followed closely

by age 1+. This is contrary to other investigators who most often note that young-of-the-

year are the largest population level consumers (Kraft 1992). My findings may be the

result gill-net selectivity for age 1+ and larger perch, which in turn may have led to

overemphasing the importance of age 2+ perch.

Age and size distribution of Sacramento perch in Abbotts Lagoon in 2001 and

2002 was similar to the size distribution reported by Saiki and Martin (2001). Age 2+

perch made up a similar proportion of the total perch collected during both my study and

for Saiki and Martin (2001). However, I found that the proportion of age 1+ perch in the

population was greater, while the proportion of age 3+, 4+ and 5+ perch was lower than

Saiki and Martin (2001) reported. Low rates of capture by the gillnets of ages 0+ and 1+

Sacramento perch, however, make comparison of difficult.

Since population estimation was not a primary objective of this study, I could not draw conclusions about absolute abundance of Sacramento perch in Abbotts Lagoon. Relative abundance appeared to be high and consistent with numbers encountered by Saiki and Martin (2001). However, distribution of length frequency from catches demonstrated the selective nature of the gill nets. I collected very low numbers of young-of-the-year and juvenile perch, with perch becoming vulnerable to the gill nets at about age 2+. Smaller mesh sizes were quite visible in the water and most likely led to the low catch of juvenile perch (Hamley 1975). Although length-frequency is an established method for assigning age classes (Bagenal and Tesch 1978), it is prone to subjectivity (Campana 2001) and, as was the case with this study, assigning ages if often difficult in older fish. Although I did attempt to correct for these biases by obtaining scale samples from a sub-sample of perch, assigning ages to fish older that 3+ was difficult. Other methods could improve age classification for perch in Abbotts Lagoon, although they were beyond the scope of this study. Aging fish from otoliths is often used when scales are difficult to read. This method does, however, require sacrificing fish for otolith collection. Another method that could prove useful is power analysis of length frequency histograms. Improving age classifications of perch will not only increase the robustness of the model, but will also provide a greater understanding of the population dynamics of perch in Abbotts Lagoon.

I estimated mortality of Sacramento perch from a simple catch curve. Catch curve estimates of mortality rely on several assumptions; survival rate is uniform with ages, the population is sampled randomly, and recruitment is constant each year (Allen

1997). I believe my sampling design met the assumption of random sampling. However, the number of Sacramento perch I collected was not large enough to discern uniformity of survival within age classes. In addition I sampled the population for only 13 months, thus I could not assess the constancy of recruitment (Ricker 1975). Including another year of sampling with gill nets, in addition to the data collected by myself and Saiki and Martin (2001) would provide useful information about whether the catch curve assumptions are being met. Allen (1997) stated that sampling without an idea of past recruitment could lead to a biased mortality estimate because with shorter-lived fish, such as perch, the regression line may be derived from as few as three points (as was the case with this study). However, Allen (1997) did suggest that catch curve analysis on shorter-lived fish would likely approximate annual survival rate (from which mortality can be derived) to within $\pm$ 10%, which is adequate for this study. Revisiting Abbotts Lagoon with an intention of collecting abundance and mortality estimates will improve the population portion of the bioenergetics models, and would be a fairly simple and informative study.

Increases in water temperature of Abbotts Lagoon could have deleterious effects on the perch population. Although my laboratory studies found maximum temperatures for metabolism above the temperatures recorded for Abbotts Lagoon, model results show high temperatures to be stressing perch, contrary to field reports by Moyle (2002). Water temperatures in Abbotts Lagoon never reach the optimum temperatures I found for maximum consumption or respiration, which may explain the lowered respiration rates,

consumption rates and growth rates predicted by the model. This point is validated further by noting increased consumption and respiration rates at higher temperatures.

I found that growth rates varied with age, but were generally higher in winter than in summer. Seasonal differences in growth rates were most pronounced in age 2+ and older Sacramento perch. Growth of these older age classes was greater in winter than in summer. This seasonal pattern was the result of respiration rates declining during winter and making more energy available for growth, even though consumption decreased during winter. Age 2+ perch were the only age class to display higher growth rates from winter through spring and into June 2002. This period of increased growth rate corresponded with a shift in diet of age 2+ perch from *Daphnia* to *Hyalella azteca*.

