Individual-level and Population-level Historical Prey Demand of San Francisco Estuary Striped Bass using a Bioenergetics Model

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Abstract

Striped bass are both a major predator of native fishes and support a recreational fishery in the San Francisco Estuary (SFE). Quantifying their demands on their prey is important for understanding long-term trends of fish in the SFE, and the recent sudden declines in certain species. In this study, we: (1) applied a bioenergetics model of sub-adult (age 1 and age 2) and adult (age 3+) striped bass (*Morone saxatilis*) to quantify long-term consumption patterns from 1969 through 2004 in the SFE; (2) developed a method to estimate the abundances of sub-adult striped bass; (3) evaluated how consumption varied by age and sex; and (4) identified factors impacting the resulting consumption estimates. On a 'per capita' basis, modeled individual prey fish consumption by striped bass increased after 1990 for age-1 cohorts, and individual total and prey fish consumption increased after 1994 for age-2 cohorts. Conversely, individual total and prey fish consumption by adult striped bass decreased over the period analyzed. This decline in individual consumption over the study period was related to a decline in mean length at age of adult cohorts. As expected, long-term trends in population consumption (total and prey fish) by all striped bass cohorts (ages 1 though 6) closely followed their respective population abundance trends. Population total consumption and prey fish-specific consumption by sub-adult striped bass was found to be similar to the population consumption by adult striped bass, due largely to the high abundance of sub-adults. Unlike adult striped bass that may emigrate and forage in the Pacific Ocean, the majority of sub-adult striped bass reside permanently within the SFE; hence, consumption by the relatively abundant sub-adult population may have significant impacts upon their estuarine prey species.

Key Words: Biogenetic model, striped bass, *Morone saxatilis,* consumption, abundance, San Francisco Estuary, pelagic fish

Introduction

In the San Francisco Estuary (Figure 1; herein referred to as SFE), abundance of striped bass (*Morone saxatilis*), threadfin shad (*Dorosoma petenense*), delta smelt (*Hypomesus transpacificus*), and longfin smelt (*Spirinchus thaleichthys*) has fluctuated greatly over time, with a sharp decline beginning around 2000 (Feyrer et al. 2007; Sommer et al. 2007). Numerous factors have been implicated in the Pelagic Organism Decline (POD) (Sommer et al. 2007) and are thought to include: (a) effects of reduced stock (Bennett 2005; Feyrer et al. 2007; Feyrer et al. 2009); (b) habitat changes (Atwater et al. 1979; Nichols et al. 1986; Lehman et al. 2005; Feyrer et al. 2007; Ostrach et al. 2008); (c) water project entrainment (Kimmerer 2008; Kimmerer and Nobriga 2008; Grimaldo et al. 2009); (d) food web effects (Kimmerer 2008); and (e) predation (Nobriga and Feyrer. 2007; Sommer et al. 2007). The work reported herein specifically focuses on quantifying long-term trends in the consumption by SFE striped bass as a measure of long-term changes in predation of fish by striped bass.

Striped bass, inclusive of all ages, are found throughout the SFE, while adults (age 3 and older) are additionally found along the California coastline (for brevity, striped bass that spawn in the SFE are herein referred to as SFE striped bass). Originally introduced into the SFE over 100 years ago, SFE striped bass quickly 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; Nobriga and Feyrer 2007). Largely to support this valuable recreational fishery, sub-adult striped bass were stocked into the SFE from 1980 to 2001. Spawning occurs annually in the fresh waters of the Sacramento

