

Bioenergetic Modeling of Striped Bass Predation in California from 1969-2004

Erik Loboschefskey¹, Gina Benigno², Ted Sommer³, Timothy Ginn⁴, Arash Massoudieh⁵, Kenny Rose⁶, Frank Loge⁷

Prepared for:

¹Department of Civil & Environmental Engineering, University of California, Davis, One Shields Ave, Davis CA 95616. elobo@ucdavis.edu, 530-848-1041.

²Department of Water Resources, 3500 Industrial Blvd, West Sacramento CA 95691. gbenigno@water.ca.gov

³Department of Water Resources, 3500 Industrial Blvd, West Sacramento CA 95691. tsommer@water.ca.gov.

⁴Department of Civil & Environmental Engineering, University of California, Davis, One Shields Ave, Davis, CA 95616. trginn@ucdavis.edu.

⁵ Department of Civil & Environmental Engineering, University of California, Davis, One Shields Ave, Davis, CA 95616. amassoudieh@ucdavis.edu.

⁶Department of Ocean and Coastal Sciences, Louisiana State University, 218 Wetland Resources, Baton Rouge, LA 70803. karose@lsu.edu

⁷Department of Civil & Environmental Engineering, University of California, Davis, One Shields Ave, Davis, CA 95616. fjloge@ucdavis.edu.

Introduction

While fisheries collapses are increasingly common, discerning the causes can be complex because of the multiple factors and time scales (Worm et al. 2006; Lotze et al. 2006). A case in point is the San Francisco Estuary, including its downstream bays and upstream Delta (collectively referred to as “Estuary” in this document). The Delta is comprised of the confluence of two major rivers, the Sacramento and San Joaquin Rivers, which together drain approximately a 100,000 km² watershed (Figure 1), consisting of runoff from the Central Valley, Sierra Nevada’s and Coastal Mountains (Feyrer et al. 2007). The majority of the Delta is now channelized to provide navigation and flood control in addition to diversions for agricultural and consumptive water uses. For example, the southern end of the Delta has two of the largest water diversion facilities in the world, the State Water Project (SWP) and the federally-operated Central Valley Project (CVP). Water diversions from these facilities are the domestic supplies of water for over 23 million Californians and a multi-billion dollar annual agricultural industry, the largest in North America. Urbanization, rural population growth and agricultural practices throughout the Estuary’s watershed have resulted in higher contaminant loading into the waterways and, in turn, have led to declining water quality (Atwater et al. 1979; Nichols et al. 1986). Invasive species, from aquatic vegetation to species of invertebrates and vertebrates, also characterize the Estuary, largely a product of the discharge of ballast water from overseas cargo ships. Such anthropogenic modifications of this Estuary (i.e. channelization, urbanization, declining water quality, invasive species) have resulted in habitat loss for fish populations and created long-standing concerns about the effect of these modifications upon resident fish populations (Feyrer et al. 2007; Sommer et al. 2007).

Given the extensive modifications to the Estuary, it is not surprising that the status of many fish populations has deteriorated. These changes are fairly well-documented in the San Francisco Estuary, where a partnership of state and federal agencies has been monitoring fish populations in the Estuary for over 40 years, creating one of the longest and comprehensive fisheries datasets in the world (Sommer et al. 2007). One of the most widely used abundance indices is the Fall Midwater Trawl (FMWT) Index, regularly conducted since 1967 by the California Department of Fish and Game (DFG) to capture pelagic fishes. The FMWT encompasses the inner portion of the Delta including San Pablo Bay. Among other species, the FMWT samples: (i) introduced threadfin shad *Dorosoma petenense*, and striped bass *Morone saxatilis* (only “Age-0”, approximately six month old striped bass are sampled by the FMWT), and (ii)

native delta smelt *Hypomesus transpacificus* and longfin smelt *Sprinchus thaleichthys*. As determined by the FMWT, the indices of the four species fluctuated greatly over time, with all indices experiencing sharp declines around 2000 (Feyrer et al. 2007; Sommer et al. 2007). Further strengthening the significance of this collapse was the failure of these populations to recover despite the moderate to above average inflows experienced in the early to mid 2000's, conditions that historically had resulted in at least partial recovery. The continued decline in the abundance indices of these four pelagic species, combined with the subsequent failure of the recovery of these species has become known as the Pelagic Organism Decline (POD) (Sommer et al. 2007). Long-term and recent declines have lead to the listing of delta smelt as threatened under the federal Endangered Species Act (ESA) and endangered under the California Endangered Species Act (CESA), and longfin smelt as threatened under the CESA. As a consequence of these declining pelagic fishes and conflicts over water use, resource managers presently face a major crisis in the Estuary.

Numerous factors have been implicated in the declines (Sommer et al. 2007). The simple conceptual model developed by the study team examining the POD includes the following mechanisms: (1) prior fish abundance, where continued low adult abundance has reduced egg supply; (2) habitat, where changes in water quality parameters, diseases, toxic algal blooms, and contaminants have negatively affected survival and reproduction; (3) "top-down" forcing, where predation and water project entrainment affect mortality rates; and (4) "bottom-up" forcing, where food web interactions affect survival and reproduction. Some recent progress has been made in analyzing the effects of reduced stock (Bennett 2005; Feyrer et al. 2007; Feyrer et al. In press), habitat changes (Lehman et al. 2005; Feyrer et al. 2007; Ostrach et al. 2008), water project entrainment (Kimmerer 2008; Kimmerer and Nobriga 2008; Grimaldo et al. In press), and food web effects (Kimmerer 2008).

Despite this new insight into the factors contributing to the collapse of pelagic fishes, some of the major drivers have not undergone detailed evaluation. Specifically, the effects of predation are poorly understood in the Estuary. There has been a recent proliferation of aquatic weeds in the Delta, which in turn has boosted populations of inshore predators such as centrachids (Nobriga et al. 2005; Brown and Michniuk 2007). However, it is unclear if these littoral fishes could have had substantial effects on the pelagic community, where the collapse occurred. Within the pelagic community, one of the primary predators is striped bass, particularly sub-adults and adults. In contrast to age-0 striped bass indices,

the adult population have not apparently declined substantially based on long-term Peterson mark-recapture estimates of the number of legal sized (age 3+) adults (Figure 2). The reasons for the divergence between the trends in the two life stages are unclear, but may be linked to density dependent increases in juvenile survival, undersampling of juveniles because of recent behavioral changes, stocking of hatchery fish, and changes in adult demographics (Stevens and Miller 1989; Kohlhorst 1999; Kimmerer et al. 2000; California Department of Fish and Game, unpublished data). In any case, it is possible that increased adult abundance may have led to changes in predation pressure on pelagic fishes.

Striped bass were introduced into the Bay-Delta system over 100 years ago and became abundant enough to support recreational and commercial fisheries. The commercial fishery for striped bass was closed in 1935, however a popular recreational fishery still exists (Stevens et al. 1985; Hassler 1988). Adult striped bass are found throughout the entire San Francisco Estuary and Delta. Spawning occurs in fresh waters of the Sacramento and San Joaquin Rivers. Eggs and larvae disperse, following the currents, down throughout the Delta and into the salt/fresh water convergence zone (Baxter et al. 2008; Hassler 1988), where they mature to juveniles and disperse throughout the Bay-Delta. Striped bass prey ranges from invertebrates such as copepods, amphipods, and mysids to fish. Prey selection is largely dependant upon age, where adults primarily feed upon fish while the younger striped bass rely more upon invertebrate prey (Stevens 1966; Hassler 1988; Feyrer et al. 2003; Nobriga and Feyrer 2007).

In this study we focused on quantifying the consumption of prey by California stocks of striped bass through the use of a bioenergetics model. Bioenergetics models, as applied to fish species, operate off of a balanced energy budget. Energy available for growth is determined by the energy in the food consumed less the energy costs of metabolism, egestion and excretion (Hartman et al. 1995a,b; Hanson et al. 1997). When growth of a fish over time is known, a bioenergetics model can be utilized to estimate the consumption of prey over time required to meet the observed growth. Such models are particularly useful in situations where it is not feasible to directly measure loss rates in the field, and when multiple life stages and prey types are involved. Bioenergetic models have proven to be fairly effective in analyzing predation effects of a variety of species including striped bass populations in Chesapeake Bay (Hartman et al. 1995a, b) and Lake Powell (Vatland et al. 2008). In our study, we asked three key questions: (1) was there evidence of a recent increase in predation; (2) what was the relative importance of major prey groups; and (3) how did predation pressure vary by age-class and sex? Our focus was on relative trends in

consumption over time, which we considered a reasonable approach to deal with key data gaps and uncertainties about how well the model applied to California stocks of striped bass.

Methods

Our approach used a bioenergetics model to estimate the average annual consumption of all prey types and average annual consumption of prey fish by California stocks of striped bass. For juvenile striped bass, considered as age 1 through age 2 fish, average annual total and prey fish consumption (for each age cohort) was estimated only on an individual basis (due to the lack of juvenile striped bass abundance data) from 1981 through 2003. For adult striped bass, considered as ages 3 through 6, average annual total and prey fish consumption (for each age cohort) was estimated on the individual and population level basis, from 1969 through 2004. These time periods were selected based on the availability of long term datasets.

The bioenergetics model used herein follows the Wisconsin bioenergetic modeling approach (Hanson et al. 1997), which is based largely on physiological and allometric relationships that regulate fish growth. This approach is driven primarily by field-derived observations on water temperature, food availability, and the annual growth and weight of the fish being modeled (Hanson et al. 1997; Vatland et al. 2008). For this study we obtained previously developed striped bass parameters from laboratory studies performed on Chesapeake Bay stocks of striped bass (Hartman 1995a, b). Historical datasets from the San Francisco Estuary and surrounding California coastal waters of striped bass weights, diets, water temperatures, and abundance estimates (adult striped bass only) were used as inputs to the model and are discussed below in more detail, followed by a description of the bioenergetics modeling process.

Empirical Data Sources

Datasets on striped bass weight, water temperatures, striped bass diet and abundance estimates were required inputs into the bioenergetics model. Advantageous to California stocks of striped bass are the large and comprehensive historical datasets available that allow this bioenergetics modeling process to be applied. Each dataset used in this study is discussed in detail below.

Striped Bass Weight: Two historic databases contain fork lengths of different age groups of striped bass: (1) Bay Study database with focus on age 1 through age 2

fish (not subdivided by sex) from 1980 through 2004, and (2) mark-recapture database with focus on age 3 through 7 male and female fish from 1969 through 2004 (Appendix Table A1). Both sampling programs collect data during the spring of each year, however only April and May were recorded consistently. Therefore, only fork lengths from April and May of each year were converted into weights as per the following Equation (Kimmerer *et al.* 2005):

$$W = \frac{(0.0066 \times L^{3.12})}{1000} \quad (1)$$

where length (L) is fork length in millimeters and weight (W) is in grams.

Individual weights were then grouped into cohorts. Weights from the Bay Study database were grouped into an age 1 cohort (inclusive of fish between the age 1 and 2) and an age 2 cohort (inclusive of fish between the age of 2 and 3). Weights from the mark-recapture database were grouped into 8 cohorts representing age 3, 4, 5, and 6 cohorts for both female and male fish. The mean (Appendix Table A2) and standard deviation of weight were calculated for each cohort based on empirical data collected specifically during the months of April and May.

Limitations of the Bay Study included extremely low sample numbers of striped bass in the age 2 cohort and a constrained study area for both age 1 and 2 cohorts. Both limitations bring into question how representative sample statistics are of the population of age 1 and age 2 cohorts. Additionally, fork length data was not available for age 2 fish; the method of addressing the lack of this fork length data is discussed later in this document. Despite limitations, the Bay Study database is the only source of historical size data on young striped bass.

Limitations of the mark-recapture study included (1) skewed length, and subsequently weight, data for age 3, and to a lesser extent age 4, cohorts, and (2) missing data in selected years during the mid to late 1990s. Length, and subsequently weight, data were skewed due to a legal take size restriction of 42 cm FL for striped bass in California. To estimate the impact of take size restriction on calculated cohort mean weights, a normal distribution was fit through the histogram of weights for age 3 and age 4 cohorts (data not shown): the weights of approximately half of the age 3 cohort and one sixth of the age 4 cohort were not sampled in the mark-recapture study. For the age 3 and age 4 cohorts, the weights generated by fitting a normal distribution to the empirical weight data were used to estimate the mean weight used in the bioenergetics model. Additionally, the mark-recapture study did not collect fork length data

for any cohorts in 1995, 1997, 1999 and 2001. The method of addressing the lack of data for these years is discussed later in this document.

Water Temperature: Water temperature data from the San Francisco Estuary were compiled from three different datasets to span 1969 through 2004. Monthly water temperatures from United States Geological Survey (USGS) Water Quality Cruises were applied from 1969 through 1975. Bi-monthly water temperatures from Department of Water Resources (DWR) discrete monitoring data were applied from 1976 through 1982. Finally, averaged daily water temperatures from four DWR monitoring stations in the Delta were applied from 1983 through 2004.

Because the temporal resolution of data was not consistent among the three data sources, the available data was used to calibrate a temperature function for each year from 1969 to 2004:

$$T = B\cos(A + \frac{2\pi j}{J}) + C \quad (2)$$

where j is ordinal day, J is total number of days in the year, A is the phase shift of the sinusoidal function, B is the amplitude of the sinusoidal function, and C is the average yearly water temperature in degrees Celsius. For each year modeled extending from May 1 through April 30, new parameters of A , B and C were determined by fitting the temperature function to empirical data using the method of least squares. The calibrated model was then used to predict water temperature on a daily basis for a given year.

Modeled daily water temperature was used in place of empirical data for two primary reasons. First, prior to 1983 there was no consistent daily water temperature dataset available. Second, while a dataset containing daily water temperatures was available after 1983, the data was incomplete: temperatures for periods of days to weeks were often missing in multiple years.

The primary limitation of the water temperature datasets was their spatial resolution. Water temperatures vary throughout the Estuary and coastal areas, and the use of an average daily value does not capture this variation. Since striped bass are found throughout the Estuary and areas along the California coast, this limitation calls into question how representative the average daily water temperature was to actual striped bass exposure. However, these datasets represent the best available historic temperature data.

Striped Bass Diet: Diet composition of striped bass prey consumed was compiled from a variety of sources to span the period from 1969 to 2004. In each of the datasets, the proportions of different prey consumed were determined from analysis of striped bass stomach contents. Data from September 1963 to August 1964 (Stevens 1966) was applied to adult striped bass (age 3-7) from 1969 through 1979. Data from August 1979 to May 1983 (Feyrer et al. 2003) was applied to all cohorts from 1980 through 1989. Also from Feyrer et al. (2003), data from April 1998 to January 1999 was applied to age 1 and 2 cohorts from 1990 through 2004. The adult striped bass diets from 1990 through 2004 were taken from DFG field data and broken down into two time blocks, one from 1990 through 1999 and the other from 2000 through 2004. For each of these data sets, we chose to combine several prey types to simplify the bioenergetic modeling process. Thus, the dietary categories summarized in Table 1 reflect empirical data as applied in the bioenergetics model.

There were two primary limitations of the diet datasets. First, relatively few diet studies were available over the modeled time-period (1969-2004). Since numerous years were not captured in the empirical diet data, it was necessary to assume that the striped bass diet during the non-sampled years was similar to the most recent prior diet study. Second, some of the diet studies did not sample striped bass throughout the Estuary nor did samples include any striped bass captured along the California coast, so any spatial variations in prey type consumption were not reflected in those studies.

Striped Bass and Striped Bass Prey Energy Densities: Energy content is an important property of all living organisms. For example, the energy needed by striped bass for growth, movement, reproduction, etc, is derived from the prey they eat. Energy content of an organism is typically measured in units of energy, such as calories or joules. Moreover, an energy density of an organism is generally calculated by simply dividing the total energy content of the organism by its weight (i.e. $\text{Joules} \cdot \text{g}_{\text{prey}}^{-1}$ or $\text{Joules} \cdot \text{g}_{\text{bass}}^{-1}$). Often, this energy density can vary by species, age and/or season.

Energy density of different striped bass prey types (Table 1) were obtained from literature sources (Steimle and Terranova 1985; Pope et al. 2001; Chips and Bennett 2002; Vatland et al. 2008). Since striped bass consume multiple prey types with different energy densities, a weighted average of energy density (\bar{e}_p) was taken based upon the proportions of each different prey type consumed:

$$\bar{e}_p = \sum_{j=1}^n \alpha_j e_{p,j} \quad (3)$$

where, j represents the number of different prey types, α_j is the fractional proportion of prey j out of the total prey consumed and $e_{p,j}$ is the energy density of prey type j ($\text{J} \cdot \text{g}_{\text{prey}}^{-1}$). Note that the sum of the fractional proportions of prey type j (α_j) must equal one. Seasonal variations in prey energy densities can occur, however such variations were not incorporated into this study.

Striped bass energy density was considered on a seasonal basis following Hartman et al. (1995b). Several simple regression functions were utilized to determine the approximate striped bass energy density as a function of age and ordinal day as detailed in Figure 3 and Table 2.

Striped Bass Abundance Estimates: Peterson abundance estimates of adult striped bass cohorts (ages 3-7) were obtained from DFG's mark-recapture survey for 1969 through 2004 (Figure 4, Appendix Table A3). Since adult striped bass are known to migrate up and down the California coast, the abundance estimates of this mark-recapture survey capture the abundance estimates of adult striped bass throughout California and are not exclusive to the San Francisco Estuary (i.e. the relative abundances within either region are not designated by this dataset). Moreover, during certain times of the year, the relative abundance of adult striped bass found along the California coast as compared to the abundance in the San Francisco Estuary vary, thus this abundance dataset in its entirety was considered.

The different colored column bars in Figure 4 represent each adult striped bass cohort, with the abundance estimate of each cohort represented by the length of the bar. Striped bass abundance estimates were not available for 1995, 1997, 1999 and 2001 as no survey data were collected during those years. The abundance estimates during these missing years were estimated by averaging the prior and subsequent year's abundance for each respective cohort. As illustrated in Figure 4, adult striped bass abundance estimate lows occurred in the late 1980s through the mid 1990s, with abundance estimate peaks occurring in the early 1970s and late 1990s.