Stunted populations of Sacramento perch often occur when temperatures are low and there is no large prey (Moyle 2002). However, the perch population in Abbotts Lagoon does not appear to be stunted, despite low growth during the summer months, and low temperatures. He et al. (1993) found that when larger largemouth bass did not switch from smaller prey to larger prey, such as fish, they exhibited lower growth rates than largemouth bass that did make the ontogenetic switch to larger prey. Diet analysis and the bioenergetics model suggest larger perch, ages 4+ and 5+, rely on relatively smaller prey such as Chironomidae and *Daphnia*, instead of larger prey. Drawing conclusions about growth rates from prey size is difficult, because abundance and availability of smaller prey may provide more energy than larger prey if the latter are less abundant or energetically costly to capture. Bosclair and Leggett (1989) concluded that

factors other than food consumption, such as respiration, play a role in growth rate differences within and among populations.

Bioenergetics model parameters I estimated for Sacramento perch are similar to those published for bluegill (*Lepomis macrochirus*) and smallmouth bass (*Micropterus dolomieu*) (Hansen et al. 1997). Exceptions include CB, CTO, RB, and RTO. Agreement of perch model parameters with other closely related species of Centrarchidae lends credibility to the laboratory derived model parameters. Parameters lacking agreement, the slopes and optimum temperatures for consumption and respiration, likely indicate areas for future model improvement. The allometric mass functions I obtained for these equations were developed from relatively few observations. Furthermore, I did not measure either consumption or respiration at temperatures warmer than 26 ^{o}C. Increasing replicates in the laboratory and extending the range of temperatures examined would, presumably, improve these allometric mass functions.

Bioenergetic models are only as good as the data collected to create them, and inconsistencies are only made worse when data are extrapolated to the population level (Essington 2003). Sensitivity analysis for age 2+ Sacramento perch showed the model to be generally robust for all parameters, with sensitivity greatest for respiration parameters, start weight, end weight and p-value. With the exception of p-value, the above mentioned parameters were also identified were also identified as needing improvement during laboratory experiments and model building. I had difficulty obtaining constant temperatures during respiration experiments and in reaching temperatures above 26ºC. Additionally equipment used during respiration experiments, while acceptable and

unavoidable for this study, was very basic. More innovative and accurate equipment is available for measuring respiration (Cech 1990), and reproducing the respiration experiments using the improved equipment may increase the robustness of the model.

Besides the above mentioned improvements, model sensitivity should be tested at the population level, and perhaps for each age class of Sacramento perch. Essington (2003) identified differences in sensitivity for models applied at the individual level and at the population level for skip-jack tuna (*Kastuwonus pelamis*). These differences also demonstrated themselves in Essington's (2003) model, where reproductive costs became less important in the population-level model than in individuals.

Testing the validity of a bioenergetics model is important for creating an applicable and useful model. I approached testing my model through sensitivity analysis. While this analysis identifies those model parameters most sensitive to change in environmental conditions, it does not validate the overall model. Testing the model using controlled field trials, as suggested by Boisclair and Sirois (1993) or Beauchamp et al. (1989) would help to validate model performance.

Sediment-laden agricultural runoff from dairy farms is filling in the upper basin of the lagoon (Anima 1990). This study has identified the upper basin of Abbotts Lagoon to be an important basin for juvenile Sacramento perch. Any further loss of this habitat may have detrimental effects on perch in Abbotts lagoon. The shallower water may also lead to higher temperatures in this basin, which in turn, may lead to even lower growth rates in the summer.

The National Park Service has developed a management plan to "clean up" Abbotts Lagoon to improve habitat for the endangered red-legged frog (*Rana aurora*). This plan includes decreasing the agricultural runoff to the lagoon and improving water quality. If implemented this plan will likely benefit Sacramento perch. Slowing or stopping the filling of the lagoon, especially the upper basin, would protect habitat that appears to be important habitat for young Sacramento perch. Improving water quality of the lagoon could also change the structure of the invertebrate community in Abbotts Lagoon, but is likely to favor larger bodied prey species. The bioenergetics model created for Sacramento perch will be valuable in determining the effect such a shift in diet would have on the perch.

LITERATURE CITED

Aceituno, M. E., and S. J. Nicola. 1976. Distribution and status of the Sacramento perch, *Archoplites interruptus* (Girard), in California. California Fish and Game 62:246-254.