River and historically occurred during high flow years in the San Joaquin River (Turner and Chadwick 1972). The typical life history pattern is for eggs and larvae to disperse down into the upper SFE and the salt/fresh water convergence zone, where they develop into juveniles and disperse throughout the SFE (Turner and Chadwick 1972; Stevens et al. 1985; Hassler 1988). Striped bass are opportunistic predators. Prey selection is largely mouth gape dependent, ranging from invertebrates such as copepods, amphipods, and mysids to fish (e.g., Nobriga and Feyrer 2008; Nobriga and Feyrer 2007; Kimmerer et al. 2000). Evaluating the diets of striped bass at different life-stages is important, because the consumption of certain prey types can lead to more (or less) energy available for growth (Hartman and Brandt 1995a, 1995b; Hanson et al. 1997). For example, adult striped bass in the SFE primarily feed upon fish, a relatively high-energy source, while the younger striped bass rely more upon lower-energy invertebrate prey (Stevens 1966; Hassler 1988; Feyrer et al. 2003; Nobriga and Feyrer 2007). Conceptually, both the type and quantity of prey consumed are important regulators in striped bass growth. The present study is focused on broad categorical prey types (e.g., fish, decapods, isopods, mysids) and not specific prey species (e.g., delta smelt, longfin smelt, threadfin shad) due to the coarse resolution of the available empirical data.

While other studies have evaluated cumulative annual consumption by striped bass (Hartman and Brandt 1995b; Cyterski et al. 2002) and consumption over shorter time periods (Nelson et al. 2006; Tuomikoski et al. 2008; Vatland et al. 2008), none have evaluated consumption over extended periods of time (i.e., decades). Relationships between striped bass prey consumption, observed growth and abundance, as well as water temperature, have been established through bioenergetics models for stocks in Chesapeake Bay (Hartman and Brandt 1995a, 1995b) and

Lake Powell (Vatland et al. 2008), but have yet to be established for the Pacific Coast stocks (i.e., fish that spawn in SFE or Coos Bay, OR). Bioenergetics models, as applied to fish species, use an energy budget approach for the growth of an individual fish and are typically used to calculate cohort or population-level consumption. Energy available for growth is determined by the energy of the food consumed less the energy costs of metabolism, egestion, excretion, and reproduction (Hartman and Brandt 1995a, 1995b; Hanson et al. 1997).

In this study, we estimated time-series values of individual and population consumption by SFE striped bass, stratified by age and sex, to address three questions: (1) is there evidence of temporal trends in consumption; (2) did consumption vary by age-class and gender; and (3) what factors influenced consumption by the SFE striped bass population? Given the lack of a bioenergetics model calibrated specifically to SFE striped bass, we used the model calibrated by Hartman and Brandt (1995a) for Chesapeake Bay striped bass. Our focus in this study was on trends in consumption over time and among age and gender classes; examination of the trends is reasonable given the uncertainties of how well the model applied to striped bass in the SFE.

Methods

For sub-adult SFE striped bass (considered as age 1 through age 2), average annual total consumption of all prey and consumption of prey fish was estimated at the individual and population level for cohorts from 1981 through 2003. For adult SFE striped bass (considered as age 3 through age 6), average annual total and prey fish consumption was estimated at the individual and population level for cohorts from 1969 through 2004. These time periods were selected based on the availability of long-term datasets.

Our primary approach used the Wisconsin bioenergetics model (Hartman and Brandt 1995a, 1995b; Hanson et al. 1997), which is based on physiological and allometric relationships that regulate fish growth. For this study, we obtained previously developed bioenergetic parameters from laboratory studies performed on Chesapeake Bay stocks of striped bass (Table 1; Hartman and Brandt 1995a, 1995b). Historical datasets for SFE striped bass weights, diets, and water temperatures were used as inputs to the model.

Water Temperature

Water temperature data from the SFE was compiled from three different datasets to span 1969 through 2004. Monthly water temperatures from United States Geological Survey (USGS) Water Quality Cruises were used for 1969 through 1975[1]. Bi-monthly water temperatures from California Department of Water Resources (DWR) discrete monitoring data were used for 1976 through 1982[2]. Averaged daily water temperatures from four DWR continuous monitoring[3] stations in the SFE were used for 1983 though 2004 (DWR, Division of Environmental Services, Real Time Monitoring). Several years of overlapping temperature data between each dataset were analyzed to ensure that the datasets could be reliably combined.