Several limitations were encountered in this abundance estimate dataset. First, the abundance estimate of each adult striped bass cohort was assumed constant

throughout the duration of a given year (inter-annual mortality was not considered). Second, adult striped bass abundance estimates were approximated for 1995, 1997, 1999 and 2001. Third, available datasets do not extend beyond age 7 cohorts thus abundances of striped bass greater than ages 7 were also not incorporated into this study. Finally, due to the unavailability of a time series of abundance estimates for juvenile striped bass cohorts, their abundances were not incorporated into this study. Finally, this abundance dataset does not designate relative abundances within either the San Francisco Estuary or California coast regions.

Bioenergetics Model Description

As described above, the bioenergetics model used herein follows the Wisconsin bioenergetic modeling approach (Hanson et al. 1997) Within the modeling framework, a net gain in energy allows the fish to gain weight (i.e. grow), while a net loss in energy requires the fish to lose weight. Weight loss due to the release of eggs during spawning in sexually mature female fish are sometimes incorporated into bioenergetic models when sufficient spawning data is available. The effects of striped bass spawning on weight loss were not incorporated into the model of this study due to a lack of necessary spawning information. Striped bass bioenergetic modeling studies by Vatland et al. 2008 and Hartman and Brandt. 1995 also did not incorporate spawning weight losses. The bioenergetics model employed herein follows a daily time-step to track the weight of individual fish as shown in Equation 4:

$$W_t = W_{t-1} + W_{t-1} \left[\frac{\bar{e}_p}{e_s} (C_{t-1} - (R_{t-1} + SDA_{t-1}) - F_{t-1} - U_{t-1}) \right] \Delta t \quad (4)$$

where W_t is the weight of an individual striped bass (g_{bass}) at time t , W_{t-1} is the weight of an individual striped bass (g_{bass}) at time $t-1$, e_s is the energy density of the striped bass ($J \cdot g_{\text{bass}}^{-1}$), \bar{e}_p is the average prey energy density ($J \cdot g_{\text{prey}}^{-1}$), C_{t-1} is realized consumption ($g_{\text{prey}} \cdot g_{\text{bass}}^{-1} \cdot d^{-1}$), R_{t-1} is respiration ($g_{\text{prey}} \cdot g_{\text{bass}}^{-1} \cdot d^{-1}$), SDA_{t-1} is specific dynamic action ($g_{\text{prey}} \cdot g_{\text{bass}}^{-1} \cdot d^{-1}$), F_{t-1} is egestion ($g_{\text{prey}} \cdot g_{\text{bass}}^{-1} \cdot d^{-1}$) and U_{t-1} is excretion ($g_{\text{prey}} \cdot g_{\text{bass}}^{-1} \cdot d^{-1}$). The summation of respiration and specific dynamic action ($R_{t-1} + SDA_{t-1}$) reflects the energy associated with metabolism. As Equation 4 is formulated, it was necessary to calculate realized consumption through an iterative process, which required the inputs of fish weight (W_{t-1}), diet, energy densities (α_j , e_{pj} , e_s), and major physiological processes (R_{t-1} , SDA_{t-1} , F_{t-1} , U_{t-1}). Historical datasets of striped bass weights, diets, water temperatures, and abundances, as described above, were used as inputs to the model. The major

physiological processes of consumption, metabolism, egestion and excretion all require species-specific sets of parameters in addition to the inputs of to accurately define each process. For this study we obtained previously developed striped bass parameters from laboratory studies performed by *Hartman et al.* on Chesapeake Bay stocks of striped bass (Hartman 1995a, b). These parameters as well as mathematical descriptions of the major physiological process are described below in more detail.

Consumption: Realized consumption rate (C_{t-1}), as reflected in Equation 4, refers to the energy gained by the consumption of prey consumed over a specified period of time. Therefore, the realized consumption rate reflects the actual consumption amount by the fish during a time-step that is necessary to produce a specific weight change over the same time-step. Direct calculation of this realized consumption term from Equation 3 is not possible as consumption is dependent upon species-specific constants, fish weight and water temperature. Realized consumption can further be defined as shown in Equation 5:

$$C_{t-1} = pC_{\max,t-1} \quad (5)$$

where, p is the proportion of maximum consumption (unitless) and $C_{\max,t-1}$ is the maximum consumption rate ($\text{g}_{\text{prey}} \cdot \text{g}_{\text{bass}}^{-1} \cdot \text{d}^{-1}$). A zero value of the proportion of maximum consumption (p) suggests that no consumption was occurring while a value of one suggests that the maximum consumption was achieved.

Fish, like the majority of other species, have a maximum rate at which they can consume food. This rate for a particular species can vary based on numerous physiological variables such as age, body weight, sex, and environmental temperature. The maximum consumption rate ($C_{\max,t-1}$) assumes that there is a limitless supply of easily obtainable prey, and if this were actually the case, would reflect the actual consumption rate (C_{t-1}). The maximum consumption rate ($C_{\max,t-1}$) of Equation 5 is defined as a function of fish weight (W_{t-1}), water temperature modifier ($f(T)$, unitless) and striped bass specific constants as shown in Equation 6:

$$C_{\max,t-1} = 0.3021(W_{t-1}^{-0.2523} \times f(T)) \quad (6)$$

where the striped bass specific constants of 0.3021 ($\text{g}_{\text{prey}} \cdot \text{g}_{\text{bass}}^{-2} \cdot \text{d}^{-1}$) and -0.2523 (unitless) are the intercept of the allometric mass function and the slope of the allometric mass function, respectively. Both terms were obtained from *Hartman*

et al. 1995a laboratory studies on striped bass in the Chesapeake Bay. The $f(T)$ in Equation 6 is a water temperature modifier based upon the Thornton and Lessem (1978) algorithm:

$$f(T) = K_a(\theta) * K_b(\theta) \quad (7)$$

$$K_a(\theta) = \frac{K_1 e^{\gamma_1(T-\theta_1)}}{1 + K_1(e^{\gamma_1(T-\theta_1)} - 1)}$$

$$\gamma_1 = \frac{1}{\theta_2 - \theta_1} \ln \frac{K_2(1 - K_1)}{K_1(1 - K_2)}$$

$$K_b(\theta) = \frac{K_4 e^{\gamma_2(\theta_4 - T)}}{1 + K_4(e^{\gamma_2(\theta_4 - T)} - 1)}$$

$$\gamma_2 = \frac{1}{\theta_4 - \theta_3} \ln \frac{K_3(1 - K_4)}{K_4(1 - K_3)}$$

where, T is the water temperature in degrees Celsius and all other values are life-stage specific constants obtained for striped bass (Table 3) from *Hartman et al. 1995*.

Therefore, as per Equations 5 and 6, calculation of realized consumption (C_{t-1}) at time $t-1$, requires the inputs of the water temperature modifier ($f(T)$, Equation 7), fish weight (W_{t-1}) and the proportion of maximum consumption (p). To carry out this calculation, the following steps were taken for each time step. First, the water temperature at time $t-1$ was used to calculate the temperature modifier ($f(T)$) following Equation 7. Next, the weight (W_{t-1}) of the striped bass at time $t-1$ was used to calculate the maximum consumption rate ($C_{max,t-1}$) at time $t-1$, following Equation 6. Finally, the proportion of maximum consumption (p) was used to calculate the realized consumption rate (C_{t-1}) at time $t-1$, following Equation 5.

Metabolism: Metabolism or total metabolic rate ($R_{t-1} + SDA_{t-1}$) in the bioenergetics model (Equation 4) represents the energy costs associated with respiration rate (R_{t-1}) and specific dynamic action (SDA_{t-1}). Similar to consumption rates, respiration rates can vary by species, weight, age, and activity. For this study, respiration rate is dependent upon striped bass specific constants, striped bass weight, water temperature and activity as shown in Equation 8:

$$R_{t-1} = RA * W_{t-1}^{RB} * e^{RQ*T} * ACT * OXY \quad (8)$$

where RA is the specific weight of oxygen consumed by a 1g fish at 0 degrees Celsius ($g_{O_2} \cdot g_{bass}^{-1} \cdot d^{-1}$), RB is the slope of the allometric mass function for standard metabolism (unitless), RQ is a species-specific constant (unitless), and ACT is the activity multiplier constant (unitless) obtained for striped bass (Table 3) from *Hartman et al. 1995a*. The oxycalorific factor (OXY), converts the respiration rate (R) from $g_{O_2} \cdot g_{bass}^{-1} \cdot d^{-1}$ into $g_{prey} \cdot g_{bass}^{-1} \cdot d^{-1}$ using the oxycalorific value of $13,560 J \cdot g_{O_2}^{-1}$ multiplied by the average prey energy density ($J \cdot g_{prey}^{-1}$) as determined in Equation 3 (Elliot and Davison 1975; Megrey et al. 2008).

Specific dynamic action (SDA_{t-1}) is the energetic cost associated with digestion. It is typically assumed to be a proportional constant of assimilated energy, that is consumption minus egestion, as shown in Equation 9 (Hartman et al. 1995a, b; Hanson et al. 1997):

$$SDA_{t-1} = 0.172 * (C_{t-1} - F_{t-1}) \quad (9)$$

where, 0.172 is the unitless striped bass specific proportional constant of assimilated energy.

Egestion and Excretion: Egestion (F_{t-1}) and excretion (U_{t-1}) are the fecal and nitrogenous waste energy losses of the fish. Both terms are dependent largely upon consumption, where increases in consumption lead to increase in waste losses. Egestion and excretion energy are modeled as constant proportions of consumption and assimilated energy, respectively, following Kitchell et al. 1977 (Hanson et al. 1997) as shown in Equations 10 and 11.

$$F_{t-1} = 0.104 * C_{t-1} \quad (10)$$

$$U_{t-1} = 0.068 * (C_{t-1} - F_{t-1}) \quad (11)$$

In Equations 10 and 11, the values 0.104 and 0.068 are unitless striped bass specific constants and were obtained from the laboratory experiments of *Hartman et al. 1995*.

Bioenergetics Model Implementation

One of the main objectives of this study is to calculate annual prey consumption by striped bass using the bioenergetics model (Equation 4) described above. To better understand how this is accomplished, the bioenergetics model in Equation 4 is combined with Equation 5 to include the maximum consumption ($C_{max,t-1}$) and the proportion of maximum consumption (p) terms, resulting in Equation 12:

$$W_t = W_{t-1} + W_{t-1} \left[\frac{e_p}{e_s} \left(p C_{\max, t-1} - (R_{t-1} + SDA_{t-1}) - F_{t-1} - U_{t-1} \right) \right] \Delta t \quad (12)$$

As described previously, realized consumption (the product of p and C_{\max}) ultimately governs growth, whereby for a fish to grow it must consume enough prey energy to offset other physiological losses. However, to calculate realized consumption, Equation 12 must be iteratively solved for the proportion of maximum consumption (p), as is described below.

For each simulation of the bioenergetics model, we ran the model on a daily time-step over the course of a year (365 or 366 days, depending upon leap years). At time $t=1$: (1) the initial fish weight (W_{t-1}) was obtained from the model of historical empirical field data (Equation 1), (2) the average water temperature was obtained from the model of historical empirical field data (Equation 2), and (3) we assume a value for the proportion of maximum consumption (p). We then calculate the weight of a fish (W_1) using Equation 12. With each time step, the value of p remained fixed at the assumed value, the new striped bass weight (W_t) becomes the previous weight (W_{t-1}), and a new water temperature was obtained as a function of ordinal day based upon the temperature model described above (Equation 2). At the end of the simulation year, final weight ($t=365$ or 366) was subtracted from the initial weight ($t=0$) to obtain the annual growth:

$$GR = W_{final} - W_{initial} \quad (13)$$

The modeled annual growth was compared to the observed annual growth obtained from empirical field data (Appendix Table A4). Iterative values of proportion of maximum consumption (p) were selected in the above simulation until a 0.5% difference was achieved between the values of modeled and observed annual growth (Figure 5).

Once the proportion of maximum consumption (p) was determined, annual consumption (C_T) was then calculated as the sum of daily realized consumption over the year:

$$C_T = \sum_{t=1d}^{t=365 \text{ or } 366d} C_{t-1} \quad (14)$$

where, t is time (days), C_{t-1} is daily realized consumption ($g_{\text{prey}} \cdot g_{\text{bass}}^{-1} \cdot d^{-1}$) and C_T is annual consumption ($g_{\text{prey}} \cdot g_{\text{bass}}^{-1} \cdot yr^{-1}$). Assuming a fixed proportion of maximum consumption (p) suggests that the daily realized consumption rate (C_{t-1} , Equation 5) only varies based upon the daily maximum consumption rate ($C_{\text{max},t-1}$) in a given year. This assumption is not entirely realistic: the value of p could vary on a daily basis. However, given that daily variations in p must be inversely proportional to daily variations in $C_{\text{max},t-1}$ and the product of p and $C_{\text{max},t-1}$ (Equation 6) is used as the fitting parameter in Equation 12, the value of annual consumption (C_T , Equation 14) should be unique regardless of whether or not variations in p are considered explicitly.

Two-Year Bioenergetics Model Simulations: As previously discussed, striped bass lengths were incomplete in both the Bay Study and mark-recapture databases. Specifically, lengths and subsequently weights, were missing for the age 2 cohort throughout the entire study period, and for all adult striped bass cohorts in 1995, 1997, 1999 and 2001. In both situations, the lack of data necessitated the calculation of annual growth over two years, rather than one year. Accordingly, the bioenergetics model (Equation 12) was run over a two-year period to determine the proportion of maximum consumption (p) that resulted in matching the observed two-year annual growth. Once the correct proportion of maximum consumption (p) was determined, the annual consumption (C_T , Equation 14) was calculated as described above.

Striped Bass Population Level Simulations: The average annual population level consumption and the average annual population level prey fish consumption were calculated for each adult striped bass cohort. The average annual individual consumption for each adult cohort was multiplied by the corresponding population estimate to obtain average annual population level consumption for each cohort. The average annual population level prey fish consumption by adult striped bass cohorts was then calculated by multiplying the average annual population level consumption by the respective proportion of prey fish consumed as determined from the striped bass empirical diet datasets. The adult striped bass diets (Table 1) previously applied to the bioenergetics model (Equation 12) were used to determine the proportion of total consumption attributable to prey fish.

Results and Discussion

In this study we specifically focused on quantifying the consumption of prey by California stocks of striped bass through the use of a bioenergetics model. The

first step was to determine the proportions of maximum consumption (p) for each of the juvenile and adult striped bass cohorts. Next, the mean values of daily water temperature and cohort specific weights were used to calculate the average annual individual total consumption (kilograms of prey per striped bass) for both juvenile and adult cohorts. The third step was to determine the average annual individual prey fish consumption (kilograms of prey fish per striped bass) by the adult and juvenile cohorts. The final step was to determine the average annual population level total consumption (kilograms of prey per striped bass) and average annual population level prey fish consumption (kilograms of prey fish). The appendix at the end of this document contains tabulated values used to create the figures presented and discussed below.

Proportion of Maximum Consumption (p-value)

Fish, like the majority of other species, have a maximum rate at which they can consume food. This daily rate for a particular species can vary based on numerous physiological variables such as age, body weight, sex, and environmental temperature. A daily maximum consumption rate assumes that there is limitless supply of easily obtainable prey, and would reflect the realized consumption rate if this were actually the case. Thus we can define a value that represents a proportion of the maximum consumption rate (p), which represents the fractional amount of maximum food consumed per day. The product of p and the daily maximum consumption rate yield the realized daily consumption rate (see Equation 5). The value of p ranges from zero to one, with a value of zero indicating no consumption occurred, while a value of one suggesting that the maximum consumption rate was achieved.

A large value of the proportion of maximum consumption (p) in one year relative to another year does not immediately imply a higher annual consumption (C_T). Specifically, annual consumption (C_T) is determined from the summation of daily realized consumption (Equation 14) and daily realized consumption (C_{t-1}) is the product of the proportion of maximum consumption (p) and the daily maximum consumption rate ($C_{max,t-1}$, Equation 6). It is possible that in a given year, a relatively large value of p could be multiplied by a consistently small daily maximum consumption rate ($C_{max,t-1}$, Equation 6), which would then result in a relatively small daily realized consumption (C_{t-1}). Thus the summation of this relatively small daily realized consumption (C_{t-1}) would then yield a small annual consumption (C_T).

The proportion of maximum consumption (p) was determined for each cohort of striped bass for each of the years modeled. For adult striped bass (ages 3

through 7) the modeled years span from 1969 through 2004 and for juveniles (ages 1 through 2) the modeled years span from 1981 through 2003. Selection of these modeled time periods reflect the availability of input data. The proportions of maximum consumption (p) for each cohort are illustrated in Figure 6 as a function of the modeled year, and are plotted alongside the average annual water temperature. As illustrated in Figure 6, juvenile striped bass had higher proportions of maximum consumption (p) than adults in each of the modeled years, suggesting that this cohort was feeding closer to its maximum potential. Between the adult striped bass cohorts, the proportions of maximum consumption (p) were similar in each modeled year, suggesting that each cohort was feeding at approximately the same proportion of their maximum potential. Recall that this does not imply that each cohort was consuming similar amounts of prey as the maximum consumption rate, and hence the daily consumption rates, likely differed between cohorts.

Fluctuations in the proportion of maximum consumption (p) for both adult and juvenile striped bass appeared to coincide with fluctuations in annual growth rates. A scatter plot was created and fitted (Figure 7) with a simple linear regression model to statistically evaluate the significance of the average annual growth rates of adult and juvenile cohorts on the proportion of maximum consumption (p); the linear model is not intended to be used in a predictive sense. The proportion of maximum consumption (p) was correlated to average annual growth rate for juvenile striped bass ($R^2 = 0.32$), and to a lesser extent, correlated to adult striped bass ($R^2 = 0.23$). Additional factors other than growth rate that can influence the proportion of maximum consumption (p) include water temperature and striped bass weight. Neither of these two additional factors appeared to be strongly correlated the proportion of maximum consumption (p).

Average Annual Individual Total Consumption Per Striped Bass

The next step in this study was to determine the average annual individual total consumption per striped bass (individual consumption). Individual consumption (C_T , Equation 14) refers to the total amount of all prey types consumed by an average individual modeled striped bass (i.e. kilograms of prey per striped bass) within each cohort. For adult (ages 3 through 7) and juvenile (ages 1 through 2) striped bass, individual consumption was determined from 1969 through 2004 and 1981 through 2003, respectively. The resulting individual consumption in each year is depicted as a line chart in Figures 8a and 8b for juveniles and adults cohorts, respectively. The individual consumption by each striped bass cohort in Figures 8a and 8b are represented as lines of varying color.