Aceituno, M. E., and C. D. Vanicek. 1976. Life history studies of the Sacramento perch, *Archoplites interruptus* (Girard), in California. California Fish and Game 62:5-20.

Allen, M.S. 1997. Effects of variable recruitment on catch-curve analysis for crappie populations. North American Journal of Fisheries Management 17:202-205.

Anderson, R. O., and R. M. Neuman. 1996. Length, weight, and associated structural indices. Pages 447-482 *in* B.R. Murphy and D.W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Anima, R. J. 1990. Pollution studies of Drakes Estero and Abbotts Lagoon, Point Reyes National Seashore, California, USA. United States Geological Survey Open File Report 91-145. 178 pp.

Bagenal, T. B., and F. W. Tesch. 1978. Age and growth. Pages 101-118 *in* T. B. Bagenal, editor. Methods for assessment of fish production in fresh waters, 3rd edition. International Biological Programme Handbook number 3. J. B. Lippincott Company, Philadelphia, Pennsylvania.

Baldwin, C. M., D. A. Beauchamp, and J. J. Van Tassell. 2000. Bioenergetic assessment of temporal food supply and consumption demand by salmonids in the Strawberry Creek Reservoir food web. Transactions of the American Fisheries Society 129: 429-450.

Bartell, S. M., J. E. Breck, R. H. Gardner, and A. L. Brenkert. 1986. Individual parameter perturbation and error analysis of fish bioenergetic models. Canadian Journal of Fisheries and Aquatic Sciences 43:160-168.

Beamish, F. W. H. and E. A. Trippell. 1990. Heat increment: a static or dynamic dimension in bioenergetic models? American Fisheries Society 119: 649-661.

Beauchamp, D. A. 1990. Seasonal and diel food habits of rainbow trout stocked as juveniles in Lake Washington. Transactions of the American Fisheries Society 119:475-482.

Benke, A. C., A. D. Huryn, L. A. Smock, J. B. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeaster United States. The North American Benthological Society 18:308-343.

Boldt, J. L., and L. J. Haldorson. 2002. A bioenergetics approach to estimating consumption of zooplankton by juvenile pink salmon in Prince William Sound, Alaska. Alaska Fishery Bulletin 9:111-127.

Bowen, S. H. 1996. Quantitative description of the diet. Pages 513-529 *in* B.R. Murphy and D.W. Willis, editors. Fisheries Techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Boisclair, D., and P. Sirois. 1993. Testing assumptions of fish bioenergetics models by direct estimation of growth, consumption, and activity rates. Transactions of the American Fisheries Society 122:784-796.

Boisclair, D., and W.C. Leggett. 1989. Among-populaiont variability of fish growth: I. Influence of the quanitity of food consumed. Canadian Journal of Fisheries and Aquatic Sciences 46:457-467.

Campana, S.E. 2001. Accuracy, precision and quality control in age determination, including a reiview of the use and abuse of age validation methods. Journal of Fish Biology 59:197-242.

Cech, J.J. 1990. Respirometry. Pages 335-362 *in* C.B. Schreck and P.B. Moyle, editors. Methods for fish biology. American Fisheries Society, Bethesda, Maryland.

Cummins, K.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigation in ecological energetics. Internationale Vereinigung Für Theoretische und Angewandte Limnologie 18:.

DeVries, D. R. and R. V. Frie. 1996. Determination of Age and Growth. Pages 483-508 *in* B.R. Murphy and D.W. Willis, editors. Fisheries Techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Driver, E. A., L. G. Sugden, and R. J. Kovach. 1974. Calorific, chemical, and physical values of potential duck foods. Freshwater Biology 4:281-292.

Duffy, W. G. 2000. Length-mass relationship for *Hyalell azteca*. Unpublished data.

Duffy, W.G. 1998. Population dynamics, production, and prey consumption, of fathead minnows (*Pimephales promelas*) in prairie wetlands: a bioenergetics approach. Canadian Journal of Fisheries and Aquatic Sciences 54:15-27.

Essington, T.E. 2003. Development and sensitivity analysis of bioenergetics models of skipjack tuna and albacore: a comparison of alternative life histories. Transactions of the American Fisheries Society 132:759-770.

Hamley, J.M. 1975. Review of gillnet selectivity. Journal of the Fisheries Research Board of Canada 32:1943-1969.