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[1] *http://sfbay.wr.usgs.gov/access/wqdata/query*

[2] *http://www.baydelta.water.ca.gov/emp*

[3] The four sites are: Mossdale (C7A), Stockton (P8), Antioch (D12), and Rio Vista (D24). (*http://www.baydelta.water.ca.gov/emp/Stations/D1641_station_gallery.html)*

Because the temporal resolution of data was not consistent among the three data sources, the available data was used to fit a regression model of temperature as a function of day (following Hogg et al. 2000, McCloskey 1986) for each year from 1969 to 2004:

$$T = b \cdot \cos\left(a + \frac{2\pi \cdot j}{J} \right) + c \qquad (1)$$

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 temperature model was then used to predict water temperature on a daily basis for each year.

Adult Striped Bass Abundance Estimates

Peterson abundance estimates of SFE striped bass adults (age 3 through age 7) were obtained from California Department of Fish and Game's (DFG) mark-recapture survey for 1969 though 2004 (Figure 2), except for 1995, 1997, 1999 and 2001, when no survey data were collected. In this dataset, fish age was determined from annular rings on scale samples and gender was determined by the extrusion of milt (fish lacking milt were assumed to be females). The population abundances during the missing years were estimated by averaging the prior and subsequent year's abundance for each respective cohort. This mark-recapture survey is partially inclusive of adult striped bass found in the Pacific Ocean and hence is not entirely representative of year-round population abundances found within the SFE.

Sub-Adult Abundance Estimates

The population abundance of sub-adult SFE striped bass (ages 1 and 2) has, to date, been unknown. Several different long-term survey programs, such as the DFG's Fall Midwater Trawl (FMWT), Summer Townet Survey, and the Bay Study Otter Trawl, have been used to estimate abundance indices of age-0, age-1, and age-2 striped bass for numerous years. However, these surveys were not designed to specifically estimate the population abundance of sub-adult striped bass. Additionally, due to other factors such as the location of sampling stations, the ability of striped bass to avoid the sampling gear, and a possible recent shift in sub-adult geographic distributions, it is difficult to establish a suitable method to estimate population numbers from the abundance indices obtained from the trawl surveys. As an example, we used the approach of Newman (2008) to estimate sub-adult striped bass population abundance from the FMWT survey; however, the resulting estimates of age-0 population abundance were generally lower than the corresponding age-3 population abundance, which is clearly not reasonable.

As an alternative to using trawl data, we estimated the age-1 striped bass population by coupling: (1) numbers of age-3 fish with (2) survival estimates of age-1 to age-3 hatchery striped bass stocked in the SFE between 1981 and 1990 (DFG 1999; Harris and Kohlhorst 2002). In addition, the survival estimates of hatchery fish between 1981 and 1990 were regressed against the corresponding values of the FMWT index, age-3 abundance, average estimated Delta outflow during April-June, and the average position of X2 during April-June. X2 is the distance from the Golden Gate Bridge to the 2 psu isohaline, and is used extensively as an indicator of habitat for fish in the SFE (Jassby et al. 1995). Both Delta outflow and the position of X2 were obtained from Interagency Ecological Program's (IEP) Dayflow program[4]. A stepwise linear regression