Individual consumption per cohort (kilograms of prey per striped bass) was primarily calculated to evaluate if any changes occurred in the core bioenergetics processes that influence consumption. Factors such as annual growth, water temperature, fish weight and diet can all influence average annual individual total consumption. Therefore any observed changes in the individual consumption by the striped bass cohorts may have resulted from changes in one or more of those factors. Individual consumption varied for the age 1 cohort between a maximum of 2.75 kilograms of prey per striped bass in 1987 and a minimum of 1.35 kilograms of prey per striped bass in 1992 as illustrated in Figure 8a. There did not appear to be any long-term increase or decrease in individual consumption by this cohort. Conversely, there was an apparent increase in individual consumption by the age 2 striped bass cohort, as after 1994 individual consumption by this cohort remained greater than the 1994 amount (Figure 8a). Additionally, there are several fluctuations in the individual consumption by this cohort, ranging between a maximum of 7.97 kilograms of prey per striped bass in 1996 and a minimum of 5.66 kilograms of prey per striped bass in 1986. Overall, one or more core bioenergetic processes as reflected in the bioenergetics equation (i.e. annual growth, water temperature, fish weight or diet) may have influenced individual consumption in the age 2 cohort. For the adult striped bass cohorts (Figure 8b), there appeared to be a slight long-term decreasing trend in individual consumption from 1969 through 2004. This slight decrease was particularly apparent from the decrease in individual consumption by the age 5 and age 6 cohorts. The cause of the decreasing trend in individual consumption is not clear but may be tied to changes in one or more core bioenergetic processes as reflected in the bioenergetics equation (i.e. annual growth, water temperature, fish weight or diet).

A final observation from Figures 8a and 8b is that the individual consumption (kilograms of prey per striped bass) increased with the age of fish. Typically it is assumed that larger fish will have a greater metabolic demand and must consume more prey to meet this demand versus smaller or younger fish. Therefore, this result confirms the assumption that larger striped bass consume a greater quantity of food.

Several scatter plots were evaluated to explore correlations of the individual consumption (kilograms of prey per striped bass) with the proportion of maximum consumption (p), water temperature, annual growth and striped bass weight. Each of these scatter plots were fitted with a simple linear regression model to statistically evaluate the significance of selected processes on individual

consumption; the linear models are not intended to be used in a predictive sense. The average individual consumption for adults and juveniles exhibited little dependence upon annual average water temperatures (data not shown). Average individual consumption appeared to be statistically correlated with the proportion of maximum consumption (p), and annual growth, as illustrated in Figures 9a and 9b, mainly for adult striped bass ($R^2=0.45$, $R^2=0.54$, respectively). By far, the strongest dependence of average individual consumption was on the average weight of the striped bass, with both adults and juveniles having a strong correlation (Figure 9c, adults, $R^2=0.74$; juveniles, $R^2=0.92$). From a management standpoint, the statistical correlation of average individual consumption with striped bass weight suggests that actions leading to the removal and/or reduction of larger striped bass would lessen the individual consumption demanded by these fish.

Average Annual Individual Prey Fish Consumption Per Striped Bass

After determining individual consumption per cohort (kilograms prey per striped bass), the average annual consumption of prey fish by individual striped bass (individual prey fish consumption) was determined for each cohort. Individual consumption of prey fish (kilograms prey fish per striped bass) refers to the average amount of prey fish consumed by an average individual in each cohort, and is a proportion of the previously calculated individual consumption. The proportions of prey fish were determined by stomach content analysis of each striped bass cohort as summarized in Figures 10a and 10b. Focusing upon only prey fish from Figures 10a and 10b, adult and age 2 striped bass appear to consume primarily prey fish (between 78.5% to 99.3%) while age 1 fish consume a significantly lesser amount of prey fish (between 2.5% to 12.3%). The amount of prey fish in the diets of striped bass age 2 and older did not appear to change greatly over the time periods analyzed. Conversely, the prey fish consumed by age 1 striped bass increased from 2.42% to 12.31% starting in the 1990 diet data.

Applying these empirical prey fish proportions to individual consumption (kilograms prey per striped bass) by juvenile striped bass cohorts resulted in the calculation of individual prey fish consumption (kilograms prey fish per striped bass) by the juvenile cohorts (Figure 11a). The individual prey fish consumption by juvenile striped bass cohorts are represented in Figure 11a as lines of varying colors. The individual prey fish consumption from 1981 through 2003 by the age 1 cohort (Figure 11a) varied from a maximum of 0.30 kilograms of prey fish per striped bass in 1990 to a minimum of 0.04 kilograms of prey fish per striped bass in 1982. The maximum consumption of prey fish in 1990 was the beginning of a step increase in prey fish consumption by the age 1 cohort, which was likely

largely driven by the change in the empirical diet data (Figure 10a). Individual prey fish consumption from 1981 through 2003, by the age 2 cohort, varied from a maximum of 6.5 kilograms of prey fish per striped bass in 1996 to a minimum of 4.4 kilograms of prey fish per striped bass in 1986. An increasing trend in individual prey fish consumption by this cohort was also observed starting after 1994.

Applying the prey fish proportions in the empirical diet data to the individual consumption (kilograms prey per striped bass) by adult striped bass cohorts resulted in the calculation of individual prey fish consumption (kilograms prey fish per striped bass) by adult cohorts (Figures 11b). The individual prey fish consumption by adult striped bass cohorts in Figure 11b are represented as lines of varying colors. Similar to the trend in individual consumption (Figure 8b), there appeared to be a slight long-term decreasing trend in individual consumption from 1969 through 2004. This slight decrease was particularly apparent from the decrease in individual consumption by the age 5 and age 6 cohorts. The cause of the decreasing trend in individual consumption is not clear but may be tied to changes in one or more core bioenergetic processes as reflected in the bioenergetics equation (i.e. annual growth, water temperature, fish weight or diet). Consistency between individual and prey fish consumption is not surprising for two reasons. First, since adult fish primarily consume fish, the values in any given year of individual prey fish consumption differ only slightly from the values of individual total consumption. Second, the adult striped bass diet analysis suggested that the consumption of prey fish remained nearly constant from 1969 through 2004 (Figure 10b).

The above analyses was based on the assumption that potential shifts in diet only occurred at times concurrent with the availability of empirical diet data. Only three empirical diet data sets were available for this bioenergetic analysis between 1969 and 2004. Striped bass, especially adults, are largely indiscriminate feeders and can easily switch between different prey types and species. If certain prey, such as fish, became scarce at any point between 1969 and 2004 and was not captured in the empirical diet data, the above analyses could inaccurately reflect individual prey fish consumption.

Average Annual Striped Bass Population Level Total Consumption

Average annual striped bass population level total consumption (population level consumption) refers to the total amount of all prey types consumed (kilograms of prey) by each average adult striped bass cohort. Historical abundance estimates of adult striped bass cohorts (ages 3-7) were obtained from

DFG's mark-recapture survey for 1969 through 2004 (Figure 4), which encompass estimates from the San Francisco Estuary in addition to areas along the California coast. A reliable population estimate of striped bass under 3 years of age was not available and, as a result, the juvenile cohorts were excluded from Figure 4 and subsequent results.

The abundance estimate of each adult cohort (Figure 4) was multiplied by the individual consumption (kilograms of prey per striped bass) of the respective cohort (in each of the modeled years) to obtain population level consumption (Figure 12). The resulting population level consumption, in each year, by the adult cohorts is depicted as a stacked column chart in Figure 12. The different colored column bars in Figure 12 represent each adult striped bass cohort, with the population level consumption (by each cohort) represented by the length of the bar. The population level consumption of each adult cohort declined from 1969 through 1994. Population level consumption then increased through 2000, where it began to decline thereafter. When summing the population level total consumption by the adult cohorts, consumption peaked in 1972 at a value of 3.01×10^7 kilograms of prey and reached a minimum in 1994 at a value of 7.90×10^6 kilograms of prey. These trends in population level consumption by each cohort closely mirror the striped bass abundance estimates illustrated in Figure 4; hence, population level consumption appeared to have a strong dependence upon abundance estimates. A scatter plot was created and fitted with a simple linear regression model (Figure 13) to statistically evaluate the significance of the striped bass abundance estimates on the population level consumption; the linear model is not intended to be used in a predictive sense. Population level consumption was found to be highly correlated to striped bass abundance estimates ($R^2 = 0.93$).

The population level consumption (kilograms of prey) by older striped bass cohorts was often less than that of the younger cohorts (Figure 12). Even though the older cohorts consume a greater quantity of prey on an individual basis (Figure 8b), the abundance estimate of older striped bass is less than younger fish. However, there are a few exceptions throughout the 1990s and early 2000s, where the population level consumption of several older cohorts exceeded that of younger cohorts. Specifically focusing upon the increase of population level consumption from 1995 through 2000, a large portion of the consumption increases during this period resulted from an increase in the consumption by the age 3 and age 4 cohorts. This feature is likely a product of the increase in abundance estimates of these cohorts during this time period.

While this section highlights the population level consumption by each striped bass cohort, there are several limitations of this analysis. First, of particular importance is that since the abundance estimate includes striped bass found along the California coast, the calculated population level consumption is not specific solely to the San Francisco Estuary; suggestive that the population level consumption specific to the Estuary is potentially less than the values reported herein. Since population level consumption (Figure 11) is highly correlated with the striped bass abundance estimates (Figure 4), the relative proportion of striped bass found within the Estuary is less than, or potentially equal to, the reported abundance estimates (a lower abundance would likely result in a lower population level consumption). Second, the abundance estimate of each adult striped bass cohort was assumed constant throughout the duration of a given year (inter-annual mortality was not considered). Third, due to the unavailability of abundance estimates of juvenile striped bass cohorts, the consumption demand by this population was not considered. While these younger fish consume less on an individual basis, it is likely that their larger abundance estimates could contribute a considerable amount to the total consumption demand by striped bass. Fourth, striped bass in California can live for much longer than seven years. This study, based on the available field data, only consider striped bass up through seven years of age. Following the trend that individual consumption increases with the age of the cohort (Figure 8b), the individual consumption by age 7+ cohorts is likely greater than that of the age 6 (and lesser) cohorts. However, following the trend that the striped bass abundance estimates decrease with age, it is likely that the abundance estimates of age 7+ cohorts is low. Since population level consumption is statistically correlated to abundance estimates (Figure 13), population level consumption by age 7+ cohorts is likely lower in comparison with the other cohorts.

Average Annual Striped Bass Population Level Prey Fish Consumption

Next, the average annual population consumption of prey fish (population level prey fish consumption) was determined for each adult striped bass cohort. The population level prey fish consumption (kilograms of prey fish) by each cohort is simply the proportion of the population level consumption that resulted from feeding on prey fish. The proportion of the striped bass diet that consisted of prey fish was determined by stomach content analysis as discussed previously (Figure 10b).

Since the diet of the adult striped bass cohorts primarily consists of prey fish, the population level prey fish consumption (kilograms of prey fish) was very similar to the population level consumption (Figure 14). The resulting population level

prey fish consumption, in each year, by the adult cohorts is depicted as a stacked column chart in Figure 14. The different colored column bars in Figure 14 represent each adult striped bass cohort, with the population level prey fish consumption (by each cohort) represented by the length of the bar. The population level prey fish consumption by each adult cohort declined from 1969 through 1994. The population level prey fish consumption then increased through 2000, where it again began to decline thereafter. When summing the population level consumption of prey fish by the adult cohorts, consumption peaked in 1972 at a value of 3.00×10^7 kg of prey fish and reached a minimum in 1994 at a value of 7.86×10^6 kg of prey fish. As further illustrated in Figure 14, population level prey fish consumption by each adult cohort is generally consistent with the feature that older striped bass cohorts consume less as their abundance estimates were lower than the younger cohorts. Starting in the mid 1990's, a large portion of the increases in consumption appeared to result from an increase in the consumption specifically by the age 3 and age 4 cohorts. This feature is likely a product of the increase in the abundance estimates of these cohorts during this time period.

Comparison of FMWT Prey Fish Indices to Striped Bass Population Level Prey Fish Consumption

Due to the increasing values of population level prey fish consumption (kilograms of prey fish) starting in 1995 through the subsequent peak in 2000-2001 (Figure 14), the availability of prey fish during that same time period is called into question. Since prey fish are the primary diet of adult striped bass, their abundance can be (i) important to the amount of food available for consumption and (ii) influenced by the amount consumed by the striped bass. However, due to the complicated dynamics of the San Francisco Estuary system, we can only make inferences as to how prey fish abundance indices are related to striped bass consumption.

The abundance indices of prey fish were obtained from DFG's FMWT for comparison with striped bass average population level prey fish consumption. Only the indices of delta smelt and threadfin shad were used in this comparison. The spatial extent of FMWT sampling for American shad and longfin smelt is limited and Sacramento splittail are not always effectively captured by the sampling gear (Marty Gingras, personal comm.). Additionally, age-0 striped bass FMWT index was not considered due to the recent disconnect between this index and adult striped bass population numbers. The normalized indices of delta smelt and threadfin shad were relatively high during the period of high striped bass population consumption (Figure 15), notably during 1995-2001. This

does not necessarily imply that the increase in prey abundance during this period resulted in an increase in consumption by striped bass, nor does it imply that the high consumption by striped bass during this period drove the prey abundance down after 2000. The complicated dynamics of this system only allow inferences to be made upon how the abundance indices are related to striped bass consumption, such as consumption of striped bass appears to increase in the presence of an increase in prey fish abundance.

Conclusions

Juvenile striped bass cohorts had higher proportions of maximum consumption (p) than adult cohorts in each of the modeled years. Between adult cohorts, the values of p were similar in each modeled year, suggesting that each cohort was feeding at approximately the same proportion of their maximum potential. The proportions of maximum consumption were statistically correlated to annual growth rates of both adult and juvenile striped bass cohorts.

Individual total and prey fish consumption per cohort were evaluated to assess if any changes occurred in the core bioenergetic processes reflected in the model (i.e. annual growth, water temperature, fish weight or diet) that influenced consumption. For the age 1 cohort, individual total consumption did not significantly change throughout the analyses period. However individual prey fish consumption significantly increased after 1990, largely due to a shift in diet with greater preference toward prey fish. Both individual total and prey fish consumption appeared to significantly increase after 1994 for the age 2 cohort. The total and prey fish consumption of adult cohorts displayed a slight decreasing trend over the analyses period, which appeared to be primarily driven by a decrease in individual consumption (total and prey fish) by the age 5 and age 6 cohorts.

Population level total and prey fish consumption of adult striped bass cohorts were highly correlated to striped bass abundance estimates. Both abundance estimates and the population level total and prey fish consumption of each adult cohort declined from 1969 through 1994, then increased through 2000, where they began to decline thereafter. It is likely that the slight long-term decrease in individual total and prey consumption had a negligible effect upon the modeled trends in population level consumption due to the strong dependence of population level consumption upon the striped bass abundance estimates.

The estimates of population level consumption (total and prey fish) reported herein are consumption estimates for California striped bass and do not necessarily reflect prey consumed only within the San Francisco Estuary. Very little information is available about the prey habits and relative abundances of any striped bass once they leave the Estuary and enter the Pacific Ocean. Moreover, the striped bass abundance dataset includes abundances of striped bass found throughout the Estuary as well as along the California coast and does not designate relative abundances within either region. As such the population level consumption (total and prey fish) by striped bass occurring within the Estuary cannot be accurately separated from the consumption by striped bass occurring along the California coast.

The following material is provided as a cautionary note. The normalized indices of delta smelt and threadfin shad (two prey species for striped bass) were relatively high during the period of high striped bass population level prey fish consumption, notably during 1995-2001. Correlation between prey (delta smelt and threadfin shad) and striped bass population numbers may suggest a causal predator-prey dynamic, and hence would suggest that POD was caused, in part, by elevated striped bass prey fish consumption between 1995-2000. However, no such causal link has been established in this paper, or by other researchers to-date. The San Francisco Estuary system is complex. Findings in this study related to observations and trends in striped bass consumption should not be used as the sole basis for evaluating past, present, and future management actions within the region, but rather should be integrated into a larger body of knowledge encompassing all existing empirical data and models.

Limitations and Future Work

There were several limitations of the fish length, water temperature, diet, and population number datasets that were used to calculate the individual and population level consumption by striped bass. Limitations of the fish length datasets included lack of fish lengths, and corresponding weights, from the age 2 cohort, and under-sampled lengths from the age 3 and 4 cohorts. These limitations could result in errors in calculating the maximum consumption rate ($C_{max, t-1}$, Equation 6), and the respiration rate (R_{t-1} , Equation 8). For the diet datasets, limitations included constrained temporal and spatial scales throughout the modeled time period, and the assumption of diets during modeled years when diet data were unavailable. Errors arising from these limitations of the diet datasets can directly impact the average of prey energy density (\bar{e}_p , Equation 3)

and the proportions of prey fish consumed by each cohort. Limitations of water temperature datasets included limited spatial and temporal scales as well as missing data. These limitations could result in errors in determining the temperature function (T , Equation 2) and calculating maximum consumption rate ($C_{max, t-1}$, Equation 6) and the respiration rate (R_{t-1} , Equation 8). Finally, limitations of the striped bass abundance estimate datasets included temporally limited data for the age 1 and 2 cohorts as well as no data for the adult cohorts during 1995, 1997, 1999 and 2001. Taken as a whole, errors arising from all of these datasets can influence the expected values of the individual and population level consumption for each of the striped bass cohorts. Uncertainty in the input parameters of the bioenergetic equations (Equations 5-11) can influence the value of the proportion of maximum consumption (p), which may then affect the value of daily realized consumption (C_t). Uncertainty in the daily realized consumption (C_t) may then affect the value of annual consumption (C_T , Equation 14). The lack of a comprehensive striped bass abundance dataset for the age 1 and 2 cohorts resulted in the inability to calculate population level consumption (total and prey fish) for these cohorts. Additionally, population level consumption by the age 1 and age 2 cohorts may be quite significant, with respect to the San Francisco Estuary, as it appears this area provides the only routine reproduction and rearing area in California. Finally, errors and uncertainty in the adult striped bass abundance estimate dataset can influence values of population level total consumption (and subsequently consumption of prey fish) by adult striped bass cohorts.