Hansen, M.J., D. Boisclair, S.B. Brandt, S.W. Hewett, J.F. Kitchell, M.C. Lucas, and J.J. Ney. 1993. Applications of bioenergetics models to fish ecology and management: where do we go from here? Transactions of the American Fisheries Society 122:1019-1030.

Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish Bioenergetics 3.0. University of Wisconsin, Sea Grant Institute, Madison, Wisconsin.

He, X., et al. 1993. Roles of fish predation: piscivory and planktivory. Pages 85-102 *in* S. R. Carpenter and J. F. Kitchell, editors. The trophic cascade in lakes. Cambridge University Press, Cambridge, Massachusetts.

Hewett, S. W., and B. L. Johnson. 1992. Fish bioenergetics model 2: and update of a generalized bioenergetics model of fish growth for microcomputers. Sea Grant Institute, WIS-SG-92-250, Madison, Wisconsin.

Hodar, J. A. 1996. The use of regression equations for estimation of arthropod biomass in ecological studies. Acta AEcologica 17:421-433.

Jobling, M. 1994. Fish Bioenergetics. Chapman and Hall, London, England.

Kawabata, K., and J. Urabe. 1998. Length-weight relationships of eight freshwater planktonic crustacean species in Japan. Freshwater Biology 39:199-205.

Kitchell, J. F., D. J. Stewart, and D. Weininger. 1977. Applications of a bioenergetics model to Yellow Perch (*Perca flavescens*) and Walleye (*Stizostedion vitreum vitreum*). Journal Fisheries Research Board of Canada 34:1922-1935.

Kraft, C.E. 1992. Estimation of phosphorus and nitrogen cycling by fish using a bioenenergetics approach. Canadian Journal of Fisheries and Aquatic Sciences 49:2596-2604.

Lasenby, D. C., and R. R. Langford. 1972. Growth, life history, and respiration of *Mysis relicta* in an arctic and temperate lake. Journal Fish Research Board of Canada 29: 1701-1708.

McCarraher, D. B. 1971. Survival of some freshwater fishes in the alkaline eutrophic waters of Nebraska. Journal Fisheries Research Board of Canada 28:1811-1814.

McCarraher, D.B., and R. W. Gregory. 1970. Adaptability and current status of introductions of Sacramento Perch, *Archoplites interruptus*, in North America. Transactions of the American Fisheries Society 4:700-707.

McCauley, E. 1984. The estimation of the abundance and biomass of zooplankton in samples. Pages 228-265 *in* J. A. Downing and F. H. Rigler, editors. A manual on methods for the assessment of secondary productivity in fresh waters. International Biological Programme Handbook Handbook number 17. Blackwell Scientific Publications, St. Louis, Missouri.

Merritt, R.W., and K.W. Cummings. 1996. An introduction to the aquatic insects of North America. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Moyle, P.B. 1976. Inland Fishes of California. University of California Press, Berkeley, California.

Moyle, P. B., 2002. Inland Fishes of California, Revised and Expanded. University of California Press, Berkeley and Los Angeles, California.

Moyle, P. B., S. B. Mathews, and N. Bonderson. 1974. Feeding habits of the Sacramento Perch, *Archoplites interruptus*. Transactions of the American Fisheries Society 2:399-402.

Ricker, W.E. 1975. Computation and Interpretation of Biological Statistics of Fish Populations. Bulletin of the Fisheries Research Board of Canada 191. Ottawa, Ontario, Canada.

Rudstam, L. G., F. P. Binkowski, and M. A. Miller. 1994. A bioenergetics model for analysis of food consumption patterns of bloater in Lake Michigan. Transactions of the American Fisheries Society 123:344-357.

Saiki, M. K., and B.A. Martin. 2001. Survey of fishes and environmental conditions in Abbotts Lagoon, Point Reyes National Seashore, California. California Fish and Game 87:123-138.

Self D. W., and J.F. Ranlet. 1984. Inland fish and habitats of Pt. Reyes National Seashore. Unpublished data.

Shuter and Post. 1990. Climate, population viability, and the zoogeography of temperate fishes. Transactions of the American Fisheries Society 119:314-336.

Smit, H., E. D. Van Heel, and S. Wiersma. 1993. Biovolume as a tool in biomass determination of Oligochaeta and Chironomidae. Freshwater Biology 29:37-46.

Smock, L. A. 1980. Relationships between body size and biomass of aquatic insects. Freshwater Biology 10:375-383.