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[4] *http://www.water.ca.gov/dayflow*

was used to determine the variables (i.e., FMWT index, age-3 abundance, average outflow, and average X2) that resulted in the best-fit regression. Ultimately, the additive sum of the average position of X2 (April-June) for a three-year span (e.g., for a survival estimate in year *y*, $X2_y + X2_{y+1} + X2_{y+2}$) had the most robust and statistically significant correlation ($R^2=0.93$) with survival of age-1 to age-3 hatchery striped bass stocked into the SFE between 1981 and 1990. Other researchers have shown statistical relationships between X2 and survival (Kimmerer et al. 2001). The linear model was then used to infer the survival of age-1 to age-3 striped bass for each year from 1991 to 2003 based on the corresponding known values of X2. The survival estimates between 1991 and 2003 were then used to estimate the number of age-1 striped bass based on corresponding age-3 population numbers. As a cautionary note, survival rates of hatchery-reared fish may not accurately reflect survival rates associated with wild fish. Error analyses such as Monte Carlo simulations and confidence interval construction are advisable in future studies to address errors associated with the linear interpolation scheme used to estimate age-1 to age-3 survival rates.

Annual age-2 striped bass population abundance was approximated from age-3 population estimates using natural mortality estimates for age-3 to age-4 fish. Natural mortality rates simply remove the effect of harvest (i.e., angling) from the total mortality rate. It was assumed that natural mortality rates of age-3 to age-4 fish were comparable to natural mortality rates of age-2 to age-3 fish. From DFG's mark and recapture dataset, the natural mortality rate for age-3 to age-4 striped bass was determined from 1981 through 1993 and for 2002 and 2003 (Chadwick 1968; Miller 1974; Stevens 1977, 1980; Stevens et al. 1985; White 1986; Kohlhorst unpublished, 1999). For the years when natural mortality rates could not be calculated due to the lack of tagging (1994 through 2001), rates were either estimated from DFG's Creel surveys (1995, 1997, 1999 and 2001), or by averaging the rates from the prior and subsequent year (1994, 1996, 1998, and 2000).

Striped Bass Weight and Annual Growth

Two long-term monitoring programs collected fork length data of SFE striped bass: (1) Bay Study, which sampled mainly age-1 fish from 1980 through 2004 (Armor and Hergessell 1985), and (2) mark-recapture sampling, which generally included 42 cm fork length and larger male and female fish of age 3 through age 7, from 1969 through 2004 (Kimmerer et al. 2000). Both programs collected data during the spring of each year; however, only April and May were recorded consistently every year. Fork lengths from April and May of each year were converted into weights using a length-weight relationship (based on Kimmerer et al. 2005):

$$W = \left(6.6 \cdot 10^{-6}\right) \cdot L^{3.12} \tag{2}$$

where L is fork length in millimeters and W is fish weight in grams. Individual weights were then grouped into cohorts for each study year to determine average cohort weight. Annual growth was then calculated in a given year (Y) by subtracting the average weight of an older cohort ($X+1$) in the subsequent year ($Y+1$) from the average weight of a younger cohort (X) in the given year (Y).

Striped bass size data were incomplete in both the Bay Study and mark-recapture databases. Specifically, both monitoring programs did not sample age-2 striped bass and the mark recapture sampling was not performed in 1995, 1997, 1999 or 2001. In both situations, the lack of data necessitated the calculation of annual growth over two years, rather than one year. Moreover, adult striped bass length, and subsequently weight data, were skewed for the age-3 and age-4 cohorts due to a legal take size restriction in the mark-recapture study of 42 cm fork length and larger. To account for the impact of the 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. The mean of the normal distribution was then used as the mean weight for age-3 and age-4 cohorts in the bioenergetics model. Because the DFG's mark-recapture survey is partially inclusive of adult striped bass that may have migrated to and from, or were found in, the Pacific Ocean and upstream tributaries, annual growth calculated from this dataset may not be representative of growth patterns from the SFE alone.

Striped Bass Diet

The diet composition of SFE striped bass cohorts was compiled from a variety of sources (i.e., Stevens 1966; Feyrer et al. 2003; DFG *unpublished data*) to span the period from 1969 to 2004 (Table 2). In each of the datasets, the proportions of different prey consumed were determined from analyses of striped bass stomach contents. For the purposes of this analysis, several prey types were combined to simplify the bioenergetics modeling process. Thus, the dietary categories summarized in Table 2 reflect empirical data as applied in the bioenergetics model.