Limitations of the striped bass length, diet, water temperature, and abundance estimate datasets may be resolved through changes in data collection methods as well as establishing additional studies to better capture this data on a broader spatial and temporal scale. Future collections of length (or weight) data should attempt to include a larger sample size of age 1 through age 4 fish, in addition to a broader spatial collection of age 1 through age 2. This would allow for a more deterministic approximation of the average weights of these cohorts, which would also improve the calculation of annual growth (GR , Equation 13). Future collections of diet information should begin to define how diets change by age, location and sex. Additionally, when permissible, the proportions of specific species found in the stomach contents should be recorded. With a large enough sample size, the collection of this type of data may help better refine the average of prey energy density (\bar{e}_p , Equation 3) as well as allow for the calculation of the consumption of specific species. Since the beginning of this study period (1969), numerous advances have been made in the collection of water temperature,

where current collection methods provide daily water temperatures from numerous stations throughout the Estuary. These current methods should continue, as a complete annual series of daily water temperatures (from multiple locations) would allow for actual data to be used in calculating the maximum consumption rate ($C_{max, t-1}$, Equation 6) and the respiration rate (R_{t-1} , Equation 8) in place of the temperature function (T , Equation 2). Finally, a better understanding of how the abundance estimates of striped bass are distributed spatially and temporally throughout the California would be integral to any future modeling effort. Once such dataset that may prove useful to future studies on understanding consumption specifically in the San Francisco Estuary is a mark-recapture dataset that strives to determine the relative abundance of adult striped bass within the Estuary.

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Table 1.
Striped bass diet data as determined through stomach content analysis.

Prey Type	Average ED (J•g _{prey} ⁻¹)	% Diet (by wt.)		
		Age 1	Age 2	> Age 3
1969-1976 (Stevens 1966), Age 3+ only				
Shrimp	3976	--	--	0.1
Unidentified Fish	5064	--	--	16.0
Bait Fish	4814	--	--	12.3
High Energy Density Fish	5441	--	--	70.7
Low Energy Density Fish	4185	--	--	0.9
1980-1989 (Feyrer et al. 2003), All Ages				
Insects, Annelida, Cladocera, Harpacticoid, and Copepod	2364	0.2	0	0
<i>Corophium</i> and Gammaridae	1700	1.4	2.3	0
<i>Crangon</i> , Isopoda & <i>Palaemon</i>	4615	0	1.1	0
Fish	4800	2.4	78.5	98.9
Mysidae	3140	95.9	18.5	0.2
<i>Palaemon</i>	4181	0	0	0.4
<i>Crangon</i>	4025	0	0	0.5
1990-2004 (Feyrer et al. 2003), Age 1 and Age 2 only				
Fish and Unidentified Animal	4800	12.3	82.1	--
Mysidae	3140	58.6	8.4	--
<i>Corophium</i> , Gammaridae and Annelida	2025	26.2	4.2	--
Cladocera and Isopoda	4418	3.1	1.1	--
Debris	0	0	4.2	--
1990-1999 (DFG, unpublished data), Age 3+ only				
Invertebrates	4418	--	--	0.2
Pericarids	4418	--	--	0.01
Decapods	4181	--	--	0.4
Vegetation	2090	--	--	0
Fish	4800	--	--	99.3
2000-2004 (DFG, unpublished data), Age 3+ only				
Invertebrates (Age 3+)	4418	--	--	0.6
Pericarids (Age 3+)	4418	--	--	0.1
Decapods (Age 3+)	4181	--	--	0.6
Vegetation (Age 3+)	2090	--	--	0
Fish (Age 3+)	4800	--	--	98.7

Table 2.
Striped bass energy density as a function of age, assuming a May 1 birthday.

Age Range (d)	Energy Density Equation ($\text{J} \cdot \text{g}_{\text{bass}}^{-1}$)
247 - 610	$0.114 * \text{age} + 3511.1$
611 - 990	$975.6 * \cos(1.10 * \text{age} / 365 * 2\pi) + 6860$
990+	$286.3 * \cos(1.04 * \text{age} / 365 * 2\pi) + 7681$

Table 3.
Bioenergetics constants used for this study.

Parameter	Description	Value		
		Age 1	Age 2	Age 3
θ_1	Temperature for K_1 (°C)	6.6	6.6	7.4
θ_2	Temperature for K_2 (°C)	19.0	18.0	15.0
θ_3	Temperature for K_3 (°C)	28.0	29.0	28.0
θ_4	Temperature for K_4 (°C)	30.0	32.0	30.0
K_1	Proportion of C_{\max} at θ_1 (unitless)	0.262	0.255	0.323
K_2 and K_3	Proportion of C_{\max} at θ_2 and θ_3 (unitless)	0.98		
K_4	Proportion of C_{\max} at θ_4 (unitless)	0.850	0.900	0.850
ACT	Multiplier of metabolism (unitless)	1.649		

LIST OF FIGURES

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12	Average annual population level total consumption by adult striped bass (consumption by each age/sex group is reflected in the length of each respective bar).
13	Linear regression model applied to the average annual population level total consumption of adult striped bass expressed as a function of adult abundance estimates.
14	Average annual population level prey fish consumption by adult striped bass (consumption by each age/sex group is reflected in the length of each respective bar).

- 15 Average annual population level prey fish consumption by adult striped bass and abundance indices of delta smelt, threadfin shad, and Age-0 striped bass.