Stewart, D., J., D. Weininger, D. F. Rottiers, and T. A. Edsall. 1983. An energetics model for Lake Trout, *Salvelineus namaycush*: An application to the Lake Michigan population. Canadian Journal of Fisheries and Aquatic Sciences 40:681-698.

Tolonen, K.T., J. Karjalainen, S. Staff, and M. Leppa. 2000. Individual and population-level food consumption by cyprinids and percids in a mesotrophic lake. Ecology of Freshwater Fish 9:133-162.

Vinyard, G. L. 1982. Variable kinematics of Sacramento perch (*Archoplites interruptus*) capturing evasive and nonevasive prey. Canadian Journal of Fisheries and Aquatic Sciences 39:208-211.

APPENDIX A. List of all prey items found in stomachs of 299 Sacramento Perch collected from Abbotts lagoon (life stages in parentheses). Ecology, length-weight equations, joules/g dry mass, and sources used in diet analysis and bioenergetics modelling.

Class	Order	Sub-Order	Family	Genus (species)	Common Name	Ecology	Length-weight equation	Source	Joules/g Dry Mass	Source
**	**	**	**	**	Round Worm	Parasite	not used	**	**	**
Oligochaeta	Lumbriculida	**	Lumbricidae (A)	**	Terrestrial Earthworm	Bottom Feeders mix soil	Vr=7.78D11^2.68	Smit et al (1993)	3503	Cummins and Wuycheck (1971)
Hirudinea	Pharyngobdellida	**	Erpobdellidae (A)	**	Leech	Scavenger; feed on small inverts	Y=0.0755-0.0086	Collected Data; Smit et al. (1993)	5443	Cummins and Wuycheck (1971)
Hirudinea	Rhynchobdellida	**	Glossiphonidae (A)	**	Leech	Blood; dead animal matter, inverts	Y=0.1869-4.2824	Collected Data; Smit et al. (1993)	5443	Cummins and Wuycheck (1971)
Branchiopoda	Cladocera	**	Daphnidae (A)	Daphnia	Water Flea	Algae, Protozoa, detritus, bacteria	lnW=1.7998+2.6345lnL (ug)	McCauley (1984)	5028	Cummins and Wuycheck (1971)
Copepoda (A)	**	**	**	**	Copepod	Filter	lnW=1.8336+2.2288lnL (ug)	Benke et al. (1999)	5788	Cummins and Wuycheck (1971)
Malacostraca	Mysidacea	Mysina	Mysidae (A)	**	Opossom Shrimp	Filter	Y=0.00272L^2.00 (mg)	Lasenby and Langford (1972)	5400	Lasenby and Langford (1972)
Malacostraca	Isopoda	Flabillifera	Sphaeromatidae (A)	**	Pill Bug, Sow Bug	Scavenger	Y=0.0054L^2.948 (mg)	Benke et al. (1999) general isopod	3004	Cummins and Wuycheck (1971)
Malacostraca	Isopoda	Asellota	Asellidae (A)	**	Pill Bug, Sow Bug	Scavenger	Y=0.0054L^2.948 (mg)	Benke et al. (1999)	3004	Cummins and Wuycheck (1971)
Malacostraca	Amphipoda	Gammaridae	Corophiidae (A)	Corophium	Side-swimmer	Scavenger, detritus, omnivores	Y=0.0058L^3.015 (mg)	Benke et al. (1999) general amphipod	3761	Cummins and Wuycheck (1971)
Malacostraca	Amphipoda	Gammaridae	Talitridae	Hyalella (azteca) (A)	Scud	Scavenger, detritus, omnivores	LnW=0.0081LnL+0.0118	unpublished data	3761	Cummins and Wuycheck (1971)
Arachnoidea	Acarina	Trombidiformes	Arrenuridae	Arrenurus (A)	Water Mite	Carnivorous, parasitic	Y=0.0530L^2.494 (mg)	Hodar (1996)	5148	Driver, Sugden, Kovach (1974)
Gastropoda	**	**	**	**	Snail	Vegetarians	Y=0.01749L^3.0304 (mg)	Benke et al. (1999)	2620	Boldt and Haldorson 2002
Pelycopoda (Bivalvia)	**	**	Sphaeriidae (A)	**	Seed shells, pea, pill, fingernail clam	Fine Organic Detritus	Y=.0163L^2.477 (mg)	Benke et al. (1999)	4530	Cummins and Wuycheck (1971)
Insecta	Collembula	**	**	**	Springtail		Y=0.0024L^3.676 (mg)	Hodar (1996)	not used	**
Insecta	Odonata	Zygoptera	Coenagrionidae (N)	**	Damselflies	Predators	Y=0.0051L^2.785 (mg)	Benke et al. (1999)	2680	Driver, Sugden, Kovach (1974)