Striped Bass and Striped Bass Prey Energy Densities

Energy densities of SFE striped bass and their prey were obtained from several literature sources. Striped bass energy densities were approximated as a function of age using one of two life-stage-dependent regression models derived in this study from the data of Hartman and Brandt (1995b):

$$e_b = k \cdot (A / 365) + l \tag{3}$$

$$e_b = k \cdot \sin\left(2\pi \cdot (A / 365)\right) + m \cdot \cos\left(2\pi \cdot (A / 365)\right) + l \tag{4}$$

where e_b is the striped bass energy density ($J \cdot g_{bass}^{-1}$), A is striped bass age (d), the value 365 converts age from days into years, and k, l and m are parameters (Table 1) with units of ($J \cdot g_{bass}^{-1} \cdot yr^{-1}$). Equation 3 is applicable to striped bass from 365 through 690 days of age, and Equation 4 is applicable to striped bass greater then 690 days of age. Energy densities of different striped bass prey types were obtained from the literature (Steimle and Terranova 1985; Pope et al. 2001; Chipps and Bennett 2002; Vatland et al. 2008). Because striped bass consume multiple prey types with different energy densities, a weighted average of energy density ($\overline{e_p}$) was taken based upon the proportions of each different prey type consumed:

$$\overline{e_p} = \sum_{z=1}^{z=n} \left(\alpha_z \cdot e_{p,z} \right) \tag{5}$$

where z represents the number of different prey types, α_z is the fractional proportion of prey z out of the total prey consumed, and $e_{p,z}$ is the energy density of prey type z ($J \cdot g_{prey}^{-1}$) (Table 2).

Striped Bass Reproduction

The energy losses associated with reproduction (i.e., gonad development and gamete production) were accounted for in the bioenergetics model for both male and female adult striped bass. Ripe gonad weights in both male and female fish were assumed a function of fish weight. Hence, an empirical relationship was developed relating gonad weights of both males and females to fish weight using empirical field data from age-4 through age-7 fish collected by DFG in 2008 and 2009 (DFG *unpublished data*):

$$W_g = r_c \cdot W_{ts} + r_i \tag{6}$$

where W_g is gonand weight (grams), W_{ts} is the striped bass weight on the day of spawning (grams), and r_c (unitless) and r_i (unitless) are gender-specific parameters (Table 1). On the selected day of spawning (i.e., April 30) of each year, the reproductive losses were computed and subtracted from the weight of the spawning fish at the time. Additionally, we assumed that the 'ripe' gonad mass was equal to the mass of gametes produced, thus upon the release of gametes, the gonad mass returns to a nominal value. Reproductive losses were not considered for striped bass younger than age 4 due to: (i) limitations of the empirical gonad dataset, and (ii) the unknown fraction of sexually mature age-3 striped bass.

Bioenergetics Model Simulation

The bioenergetics model as described by Hartman and Brandt (1995a, 1995b) is based upon an energy balance whereby net growth (defined as a change in weight per unit time) is governed by:

$$Growth = \frac{\overline{e_p}}{e_b} \cdot \left(Consumption - Metabolism - Egestion - Excretion\right) \cdot W \tag{7}$$

where *Consumption*, *Metabolism*, *Egestion*, and *Excretion* have units of $g_{prey} \cdot g_{bass}^{-1} \cdot d^{-1}$ and W is the initial striped bass weight (grams). In the present study, we modified Equation 7 to include an additional term reflecting weight loss associated with reproduction, specifically the gonad weight expressed in Equation 6. General details of the bioenergetics model are discussed elsewhere (Hartman and Brandt 1995a, 1995b); values of model parameters used in this study are summarized in Table 1. Details of the bioenergetics model specific to this study are discussed below.