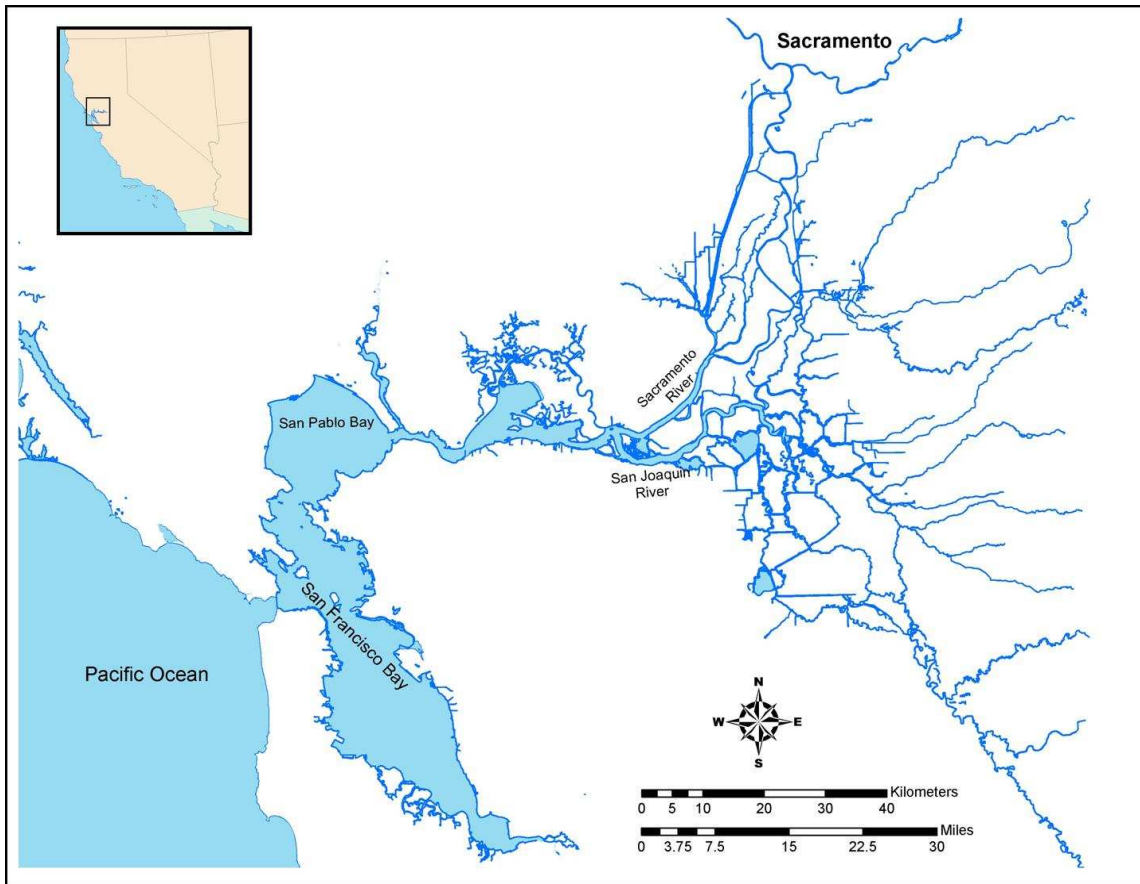


Figure 1

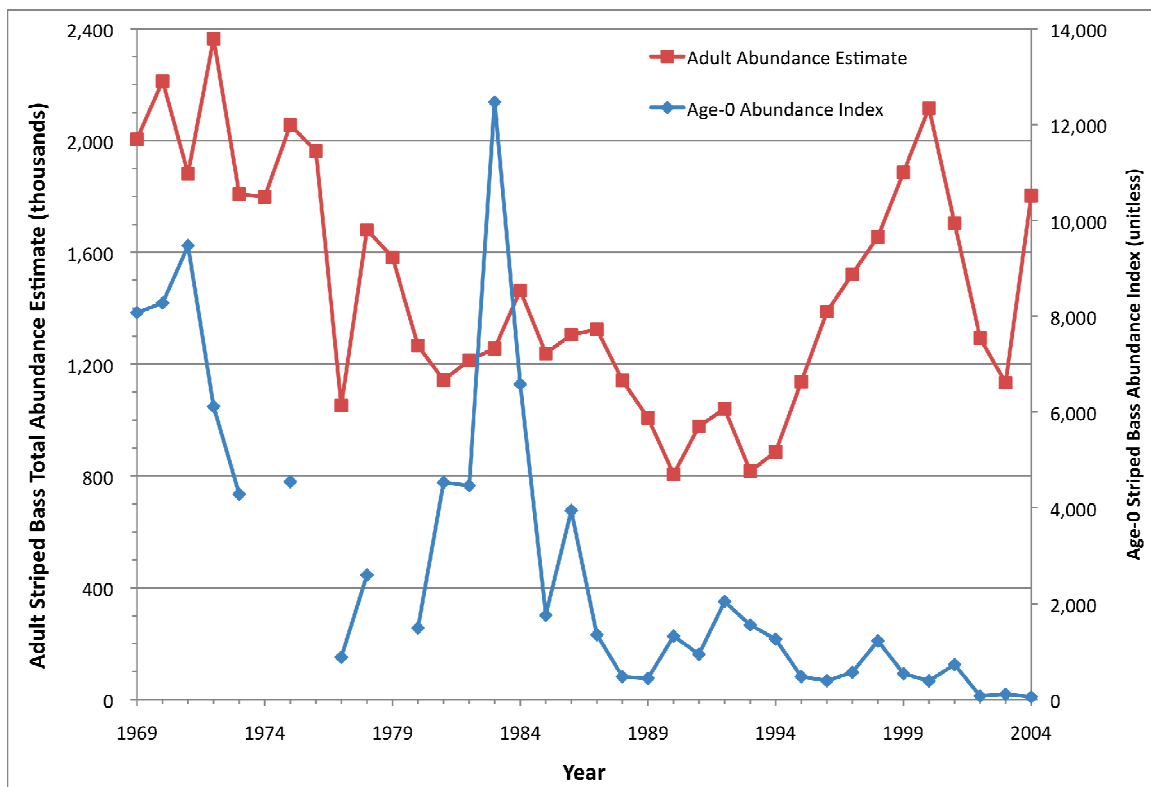


Figure 2

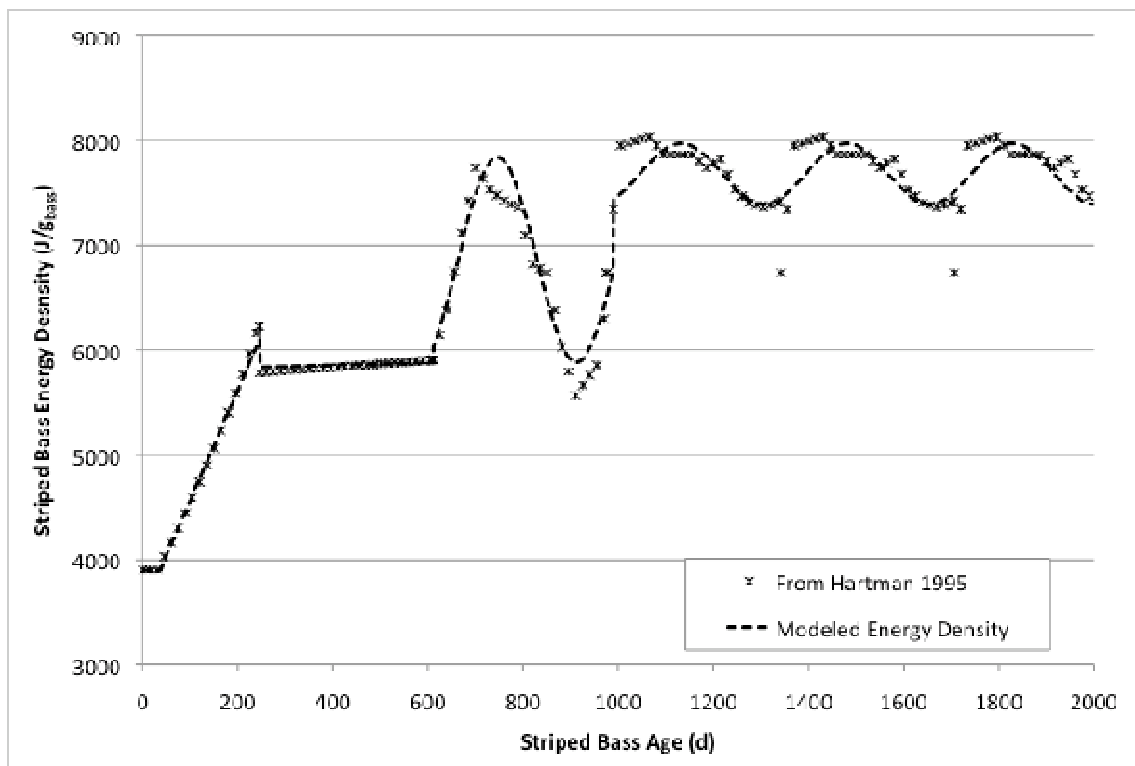


Figure 3

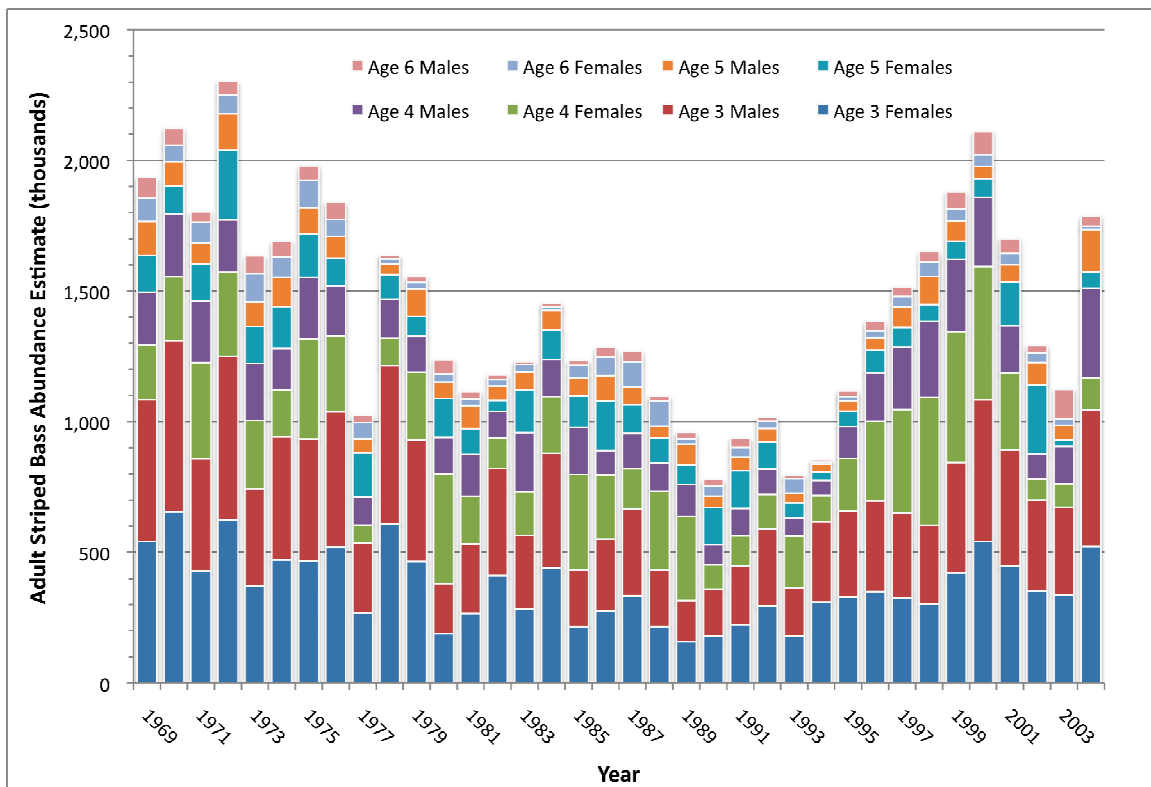


Figure 4

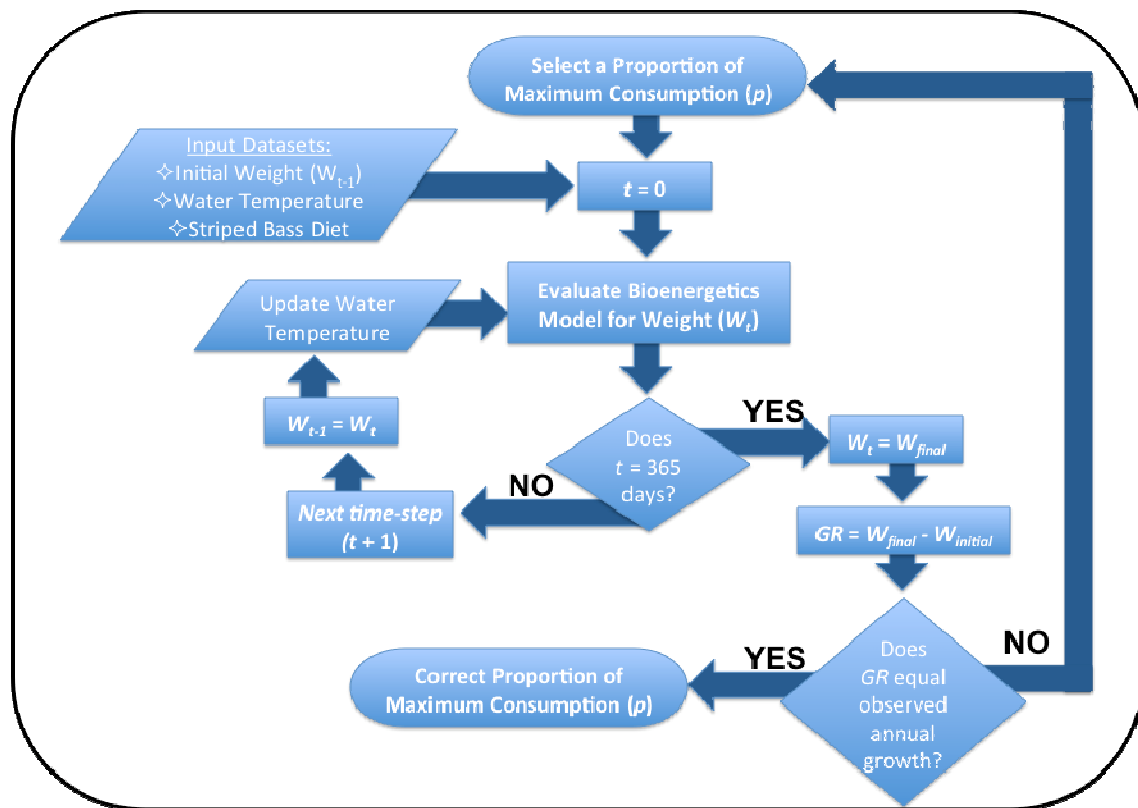


Figure 5

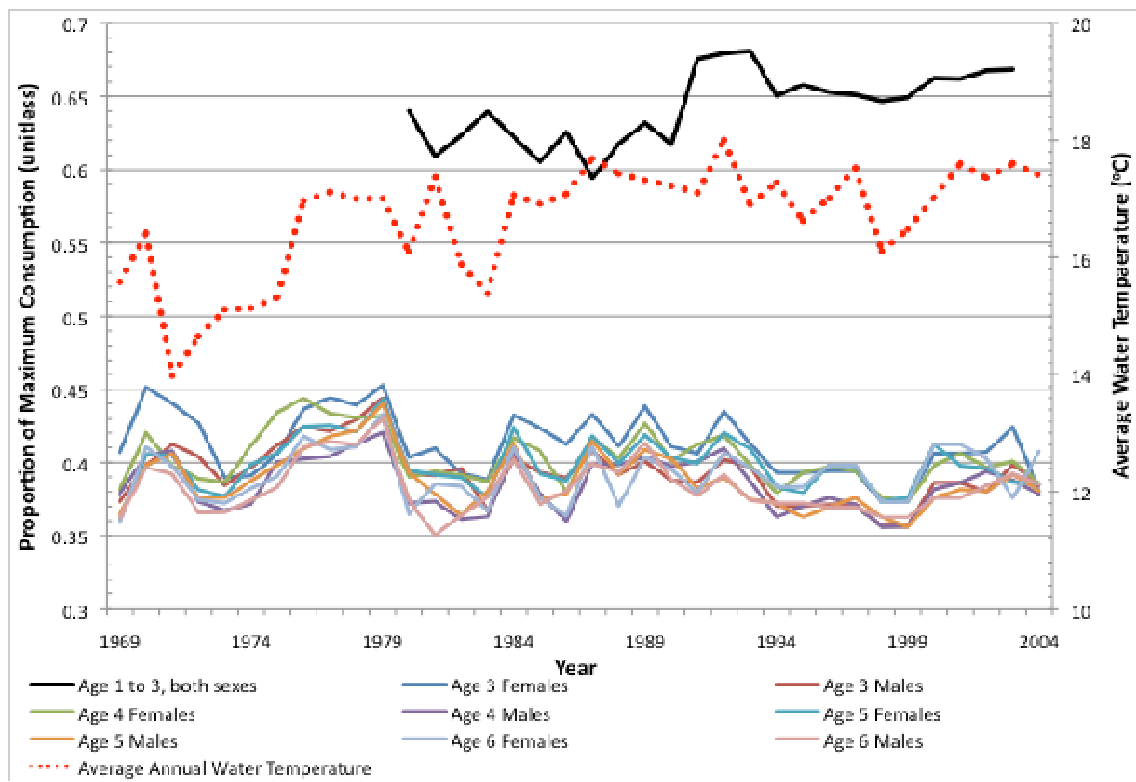


Figure 6

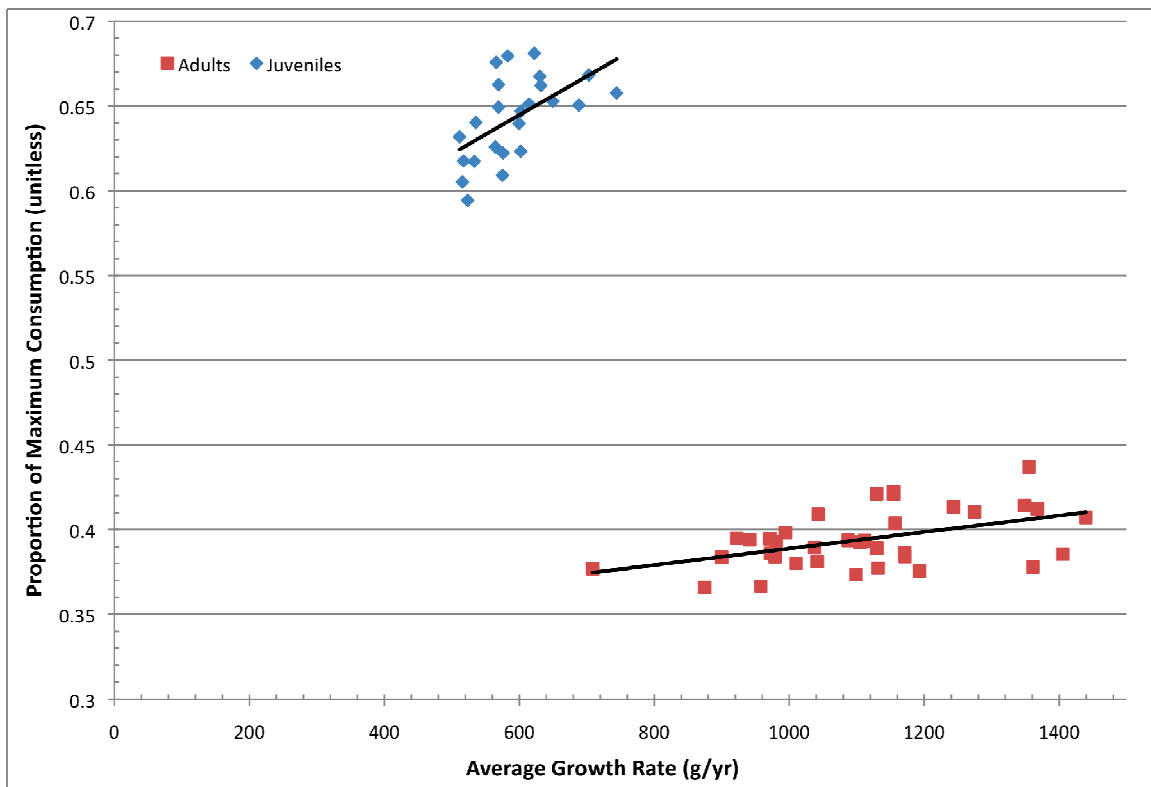


Figure 7

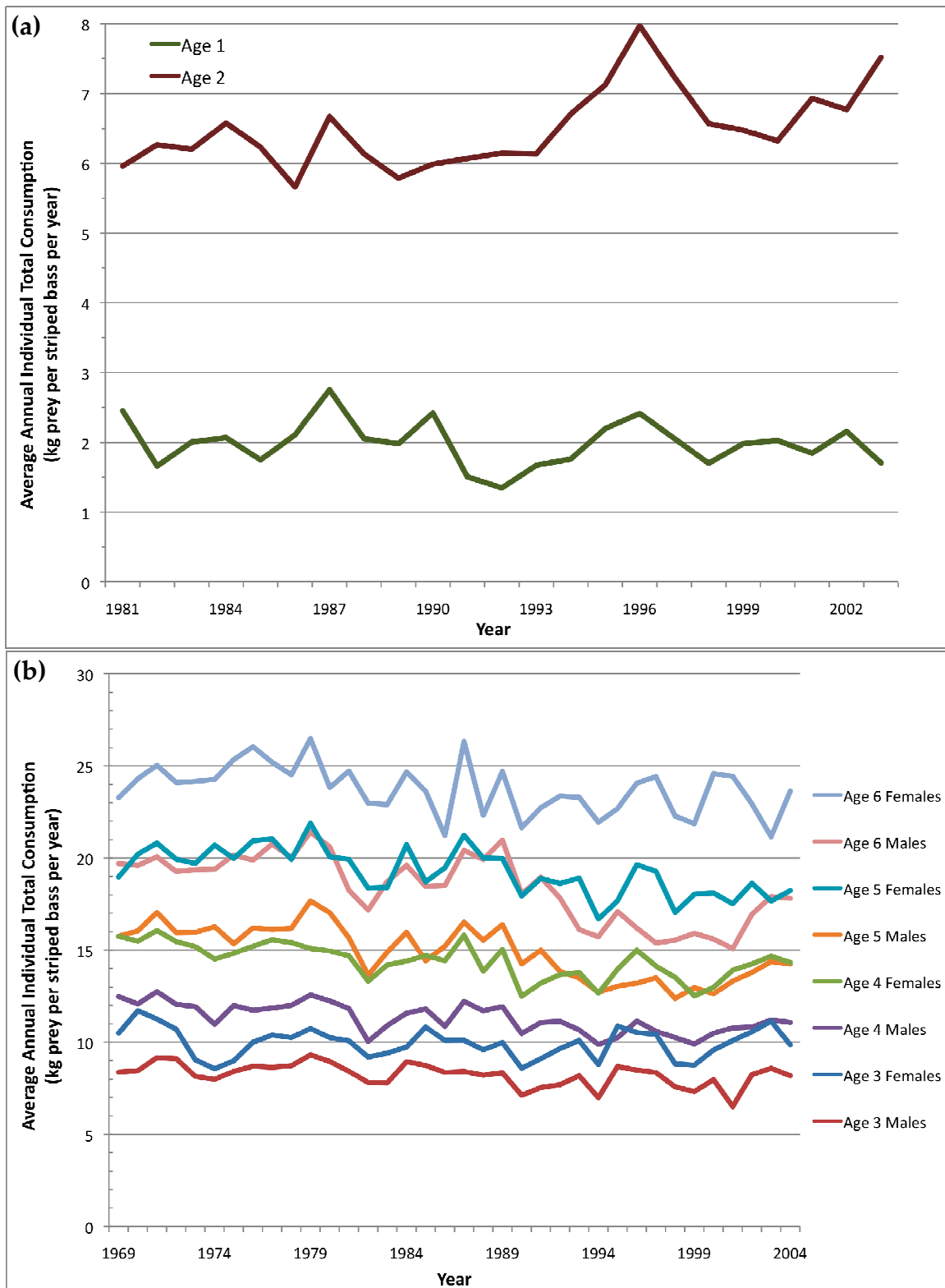


Figure 8