APPENDIX A. (Continued) List of all prey items found in stomachs of 299 Sacramento Perch collected from Abbotts lagoon (life stages in parentheses). Ecology, length-weight equations, joules/g dry mass, and sources used in diet analysis and bioenergetics modelling.

Class	Order	Sub-Order	Family	Genus (species)	Common Name	Ecology	Length-weight equation	Source	Joules/g Dry Mass	Source
Insecta	Odonata	Anisoptera	Aeshnidae (N)	**	Dragonflies	Predators	Y=0.0082L^2.813 (mg)	Benke et al. (1999)	5122	Driver, Sugden, Kovach (1974)
Insecta	Odonata	Anisoptera	Libellulidae (N)	**	Dragonflies	Predators	Y=0.0019L^2.809 (mg)	Benke et al. (1999)	5098	Cummins and Wuycheck (1971)
Insecta	Hemiptera	Homoptera (A)	**	**	Terrestrial True Bug	Predators	Y=0.0548L^2.354 (mg)	Hodar (1996)	not used	**
Insecta	Hemiptera	Heteroptera	Corixidae (A, L)	**	Water Boatmen	Piercers	Y=0.0031L^2.904 (mg)	Benke et al. (1999)	5362	Driver, Sugden, Kovach (1974)
	Hemiptera	Heteroptera	Ochteridae (A)	Ochterus		Predators, Piercer	Y=0.01023L^2.74 (mg)	Benke et al. (1999)	not used	**
Insecta	Coleoptera	**	**	**	Beetle		Y=0.0664L^2.192 (mg)	Hodar (1996)	3539	Cummins and Wuycheck (1971)
Insecta	Coleoptera	**	Haliplidae (A)	**	Crawling Water Beetles	Shredders, herbivores	Y=.0271L^2.744 (mg)	Smock 1980	3539	Cummins and Wuycheck (1971)
Insecta	Coleoptera	**	Dytiscidae (A)	**	Predaceous Diving Beetles	Predators	Y=0.0618L^2.502 (mg)	Smock 1980	3539	Cummins and Wuycheck (1971)
Insecta	Coleoptera	**	Staphylinidae (A)	**	Rove Beetles	Predators	Y=0.0023L^3.332 (mg)	Hodar (1996)	3539	Cummins and Wuycheck (1971)
Insecta	Coleoptera	**	Curculionidae (A)	**	Weevils	Shredders, herbivores	Y=0.1281L^2.254 (mg)	Hodar (1996)	3539	Cummins and Wuycheck (1971)
Insecta	Diptera	Nematocera	Tipulidae (L)	**	Crane Fly	Shredders, detritovores,	Y=0.0029L^2.681 (mg)	Benke et al. (1999)	not used	**
Insecta	Diptera	Nematocera	Ptychopteridea (L)	**	Phantom Crane Flies (Rat-Tail Maggot)	Burrowers	Y=0.00383L^2.6538 (mg)	Benke et al. (1999)	1763	Cummins and Wuycheck (1971)
Insecta	Diptera	Nematocera	Chironomidae (L)	**	Midges	Burrowers, Predators	Y=0.0018L^2.617 (mg)	Benke et al. (1999)	2742	Driver, Sugden, Kovach (1974)
Insecta	Diptera	Nematocera	Chironomidae (P)	**	Midges	Burrowers, Predators	Y=.0018L^2.618 (mg)	Benke et al. (1999)	2742	Driver, Sugden, Kovach (1974)
Osteichthyes	Gasterosteiformes	**	Gasterosteidae	Gasterosteus (aculeatus) (A)	Threespine Stickleback	Insectivore	not used	**	not used	**
Osteichthyes	Perciformes	**	Centrarchidae	Archoplites (interruptus) (L)	Sacramento Perch	Insectivore, Piscivore	Y=0.00006L^2.7811 (g)	collected Data	4677	Cummins and Wuycheck (1971)