The consumption term in Equation 7 explicitly refers to the actual consumption rate, which is expressed as a proportion of the fish's maximum consumption rate. Fish, like the majority of other species, have a maximum rate at which they can consume food and that varies based on numerous physiological variables such as age, body weight, sex, and ambient temperature. The maximum consumption rate ($C_{\max}$) is computed as:

$$C_{\max} = CA \cdot W^{CB} \cdot f(T) \tag{8}$$

where $C_{\max}$ has units of ($g_{prey} \cdot g_{bass}^{-1} \cdot d^{-1}$); CA ($g_{prey} \cdot g_{bass}^{-1} \cdot d^{-1}$) and CB (unitless) are parameters (Table 1); and *f(T)* is the Thornton and Lessem (1978) temperature dependence function (unitless), which utilizes constants from Table 1 (Thornton and Lessem 1978; Hartman and Brandt 1995a). The maximum consumption rate assumes a fish is feeding *ad libitum*. The actual consumption rate is a proportion of the maximum consumption:

$$C = p \cdot C_{\max} \tag{9}$$

where C has units of ($g_{prey} \cdot g_{bass}^{-1} \cdot d^{-1}$) and the proportion of the maximum consumption (p) is unitless and has values between zero and 1. The proportion of maximum consumption can be viewed as a measure of prey availability; when prey are scarce, p is small.

The metabolism term in Equation 7 refers to total metabolism, determined by the additive sum of routine metabolism (i.e., respiration) and specific dynamic action (i.e., digestion). Routine metabolism (R) is dependant upon fish weight, age, water temperature, activity, and the type of prey consumed:

$$R = RA \cdot W^{RB} \cdot e^{(RQ \cdot T)} \cdot ACT \cdot \left(OXY \cdot \overline{e}_p^{\,-1} \right) \tag{10}$$

where R has units of ($g_{prey} \cdot g_{bass}^{-1} \cdot d^{-1}$); RA ($g_{O2} \cdot g_{bass}^{-2} \cdot d^{-1}$), RB (unitless), and RQ (˚C^{-1}) are parameters (Table 1); ACT (unitless) is the activity multiplier of metabolism (Table 1 and Hartman and Brandt 1995a); and OXY ($J \cdot g_{O2}^{-1}$) is the oxycalorific coefficient (Elliott and Davison 1975). Specific dynamic action (SDA) is typically calculated as a proportion of consumption and egestion (Table 1; Hartman and Brandt 1995a; Hanson et al. 1997).

The bioenergetics model simulations were run on a daily time-step over the course of a year (365 or 366 days, depending upon leap years). At the model start time (t = day 1): (i) the initial fish weight was obtained from the historical empirical field data, (ii) the average water temperature was obtained from the temperature model (Equation 1), and (iii) a value for the proportion of maximum consumption (*p*) was assumed. The combination of this information then allowed for the calculation of a new fish weight (Equation 7) for the next day. With each subsequent time step, the value of *p* remained fixed at the assumed value, the new striped bass weight becomes the previous weight, and a new water temperature was obtained from the temperature model (Equation 1). Unlike the other terms of Equation 7, the reproductive term was only applied on a single day (i.e., April 30, the selected spawning day) as described above for sexually mature adult striped bass. At the end of the simulation year (t = 365 or 366 days), final fish weight (W_{final}) was subtracted from the initial fish weight ($W_{initial}$) to obtain the annual growth (*G*) in grams for that year:

$$G = W_{final} - W_{inital} \tag{11}$$

The modeled annual growth was compared to the observed annual growth obtained from empirical field data. Values of the proportion of maximum consumption (*p*) were adjusted iteratively in the above simulation until a 0.5% difference (or less) was achieved between the values of modeled and observed annual growth.