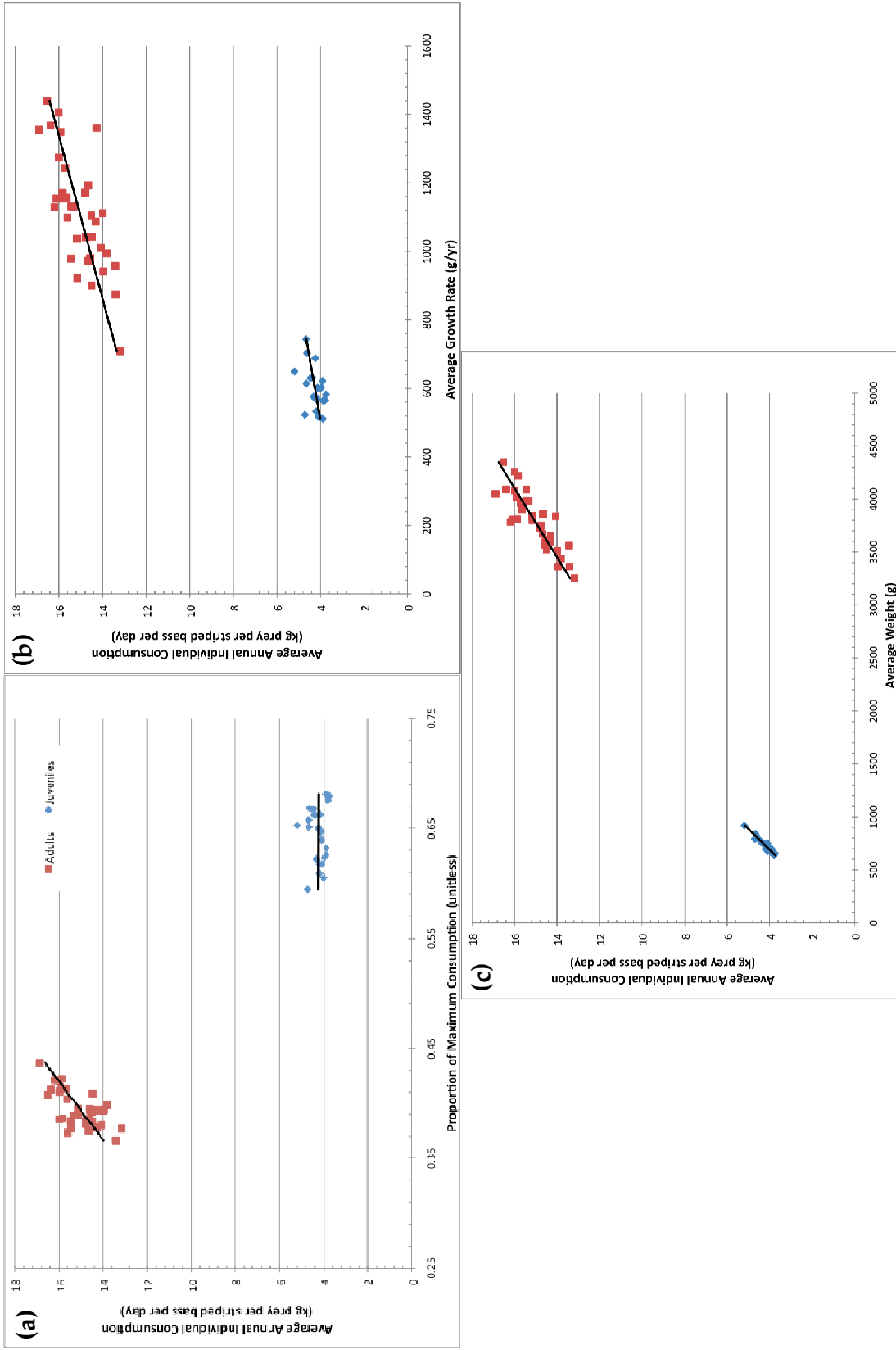


Figure 9

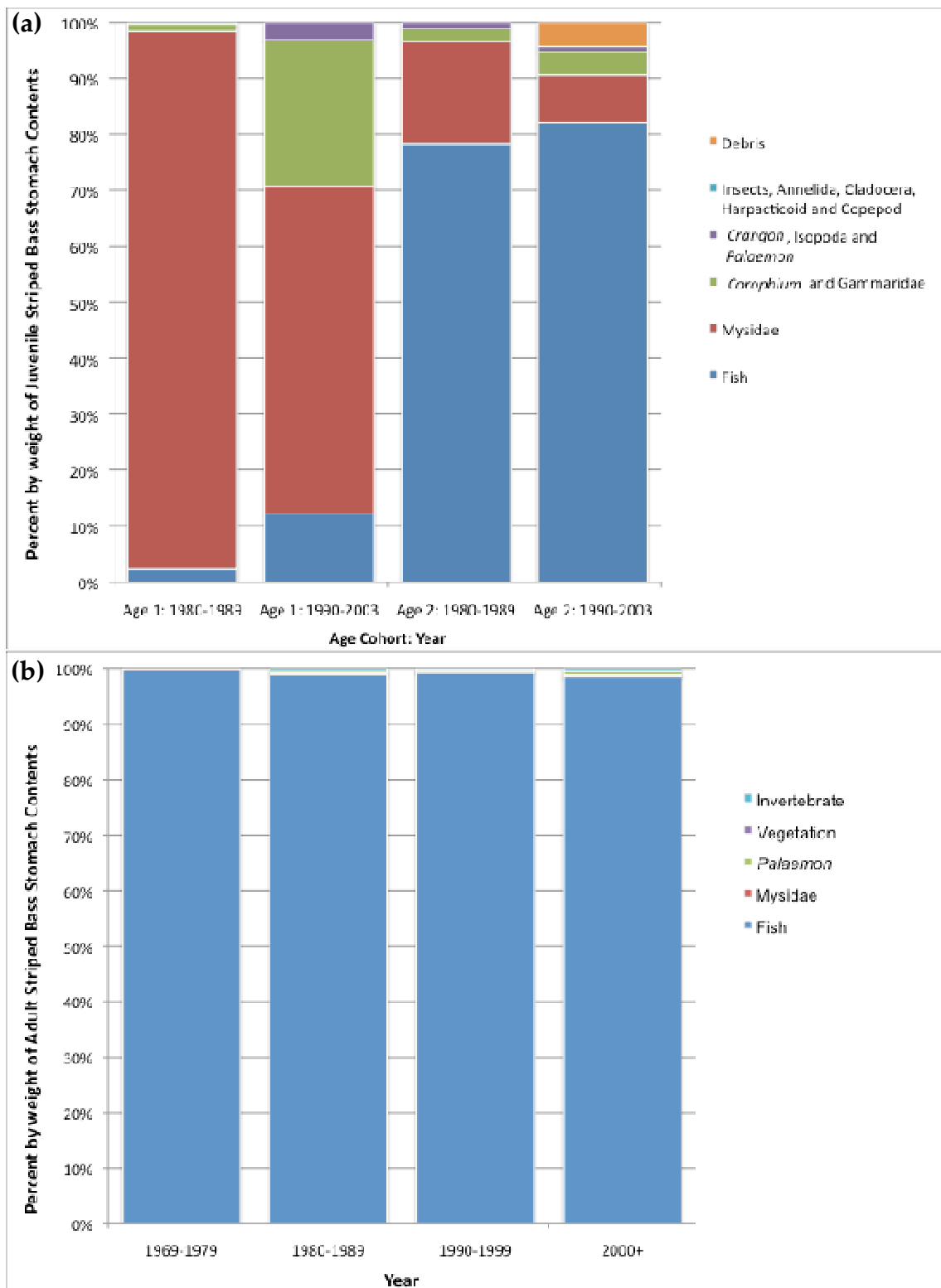


Figure 10

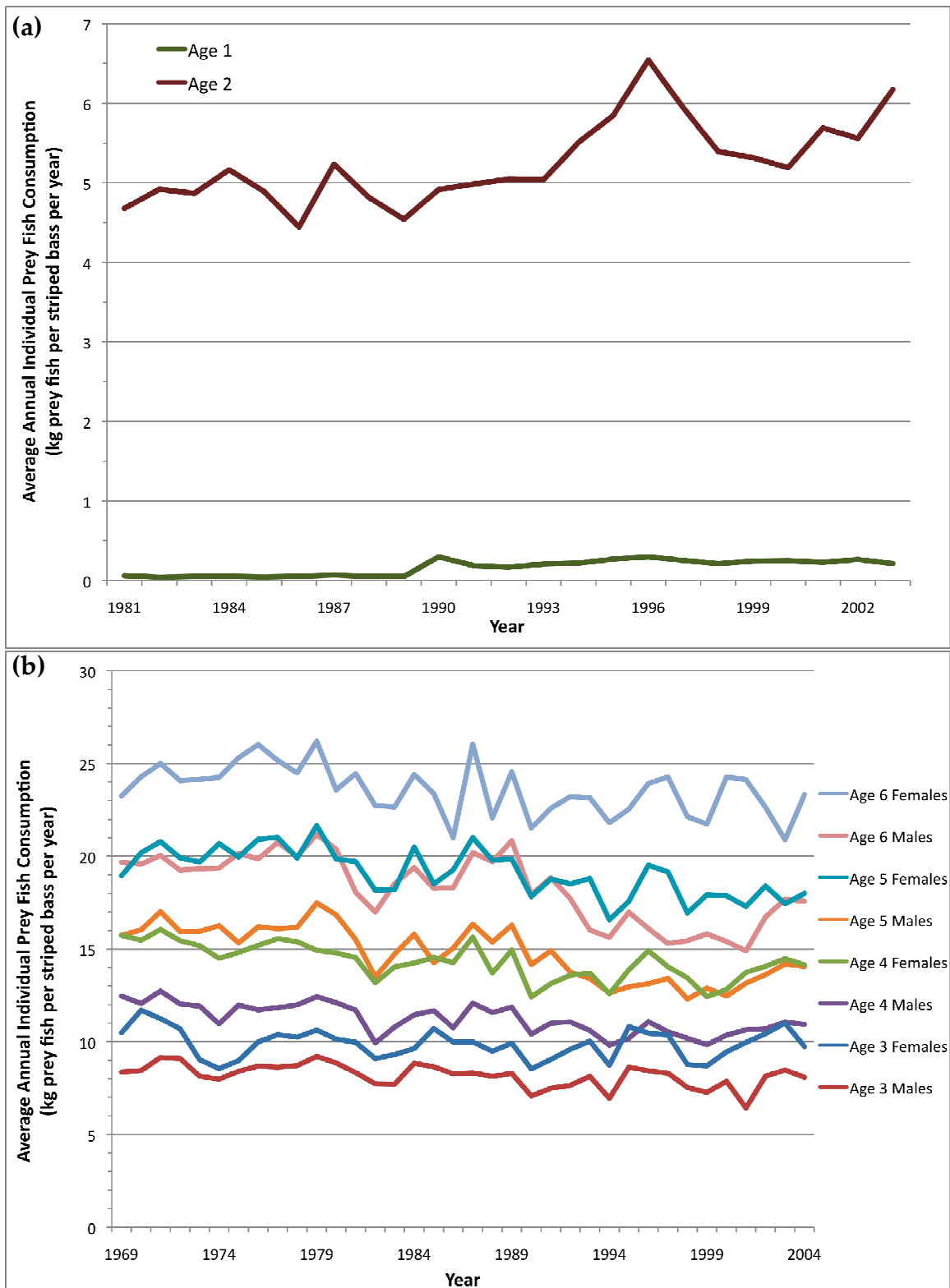


Figure 11

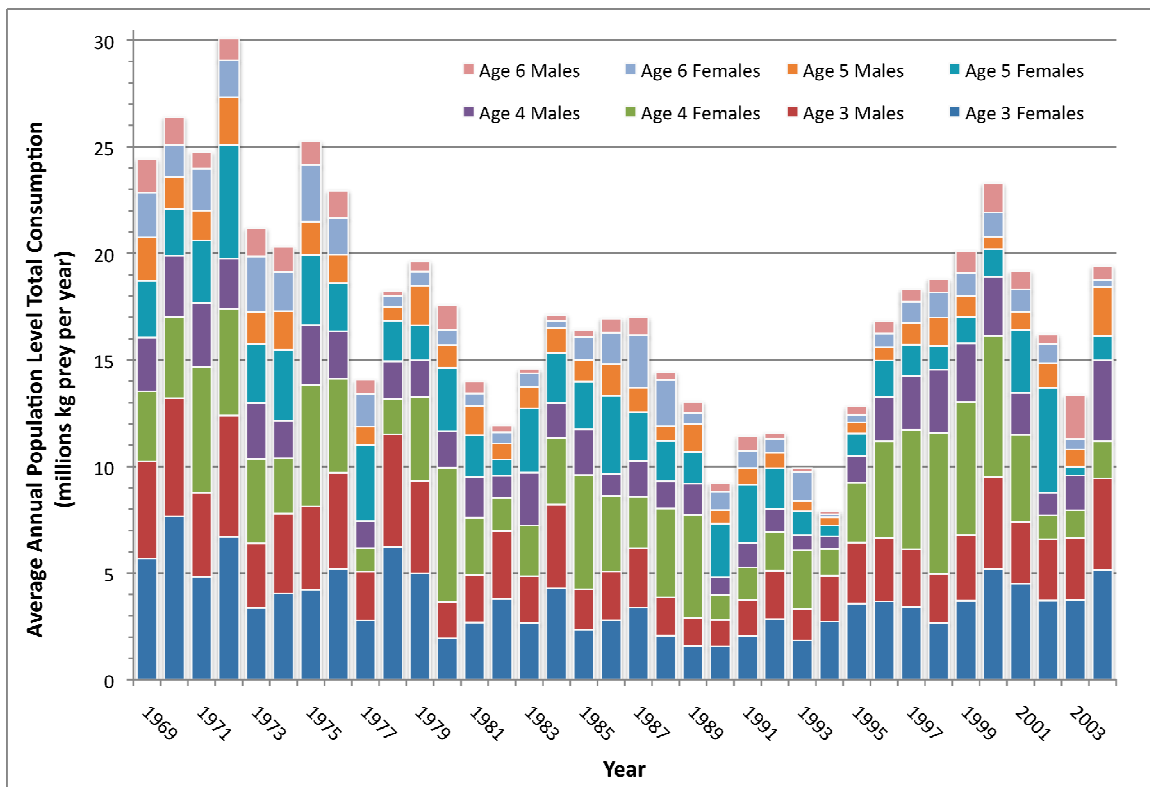


Figure 12

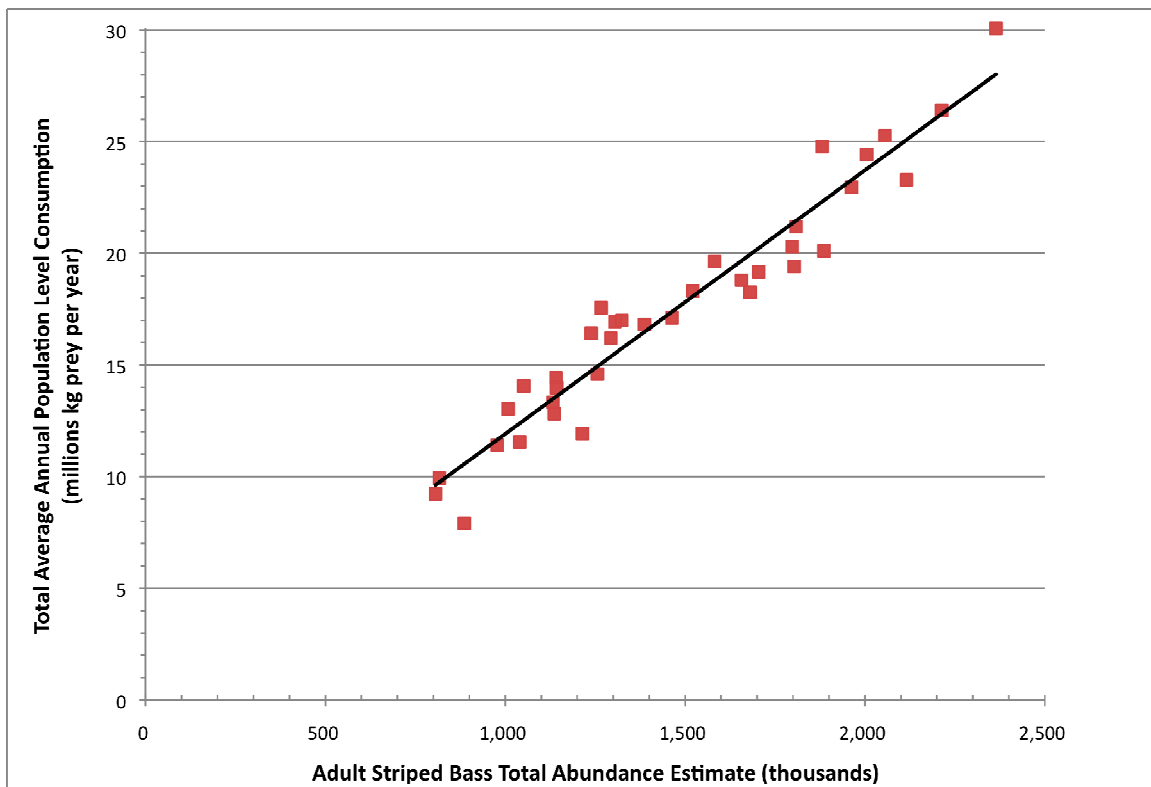


Figure 13

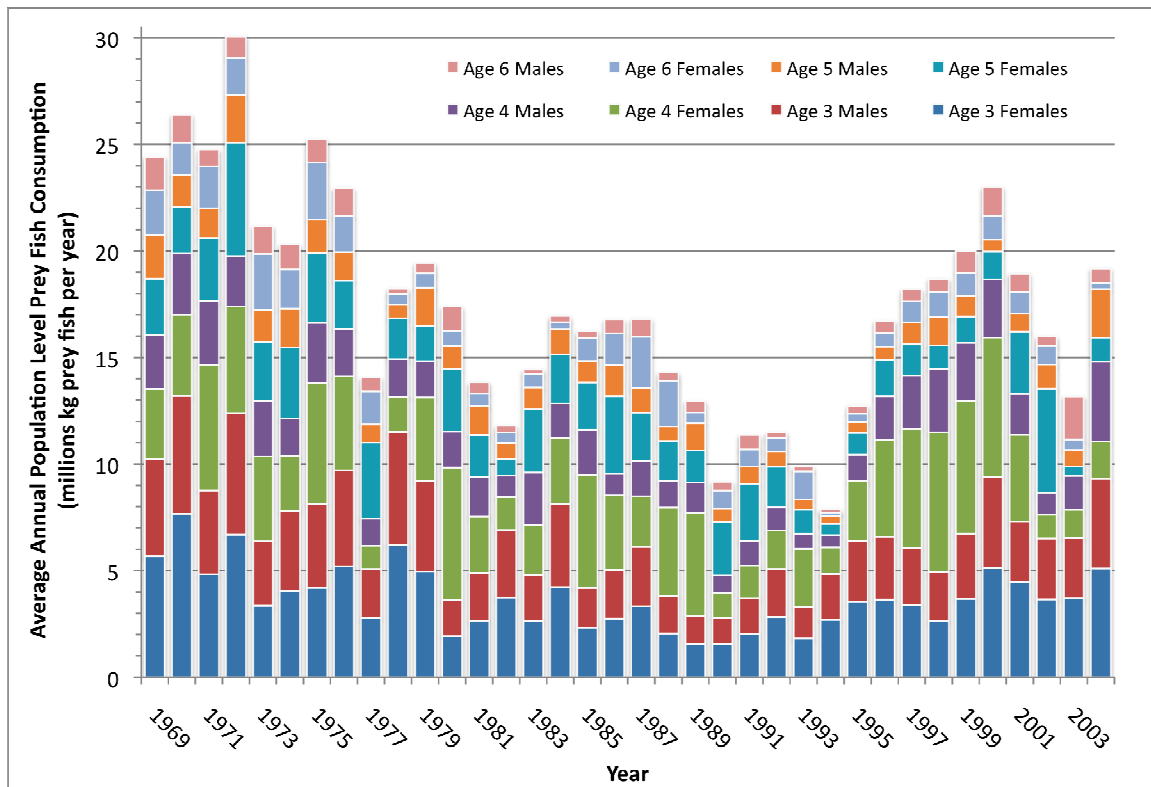


Figure 14

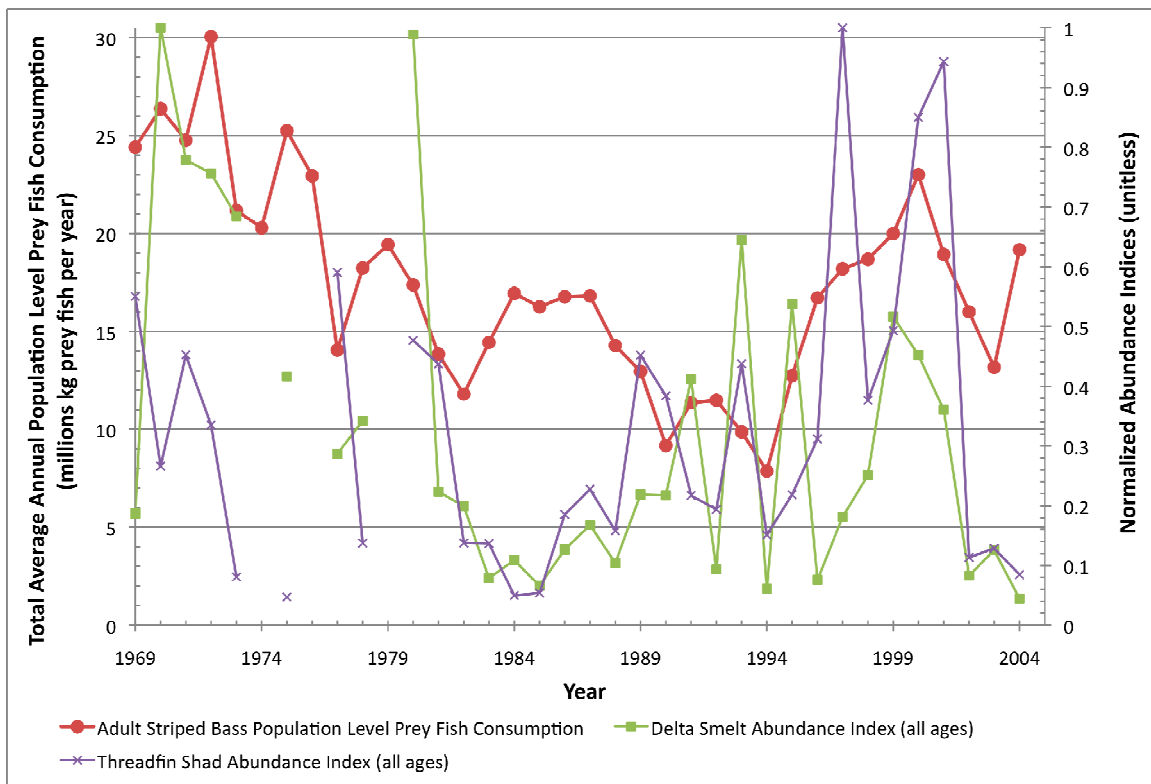


Figure 15

APPENDIX

Table A1: Average striped bass starting lengths (centimeters).

DATE	Age 1	Age 3 ¹		Age 4		Age 5		Age 6	
		Males	Females	Males	Females	Males	Females	Males	Females
1969	--	43.50	42.80	56.00	50.59	64.08	58.44	70.60	64.85
1970	--	45.00	43.80	55.40	50.73	64.24	58.73	69.46	64.53
1971	--	44.50	43.00	58.00	51.00	64.41	58.27	71.24	65.13
1972	--	44.00	43.00	57.50	53.00	65.67	60.07	72.65	66.86
1973	--	44.00	42.50	56.50	53.00	65.16	59.09	72.16	66.11
1974	--	43.50	41.50	53.00	51.00	64.56	59.04	71.74	65.83
1975	--	43.50	41.50	51.50	50.20	62.70	56.43	72.41	65.84
1976	--	43.50	42.00	52.00	50.80	62.87	57.70	70.33	63.38
1977	--	43.20	42.00	53.50	50.70	62.37	56.41	70.40	63.69
1978	--	44.00	41.80	54.10	50.30	62.55	56.43	69.96	63.42
1979	--	44.00	42.00	54.20	51.00	62.81	57.12	69.68	63.94
1980	11.70	44.60	43.00	55.00	52.10	62.22	57.86	71.71	65.92
1981	19.94	45.10	43.50	55.80	53.00	64.27	59.39	71.72	67.39
1982	14.67	45.80	42.00	54.80	51.20	63.18	58.23	71.04	64.85
1983	14.41	44.50	43.00	54.00	50.70	62.41	55.87	70.33	62.89
1984	17.50	43.50	44.80	54.00	50.20	62.96	57.08	69.82	64.03
1985	16.75	45.00	44.00	54.00	52.00	62.27	57.57	71.67	64.72
1986	16.07	44.00	42.50	56.20	51.80	63.05	57.83	69.14	62.65
1987	22.79	43.00	42.00	55.00	50.90	62.82	56.37	70.34	64.26
1988	18.08	45.00	44.00	54.50	50.69	64.06	58.17	71.74	65.18
1989	16.50	42.80	43.30	53.50	50.40	61.62	57.50	70.31	63.83
1990	21.27	42.50	42.00	54.60	50.90	63.52	57.98	70.40	65.29
1991	13.36	43.50	42.00	51.00	48.00	61.43	57.50	70.14	64.76
1992	13.14	43.00	42.00	52.35	48.72	60.22	56.00	68.66	62.90
1993	13.41	45.00	42.50	53.63	49.00	60.69	56.20	68.37	60.84
1994	15.82	45.10	43.00	54.86	50.70	61.44	55.78	69.41	61.17
1995 ¹	14.34	46.12	43.81	51.77	47.34	59.52	53.81	66.26	59.71
1996	17.44	47.10	45.10	55.00	50.40	62.24	55.36	68.08	60.63
1997 ¹	17.08	48.47	46.36	55.57	51.05	63.48	56.63	70.57	60.72
1998	14.40	46.25	44.80	55.50	51.40	61.99	55.19	69.84	60.90
1999 ¹	14.76	45.20	43.54	53.08	49.96	62.24	56.13	68.16	60.57
2000	16.30	45.10	43.50	53.00	49.70	59.44	54.57	68.45	60.29
2001 ¹	15.29	46.49	39.96	53.83	50.12	60.45	55.53	68.33	59.57
2002	15.43	46.00	44.00	54.00	48.00	61.31	55.50	66.61	60.05
2003	14.66	46.00	43.50	55.35	50.35	61.77	55.70	68.67	61.27
2004	--	48.30	44.00	56.50	51.20	62.72	56.48	67.13	61.99
2005	--	45.60	44.20	54.08	50.50	62.48	56.64	68.39	61.93

¹Striped bass starting lengths estimated. See main document for further details.

Table A2: Calculated striped bass starting weights (grams).

DATE	Age 1	Age 3 ¹		Age 4		Age 5		Age 6	
		Males	Females	Males	Females	Males	Females	Males	Females
1969	--	1126.2	1070.7	2476.8	1804.0	3771.8	2829.3	5101.8	3915.6
1970	--	1251.9	1150.6	2394.9	1819.6	3801.6	2873.1	4850.2	3855.0
1971	--	1209.0	1086.3	2763.4	1850.0	3833.0	2803.1	5248.8	3968.5
1972	--	1167.1	1086.3	2689.7	2085.9	4072.2	3082.7	5580.6	4305.1
1973	--	1167.1	1047.4	2546.4	2085.9	3972.7	2929.2	5462.6	4156.0
1974	--	1126.2	972.4	2085.9	1850.0	3860.1	2920.5	5364.5	4102.5
1975	--	1126.2	972.4	1907.1	1760.9	3523.6	2536.8	5522.4	4103.3
1976	--	1126.2	1009.4	1965.5	1827.4	3553.4	2719.0	5041.4	3645.2
1977	--	1102.2	1009.4	2147.9	1816.2	3465.7	2533.6	5058.7	3699.6
1978	--	1167.1	994.5	2223.9	1771.9	3497.3	2536.2	4959.0	3651.5
1979	--	1167.1	1009.4	2236.8	1850.0	3543.0	2634.9	4897.8	3745.9
1980	18.7	1217.5	1086.3	2341.4	1977.3	3440.8	2741.9	5356.4	4120.5
1981	98.8	1260.6	1126.2	2449.3	2085.9	3806.3	2976.0	5360.6	4413.8
1982	37.9	1322.6	1009.4	2314.9	1872.7	3608.3	2797.6	5201.6	3914.9
1983	35.9	1209.0	1086.3	2211.1	1816.2	3473.6	2458.4	5043.0	3558.1
1984	65.7	1126.2	1234.6	2211.1	1760.9	3570.2	2629.2	4928.1	3761.9
1985	57.3	1251.9	1167.1	2211.1	1965.5	3449.0	2699.6	5348.8	3890.2
1986	50.4	1167.1	1047.4	2504.5	1942.0	3585.6	2738.1	4781.3	3515.1
1987	150.0	1086.3	1009.4	2341.4	1838.7	3544.3	2528.1	5044.7	3804.0
1988	72.7	1251.9	1167.1	2275.6	1815.1	3767.9	2788.1	5365.4	3977.9
1989	54.7	1070.7	1110.2	2147.9	1782.9	3337.4	2689.7	5037.2	3726.7
1990	120.8	1047.4	1009.4	2288.7	1838.7	3668.8	2759.9	5058.9	3997.4
1991	28.3	1126.2	1009.4	1850.0	1531.1	3306.1	2689.7	5000.2	3898.1
1992	26.9	1086.3	1009.4	2007.1	1603.9	3107.5	2476.8	4677.5	3558.9
1993	28.6	1251.9	1047.4	2164.2	1632.9	3183.5	2504.4	4616.2	3208.5
1994	48.0	1260.6	1086.3	2322.9	1816.2	3308.4	2446.6	4840.1	3262.5
1995 ¹	35.3	1351.5	1151.8	1938.3	1466.8	2995.2	2186.7	4186.0	3025.8
1996	65.1	1443.3	1260.6	2341.4	1782.9	3443.3	2389.7	4555.9	3172.9
1997 ¹	60.9	1578.0	1373.4	2418.6	1855.8	3661.8	2565.1	5096.4	3188.7
1998	35.8	1363.6	1234.6	2408.5	1895.6	3400.5	2366.1	4933.4	3217.6
1999 ¹	38.6	1269.7	1129.2	2096.3	1734.3	3444.3	2494.6	4572.7	3163.7
2000	52.7	1260.6	1126.2	2085.9	1706.8	2983.4	2284.3	4633.9	3117.8
2001 ¹	43.1	1385.8	864.5	2190.1	1752.0	3143.7	2412.1	4608.7	3004.3
2002	44.4	1340.8	1167.1	2211.1	1531.1	3285.1	2408.5	4255.9	3079.0
2003	37.8	1340.8	1126.2	2388.2	1777.4	3363.7	2436.0	4680.2	3279.4
2004	--	1561.2	1167.1	2546.4	1872.7	3527.6	2544.3	4359.4	3400.6
2005	--	1304.7	1183.8	2221.4	1794.0	3485.2	2566.8	4620.1	3390.1

¹Striped bass weights derived from estimated length data. See main document for further details.

Table A3: Adult striped bass abundance estimates (thousands).

	Age 3		Age 4		Age 5		Age 6		Total
DATE	Males	Females	Males	Females	Males	Females	Males	Females	
1969	541.72	541.72	210.13	202.32	139.77	129.47	90.93	79.58	1935.65
1970	654.55	654.55	246.32	238.04	109.14	91.90	63.00	65.93	2123.43
1971	429.29	429.29	367.09	235.26	141.93	82.43	78.12	40.24	1803.65
1972	624.98	624.98	323.42	198.13	267.35	139.74	71.91	52.31	2302.83
1973	371.26	371.26	261.78	219.04	140.24	94.49	108.52	68.18	1634.77
1974	470.68	470.68	179.05	159.64	160.75	112.17	76.02	60.18	1689.16
1975	466.85	466.85	383.69	235.37	164.05	101.61	105.62	55.11	1979.14
1976	518.84	518.84	290.50	190.05	108.28	82.31	65.65	65.07	1839.54
1977	267.02	267.02	70.29	106.60	169.93	53.24	61.63	30.63	1026.36
1978	606.79	606.79	107.16	147.78	95.74	40.29	19.87	13.22	1637.64
1979	464.68	464.68	261.00	137.35	75.23	103.98	25.68	22.81	1555.41
1980	189.85	189.85	420.91	139.30	148.66	63.00	30.36	55.15	1237.08
1981	265.96	265.96	182.76	159.83	98.86	87.82	24.11	29.93	1115.22
1982	410.79	410.79	115.67	102.10	42.09	55.77	22.78	18.52	1178.50
1983	282.23	282.23	166.81	227.76	163.42	68.65	27.65	11.68	1230.44
1984	439.56	439.56	217.00	142.02	112.80	74.22	13.43	14.49	1453.09
1985	216.39	216.39	364.46	181.01	120.14	70.18	46.45	18.25	1233.28
1986	275.45	275.45	245.11	94.46	188.63	97.68	69.89	35.69	1282.36
1987	333.54	333.54	152.70	135.12	108.63	70.01	93.42	40.75	1267.71
1988	216.50	216.50	301.49	108.05	95.11	44.31	97.01	19.02	1098.00
1989	157.31	157.31	323.32	121.53	75.09	79.28	20.19	25.68	959.71
1990	179.25	179.25	93.21	78.29	140.71	44.17	39.52	23.27	777.68
1991	223.42	223.42	117.20	103.99	143.62	53.40	35.74	35.62	936.40
1992	294.51	294.51	132.72	96.75	103.36	52.25	27.66	14.56	1016.32
1993	181.88	181.88	198.30	67.61	59.08	36.05	57.36	12.90	795.06
1994	308.71	308.71	99.34	58.63	31.21	30.70	6.80	9.02	853.11
1995 ¹	328.61	328.61	201.88	121.95	59.19	39.12	16.64	22.33	1118.32
1996	348.51	348.51	304.42	185.28	87.17	47.54	26.48	35.64	1383.54
1997 ¹	325.24	325.24	396.43	238.33	76.16	77.48	39.82	38.00	1516.70
1998	301.97	301.97	488.44	291.37	65.16	107.43	53.17	40.37	1649.87
1999 ¹	421.80	421.80	499.59	278.00	68.60	76.28	49.73	64.14	1879.93
2000	541.62	541.62	510.74	264.63	72.05	45.12	46.28	87.92	2109.99
2001 ¹	446.02	446.02	294.59	181.30	168.27	64.69	42.36	57.58	1700.82
2002	350.41	350.41	78.45	97.96	264.48	84.25	38.44	27.23	1291.64
2003	336.15	336.15	89.59	143.95	24.75	55.70	23.36	114.06	1123.71
2004	523.13	523.13	122.40	342.16	62.79	161.73	13.01	37.97	1786.32

¹Striped bass abundances were estimated from prior and subsequent year. See main document for further details.

Table A4: Striped bass growth rates (grams per year).

DATE	Ages 1 thru 2	Age 3		Age 4		Age 5		Age 6	
		<i>Males</i>	<i>Females</i>	<i>Males</i>	<i>Females</i>	<i>Males</i>	<i>Females</i>	<i>Males</i>	<i>Females</i>
1969	--	1268.7	748.9	1324.8	1069.2	1078.4	1025.7	1153.3	1121.1
1970	--	1511.5	699.3	1438.1	983.5	1447.2	1095.3	1794.5	1225.3
1971	--	1480.7	999.5	1308.8	1232.8	1747.6	1502.0	1819.3	1424.1
1972	--	1379.3	999.5	1283.0	843.3	1390.4	1073.3	1392.3	1004.4
1973	--	918.7	802.6	1313.7	834.6	1391.8	1173.3	1482.3	1134.4
1974	--	780.9	788.5	1437.7	686.8	1662.3	1182.8	1446.2	1052.8
1975	--	839.3	855.0	1646.2	958.1	1517.8	1108.5	1345.7	983.3
1976	--	1021.6	806.8	1500.2	706.1	1505.3	980.5	1563.6	1151.4
1977	--	1121.7	762.4	1349.4	720.0	1493.3	1118.0	1230.4	1240.6
1978	--	1069.6	855.4	1319.1	863.0	1400.5	1209.7	1315.5	1202.4
1979	--	1174.3	967.9	1204.0	891.9	1813.4	1485.6	1808.7	1495.4
1980	--	1231.8	999.5	1464.9	998.7	1919.8	1671.9	1427.5	1529.4
1981	1071.0	1054.3	746.5	1159.0	711.7	1395.4	938.9	1451.6	375.1
1982	1150.2	888.5	806.8	1158.7	585.8	1434.7	760.6	1567.9	877.9
1983	1204.0	1002.1	674.6	1359.1	813.0	1454.5	1303.4	1463.7	1473.3
1984	1199.1	1084.9	730.9	1237.9	938.7	1778.7	1260.9	1665.4	1249.2
1985	1151.8	1252.6	774.9	1374.4	772.5	1332.3	815.5	1108.7	865.2
1986	1031.0	1174.3	791.3	1039.8	586.1	1459.1	1065.9	947.7	1266.3
1987	1128.9	1189.3	805.7	1426.5	949.5	1821.1	1449.8	1938.1	1358.9
1988	1046.6	896.0	615.8	1061.7	874.6	1269.4	938.5	586.3	1133.5
1989	1034.5	1218.0	728.5	1520.9	977.0	1721.6	1307.7	1637.0	1677.9
1990	1022.7	802.6	521.7	1017.4	851.1	1331.5	1138.1	1300.8	992.8
1991	1066.6	880.8	594.5	1257.6	945.7	1371.4	869.2	1034.7	890.0
1992	1131.5	1077.9	623.4	1176.5	900.4	1508.7	731.8	1437.5	886.3
1993	1165.5	1071.0	768.8	1144.6	813.7	1672.5	760.7	1629.7	835.8
1994 ¹	1244.1	1075.7	734.2	1065.5	683.6	1618.5	869.1	1535.0	861.9
1995 ¹	1376.6	609.6	334.4	1104.1	792.7	1261.5	886.5	1764.0	957.7
1996 ¹	1487.8	1156.2	730.0	1151.1	642.7	1214.1	864.5	1723.1	1317.4
1997 ¹	1299.3	868.4	513.4	1309.1	770.3	1483.7	657.7	1479.1	942.8
1998 ¹	1228.5	1030.5	596.2	1038.3	554.2	1606.0	914.4	1737.8	640.6
1999 ¹	1204.8	824.1	618.0	1415.0	796.8	1246.5	686.1	1944.6	1045.1
2000 ¹	1138.6	713.6	464.8	943.1	587.5	1750.5	908.9	1368.4	965.9
2001 ¹	1263.5	814.9	898.3	963.1	697.7	1551.5	664.3	2169.2	971.3
2002	1260.4	1047.4	610.3	1152.6	904.9	1395.1	870.9	1790.5	1070.0
2003	1406.0	1205.7	746.5	1139.4	766.9	995.7	964.6	831.7	1120.2
2004	--	660.2	626.8	938.7	694.1	1092.4	845.8	1854.2	1065.7

¹Annual growth rates estimated from two-year growth rates. See main document for further information.

Table A5: Proportion of maximum consumption (p-value).

DATE	Ages 1 thru 2	Age 3		Age 4		Age 5		Age 6	
		Males	Females	Males	Females	Males	Females	Males	Females
1969	--	0.4069	0.3732	0.3815	0.3787	0.3612	0.3647	0.3587	0.3620
1970	--	0.4515	0.3978	0.4202	0.4050	0.4054	0.3980	0.4105	0.3965
1971	--	0.4402	0.4124	0.3976	0.4078	0.4047	0.4058	0.3973	0.3917
1972	--	0.4270	0.4040	0.3888	0.3731	0.3814	0.3754	0.3743	0.3659
1973	--	0.3895	0.3845	0.3864	0.3673	0.3766	0.3758	0.3722	0.3662
1974	--	0.3908	0.3966	0.4114	0.3716	0.3986	0.3874	0.3823	0.3740
1975	--	0.4057	0.4119	0.4343	0.4003	0.4064	0.3982	0.3904	0.3832
1976	--	0.4364	0.4244	0.4435	0.4025	0.4244	0.4092	0.4180	0.4106
1977	--	0.4441	0.4213	0.4335	0.4042	0.4252	0.4179	0.4086	0.4144
1978	--	0.4391	0.4293	0.4309	0.4128	0.4211	0.4217	0.4106	0.4125
1979	--	0.4527	0.4440	0.4319	0.4203	0.4429	0.4398	0.4331	0.4298
1980	--	0.4035	0.3924	0.3902	0.3720	0.3942	0.3933	0.3649	0.3744
1981	0.6403	0.4095	0.3910	0.3934	0.3733	0.3914	0.3782	0.3854	0.3503
1982	0.6091	0.3925	0.3960	0.3911	0.3611	0.3895	0.3642	0.3838	0.3639
1983	0.6233	0.3880	0.3668	0.3870	0.3630	0.3762	0.3806	0.3669	0.3762
1984	0.6396	0.4326	0.4031	0.4168	0.4071	0.4240	0.4124	0.4103	0.4024
1985	0.6223	0.4233	0.3928	0.4078	0.3788	0.3921	0.3748	0.3756	0.3714
1986	0.6051	0.4126	0.3892	0.3793	0.3595	0.3876	0.3783	0.3635	0.3807
1987	0.6258	0.4329	0.4078	0.4163	0.3992	0.4180	0.4147	0.4107	0.3992
1988	0.5943	0.4111	0.3917	0.4030	0.3985	0.3994	0.3919	0.3704	0.3931
1989	0.6176	0.4383	0.4008	0.4265	0.4038	0.4187	0.4085	0.4036	0.4134
1990	0.6319	0.4108	0.3875	0.4012	0.3975	0.4032	0.4023	0.3950	0.3882
1991	0.6173	0.4060	0.3864	0.4124	0.4006	0.3994	0.3823	0.3792	0.3773
1992	0.6758	0.4349	0.4019	0.4187	0.4094	0.4201	0.3897	0.4067	0.3914
1993	0.6795	0.4128	0.3970	0.3983	0.3871	0.4093	0.3745	0.3964	0.3740
1994	0.6811	0.3928	0.3703	0.3793	0.3628	0.3834	0.3721	0.3834	0.3721
1995	0.6505	0.3928	0.3703	0.3928	0.3703	0.3793	0.3628	0.3834	0.3721
1996	0.6577	0.3939	0.3711	0.3972	0.3756	0.3982	0.3694	0.3982	0.3694
1997	0.6528	0.3939	0.3711	0.3939	0.3711	0.3972	0.3756	0.3982	0.3694
1998	0.6511	0.3730	0.3564	0.3759	0.3558	0.3728	0.3627	0.3728	0.3627
1999	0.6470	0.3730	0.3564	0.3730	0.3564	0.3759	0.3558	0.3728	0.3627
2000	0.6493	0.4061	0.3861	0.3978	0.3816	0.4124	0.3756	0.4124	0.3756
2001	0.6627	0.4061	0.3861	0.4061	0.3861	0.3978	0.3816	0.4124	0.3756
2002	0.6622	0.4070	0.3799	0.3967	0.3936	0.3960	0.3801	0.4026	0.3842
2003	0.6675	0.4240	0.3985	0.4008	0.3878	0.3864	0.3916	0.3756	0.3921
2004	0.6683	0.3803	0.3844	0.3855	0.3783	0.3855	0.3809	0.4074	0.3852

Table A6: Average annual individual total consumption (kg of prey per striped bass).

	Age 1	Age 2	Age 3		Age 4		Age 5		Age 6	
DATE			Males	Females	Males	Females	Males	Females	Males	Females
1969	--	--	10.49	8.38	15.75	12.48	18.97	15.75	23.28	19.70
1970	--	--	11.71	8.45	15.49	12.07	20.21	16.05	24.31	19.60
1971	--	--	11.26	9.17	16.06	12.75	20.81	17.04	25.03	20.07
1972	--	--	10.71	9.11	15.46	12.05	19.94	15.95	24.10	19.27
1973	--	--	9.04	8.14	15.19	11.94	19.71	15.97	24.17	19.37
1974	--	--	8.56	7.99	14.51	10.97	20.70	16.27	24.27	19.39
1975	--	--	8.99	8.42	14.83	11.99	19.98	15.35	25.34	20.17
1976	--	--	10.00	8.70	15.21	11.73	20.94	16.21	26.05	19.89
1977	--	--	10.39	8.64	15.57	11.85	21.04	16.12	25.20	20.77
1978	--	--	10.25	8.73	15.41	12.00	19.93	16.19	24.52	20.02
1979	--	--	10.74	9.31	15.09	12.56	21.89	17.67	26.49	21.40
1980	--	--	10.25	8.96	14.95	12.24	20.07	17.03	23.83	20.61
1981	2.45	5.96	10.08	8.42	14.69	11.83	19.93	15.67	24.72	18.25
1982	1.66	6.27	9.19	7.81	13.32	10.05	18.36	13.65	22.98	17.19
1983	2.00	6.20	9.41	7.79	14.20	10.91	18.40	14.89	22.91	18.72
1984	2.07	6.58	9.74	8.94	14.40	11.58	20.73	15.97	24.67	19.61
1985	1.75	6.23	10.82	8.74	14.70	11.81	18.71	14.42	23.63	18.46
1986	2.11	5.66	10.09	8.36	14.43	10.87	19.48	15.21	21.22	18.51
1987	2.75	6.67	10.10	8.41	15.81	12.22	21.23	16.52	26.33	20.42
1988	2.05	6.13	9.59	8.22	13.85	11.70	20.01	15.54	22.32	19.93
1989	1.98	5.79	9.98	8.34	15.04	11.94	19.98	16.38	24.70	20.97
1990	2.42	5.99	8.59	7.12	12.50	10.47	17.94	14.25	21.66	18.05
1991	1.51	6.07	9.11	7.54	13.21	11.07	18.89	15.00	22.73	18.95
1992	1.35	6.15	9.65	7.69	13.67	11.13	18.62	13.84	23.36	17.83
1993	1.67	6.14	10.09	8.18	13.79	10.67	18.91	13.49	23.30	16.11
1994	1.76	6.71	8.79	6.99	12.66	9.88	16.69	12.71	21.95	15.73
1995	2.20	7.12	10.88	8.69	13.97	10.24	17.68	13.05	22.69	17.10
1996	2.41	7.97	10.53	8.48	15.00	11.15	19.65	13.21	24.07	16.20
1997	2.06	7.24	10.43	8.36	14.13	10.60	19.28	13.50	24.42	15.39
1998	1.70	6.57	8.82	7.57	13.52	10.25	17.05	12.37	22.28	15.55
1999	1.98	6.47	8.76	7.32	12.51	9.90	18.04	12.97	21.87	15.91
2000	2.03	6.32	9.58	7.96	12.98	10.49	18.10	12.63	24.58	15.60
2001	1.84	6.93	10.09	6.51	13.92	10.78	17.52	13.32	24.44	15.09
2002	2.16	6.77	10.56	8.24	14.25	10.83	18.63	13.79	22.94	16.94
2003	1.70	7.52	11.15	8.58	14.67	11.21	17.66	14.38	21.16	17.91
2004	--	--	9.86	8.18	14.33	11.08	18.23	14.25	23.63	17.81

Table A7: Average annual individual prey fish consumption (kg of prey fish per striped bass).

	Age 1	Age 2	Age 3		Age 4		Age 5		Age 6	
DATE			Males	Females	Males	Females	Males	Females	Males	Females
1969	--	--	10.48	8.37	15.74	12.46	18.95	15.74	23.25	19.68
1970	--	--	11.70	8.44	15.47	12.06	20.19	16.03	24.29	19.58
1971	--	--	11.25	9.16	16.05	12.73	20.79	17.03	25.01	20.05
1972	--	--	10.70	9.10	15.45	12.04	19.92	15.94	24.08	19.25
1973	--	--	9.03	8.14	15.18	11.92	19.69	15.95	24.14	19.35
1974	--	--	8.55	7.98	14.50	10.96	20.68	16.26	24.25	19.37
1975	--	--	8.98	8.41	14.82	11.98	19.96	15.33	25.32	20.15
1976	--	--	9.99	8.69	15.20	11.72	20.92	16.19	26.02	19.86
1977	--	--	10.38	8.63	15.55	11.84	21.01	16.10	25.18	20.75
1978	--	--	10.24	8.72	15.39	11.99	19.91	16.17	24.49	20.00
1979	--	--	10.63	9.21	14.93	12.43	21.65	17.48	26.20	21.17
1980	--	--	10.14	8.86	14.79	12.11	19.86	16.85	23.57	20.39
1981	2.35	4.68	9.97	8.33	14.54	11.70	19.72	15.50	24.46	18.06
1982	1.59	4.92	9.09	7.73	13.18	9.94	18.17	13.50	22.73	17.00
1983	1.92	4.87	9.31	7.71	14.04	10.79	18.21	14.73	22.66	18.52
1984	1.98	5.16	9.63	8.85	14.25	11.45	20.50	15.80	24.41	19.39
1985	1.68	4.89	10.71	8.65	14.55	11.68	18.50	14.27	23.38	18.26
1986	2.02	4.44	9.98	8.27	14.27	10.75	19.27	15.05	20.99	18.31
1987	2.64	5.24	9.99	8.32	15.64	12.08	21.00	16.34	26.05	20.20
1988	1.97	4.82	9.49	8.13	13.71	11.58	19.79	15.37	22.08	19.71
1989	1.90	4.54	9.92	8.29	14.94	11.86	19.86	16.28	24.55	20.84
1990	1.41	4.92	8.54	7.08	12.42	10.41	17.83	14.16	21.52	17.93
1991	0.88	4.98	9.05	7.49	13.13	11.00	18.77	14.91	22.59	18.84
1992	0.79	5.05	9.59	7.65	13.59	11.07	18.51	13.76	23.22	17.72
1993	0.98	5.04	10.03	8.13	13.70	10.61	18.79	13.41	23.15	16.02
1994	1.03	5.51	8.73	6.95	12.58	9.81	16.59	12.63	21.81	15.63
1995	1.28	5.85	10.81	8.63	13.88	10.18	17.57	12.96	22.55	16.99
1996	1.41	6.54	10.46	8.43	14.91	11.08	19.52	13.13	23.92	16.10
1997	1.20	5.94	10.37	8.31	14.05	10.53	19.16	13.42	24.27	15.29
1998	0.99	5.39	8.77	7.52	13.44	10.19	16.94	12.30	22.14	15.45
1999	1.16	5.32	8.71	7.27	12.43	9.84	17.93	12.89	21.74	15.81
2000	1.18	5.19	9.46	7.86	12.82	10.36	17.87	12.47	24.27	15.40
2001	1.08	5.69	9.96	6.43	13.74	10.64	17.30	13.15	24.13	14.89
2002	1.26	5.56	10.43	8.14	14.07	10.69	18.39	13.61	22.65	16.73
2003	1.00	6.17	11.01	8.48	14.48	11.07	17.44	14.19	20.89	17.69
2004	--	--	9.73	8.08	14.15	10.93	18.00	14.07	23.33	17.58

Table A8: Average annual population level total consumption (millions kg of prey).

	Age 3		Age 4		Age 5		Age 6		Total
DATE	Males	Females	Males	Females	Males	Females	Males	Females	
1969	5.68	4.54	3.31	2.52	2.65	2.04	2.12	1.57	24.43
1970	7.67	5.53	3.82	2.87	2.21	1.47	1.53	1.29	26.39
1971	4.83	3.94	5.90	3.00	2.95	1.40	1.96	0.81	24.78
1972	6.69	5.69	5.00	2.39	5.33	2.23	1.73	1.01	30.07
1973	3.36	3.02	3.98	2.61	2.76	1.51	2.62	1.32	21.19
1974	4.03	3.76	2.60	1.75	3.33	1.83	1.85	1.17	20.31
1975	4.20	3.93	5.69	2.82	3.28	1.56	2.68	1.11	25.27
1976	5.19	4.51	4.42	2.23	2.27	1.33	1.71	1.29	22.96
1977	2.77	2.31	1.09	1.26	3.57	0.86	1.55	0.64	14.06
1978	6.22	5.29	1.65	1.77	1.91	0.65	0.49	0.26	18.25
1979	4.99	4.33	3.94	1.73	1.65	1.84	0.68	0.49	19.64
1980	1.95	1.70	6.29	1.71	2.98	1.07	0.72	1.14	17.56
1981	2.68	2.24	2.69	1.89	1.97	1.38	0.60	0.55	13.99
1982	3.78	3.21	1.54	1.03	0.77	0.76	0.52	0.32	11.93
1983	2.66	2.20	2.37	2.48	3.01	1.02	0.63	0.22	14.59
1984	4.28	3.93	3.13	1.64	2.34	1.19	0.33	0.28	17.12
1985	2.34	1.89	5.36	2.14	2.25	1.01	1.10	0.34	16.42
1986	2.78	2.30	3.54	1.03	3.67	1.49	1.48	0.66	16.95
1987	3.37	2.80	2.41	1.65	2.31	1.16	2.46	0.83	16.99
1988	2.08	1.78	4.18	1.26	1.90	0.69	2.17	0.38	14.43
1989	1.57	1.31	4.86	1.45	1.50	1.30	0.50	0.54	13.03
1990	1.54	1.28	1.16	0.82	2.52	0.63	0.86	0.42	9.23
1991	2.03	1.68	1.55	1.15	2.71	0.80	0.81	0.68	11.42
1992	2.84	2.27	1.81	1.08	1.92	0.72	0.65	0.26	11.55
1993	1.84	1.49	2.73	0.72	1.12	0.49	1.34	0.21	9.93
1994	2.71	2.16	1.26	0.58	0.52	0.39	0.15	0.14	7.91
1995	3.57	2.86	2.82	1.25	1.05	0.51	0.38	0.38	12.81
1996	3.67	2.96	4.57	2.07	1.71	0.63	0.64	0.58	16.81
1997	3.39	2.72	5.60	2.53	1.47	1.05	0.97	0.58	18.31
1998	2.66	2.29	6.61	2.99	1.11	1.33	1.18	0.63	18.79
1999	3.69	3.09	6.25	2.75	1.24	0.99	1.09	1.02	20.12
2000	5.19	4.31	6.63	2.78	1.30	0.57	1.14	1.37	23.29
2001	4.50	2.90	4.10	1.95	2.95	0.86	1.04	0.87	19.17
2002	3.70	2.89	1.12	1.06	4.93	1.16	0.88	0.46	16.20
2003	3.75	2.89	1.31	1.61	0.44	0.80	0.49	2.04	13.34
2004	5.16	4.28	1.75	3.79	1.14	2.30	0.31	0.68	19.41

Table A9: Average annual population level prey fish consumption (millions kg of prey fish).

	Age 3		Age 4		Age 5		Age 6		Total
DATE	Males	Females	Males	Females	Males	Females	Males	Females	
1969	5.68	4.53	3.31	2.52	2.65	2.04	2.11	1.57	24.41
1970	7.66	5.53	3.81	2.87	2.20	1.47	1.53	1.29	26.37
1971	4.83	3.93	5.89	3.00	2.95	1.40	1.95	0.81	24.76
1972	6.68	5.69	5.00	2.38	5.32	2.23	1.73	1.01	30.04
1973	3.35	3.02	3.97	2.61	2.76	1.51	2.62	1.32	21.17
1974	4.03	3.76	2.60	1.75	3.32	1.82	1.84	1.17	20.28
1975	4.19	3.93	5.68	2.82	3.27	1.56	2.67	1.11	25.24
1976	5.18	4.51	4.41	2.23	2.26	1.33	1.71	1.29	22.93
1977	2.77	2.31	1.09	1.26	3.57	0.86	1.55	0.64	14.05
1978	6.21	5.29	1.65	1.77	1.91	0.65	0.49	0.26	18.23
1979	4.94	4.28	3.90	1.71	1.63	1.82	0.67	0.48	19.42
1980	1.92	1.68	6.23	1.69	2.95	1.06	0.72	1.12	17.37
1981	2.65	2.22	2.66	1.87	1.95	1.36	0.59	0.54	13.83
1982	3.74	3.17	1.52	1.01	0.76	0.75	0.52	0.31	11.80
1983	2.63	2.18	2.34	2.46	2.98	1.01	0.63	0.22	14.43
1984	4.23	3.89	3.09	1.63	2.31	1.17	0.33	0.28	16.94
1985	2.32	1.87	5.30	2.11	2.22	1.00	1.09	0.33	16.25
1986	2.75	2.28	3.50	1.02	3.63	1.47	1.47	0.65	16.77
1987	3.33	2.77	2.39	1.63	2.28	1.14	2.43	0.82	16.81
1988	2.05	1.76	4.13	1.25	1.88	0.68	2.14	0.38	14.28
1989	1.56	1.30	4.83	1.44	1.49	1.29	0.50	0.54	12.95
1990	1.53	1.27	1.16	0.81	2.51	0.63	0.85	0.42	9.17
1991	2.02	1.67	1.54	1.14	2.70	0.80	0.81	0.67	11.35
1992	2.83	2.25	1.80	1.07	1.91	0.72	0.64	0.26	11.48
1993	1.82	1.48	2.72	0.72	1.11	0.48	1.33	0.21	9.87
1994	2.70	2.14	1.25	0.58	0.52	0.39	0.15	0.14	7.86
1995	3.55	2.84	2.80	1.24	1.04	0.51	0.38	0.38	12.74
1996	3.65	2.94	4.54	2.05	1.70	0.62	0.63	0.57	16.71
1997	3.37	2.70	5.57	2.51	1.46	1.04	0.97	0.58	18.20
1998	2.65	2.27	6.56	2.97	1.10	1.32	1.18	0.62	18.68
1999	3.67	3.07	6.21	2.73	1.23	0.98	1.08	1.01	19.99
2000	5.12	4.26	6.55	2.74	1.29	0.56	1.12	1.35	22.99
2001	4.44	2.87	4.05	1.93	2.91	0.85	1.02	0.86	18.93
2002	3.65	2.85	1.10	1.05	4.86	1.15	0.87	0.46	16.00
2003	3.70	2.85	1.30	1.59	0.43	0.79	0.49	2.02	13.17
2004	5.09	4.23	1.73	3.74	1.13	2.27	0.30	0.67	19.17

Table A10: FMWT indices for “age 0” striped bass, delta smelt and threadfin shad.

	“Age 0” Striped Bass		Delta Smelt		Threadfin Shad	
DATE	Index	Normalized Value ¹	Index	Normalized Value ¹	Index	Normalized Value ¹
1969	8072	0.65	313	0.19	8398	0.55
1970	8276	0.66	1673	1.00	4063	0.27
1971	9475	0.76	1303	0.78	6906	0.45
1972	6116	0.49	1265	0.76	5113	0.33
1973	4286	0.34	1145	0.68	1232	0.08
1974 ²	--	--	--	--	--	--
1975	4548	0.36	697	0.42	718	0.05
1976 ²	--	--	--	--	--	--
1977	883	0.07	480	0.29	9016	0.59
1978	2598	0.21	572	0.34	2099	0.14
1979 ²	--	--	--	--	--	--
1980	1493	0.12	1654	0.99	7279	0.48
1981	4531	0.36	374	0.22	6674	0.44
1982	4466	0.36	333	0.20	2101	0.14
1983	12473	1.00	132	0.08	2088	0.14
1984	6581	0.53	182	0.11	757	0.05
1985	1760	0.14	110	0.07	821	0.05
1986	3943	0.32	212	0.13	2829	0.19
1987	1350	0.11	280	0.17	3475	0.23
1988	477	0.04	174	0.10	2409	0.16
1989	442	0.04	366	0.22	6897	0.45
1990	1320	0.11	364	0.22	5859	0.38
1991	944	0.08	689	0.41	3316	0.22
1992	2045	0.16	156	0.09	2958	0.19
1993	1556	0.12	1078	0.64	6678	0.44
1994	1259	0.10	102	0.06	2305	0.15
1995	478	0.04	899	0.54	3337	0.22
1996	392	0.03	127	0.08	4758	0.31
1997	568	0.05	303	0.18	15267	1.00
1998	1224	0.10	420	0.25	5748	0.38
1999	541	0.04	864	0.52	7527	0.49
2000	390	0.03	756	0.45	12977	0.85
2001	731	0.06	603	0.36	14401	0.94
2002	73	0.006	139	0.083	1731	0.113
2003	111	0.009	210	0.126	1963	0.129
2004	54	0.004	74	0.044	1294	0.085

¹Bold values are the maximum FMWT index for each species and represent the quantity to which each respective FMWT index was normalized.

²FMWT indices not available.