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

$$C_T = \sum_{t=1}^{t=t_{\max}} \left(C \cdot W\right) \tag{12}$$

where t is time (days), t_{max} is 365 or 366 days (depending upon leap year), and C_T is annual consumption ($g_{prey} \cdot yr^{-1}$) herein referred to as individual total consumption. Individual total consumption refers to the total amount of all prey types consumed by an average individual modeled striped bass. Individual prey fish consumption was calculated by multiplying the fraction of prey fish in the diet of striped bass (Table 2) by the value of individual total consumption.

For the years lacking annual growth data (as described above), growth was calculated over a two-year period. Accordingly, the bioenergetics model was run over a two-year period to determine the proportion of maximum consumption (p), and the resulting p was then applied over the respective two-year period to estimate average annual individual total consumption.

Striped Bass Population Consumption

Population total consumption and population prey fish consumption by SFE striped bass were calculated by incorporating the sub-adult and adult abundance estimates. Population total consumption reflects the total amount of all prey types consumed in a given year by a specific age cohort and was calculated by multiplying the average individual total consumption by the corresponding population numbers for that given year and cohort. Similarly, population prey fish consumption reflects the total amount of prey fish consumed in a given year by a specific age cohort and was calculated by multiplying the average individual prey fish consumption by the corresponding population numbers. Confidence intervals (CIs) on the total adult abundances (when summed across all adult cohorts), as reported by the DFG, were multiplied by the total population consumption (when summed across all adult cohorts), to determine confidence levels associated with the total population consumption. Inner-annual mortality of striped bass was not considered in this study, as seasonal estimates of sub-adult or adult abundance (or survival) were not available; hence, population total and prey fish consumption estimates reported herein are conservative estimates of actual values.

Statistical Analyses

Pearson's correlation coefficients (*r*) were used to investigate relationships among the proportion of maximum consumption, annual average water temperature, striped bass annual growth, weight, abundance estimates and individual and population consumption (both total and prey fish). Significant correlations were described by coefficients having relatively high magnitudes ($r > 0.50$) with a probability of < 0.05.

Results

Historical Datasets

Average annual water temperatures over the study area ranged from 14 to 18 ˚C for 1969 through 2004. Peterson abundance estimates for adult striped bass ranged from 800,000 to over 2 million, and were variable throughout the study period (Figure 2). For fish older than age 4, mean length at age, and subsequent calculated mean weight, began to decrease in the early 1990s. Adult striped bass diet (Table 2) consisted primarily of prey fish during all time periods analyzed and was not predicted to change significantly over time. Sub-adult striped bass became more piscivorous during the study period beginning in 1990, with a commensurate decline in mysids consumption. Prey fish in the diets of age-1 and age-2 striped bass increased from 2.5 to 12.2%

and 78.5 to 82.1%, respectively, between 1980 and 1990 (Table 2), and mysids in the diets decreased from 95.9 to 58.5% and 18.4 to 8.4%, respectively. The increase in piscivory by the sub-adults likely occurred gradually up to 1990; however, this was modeled as a step increase beginning in 1990 due to decadal-level availability of the available diet data.

Sub-Adult Abundance Estimates

Population abundance estimates for the sub-adult cohorts appeared to vary significantly from year to year, with numbers higher than the corresponding adult levels (Figures 2 and 3). Age 2 population abundance approximately doubled during the mid to late 1990s; however, no other discernable temporal trend in population abundance was apparent in either cohort. Annual survival rate estimates of age-1 fish were generally lower than age-2 fish ranging from 0.615 yr^{-1} to 0.052 yr^{-1} (mean = 0.250 yr^{-1}, std. dev. = 0.165 yr^{-1}) for age 1 to age 2 and from 0.909 yr^{-1} to 0.209 yr^{-1} (mean = 0.499 yr^{-1}, std. dev. = 0.215 yr^{-1}) for age 2 to age 3. Overall survival rates from age 1 to age 3 ranged from 0.175 yr^{-1} to 0.027 yr^{-1} (mean= 0.101 yr^{-1}, std. dev.= 0.038 yr^{-1}).

Proportion of Maximum Consumption

The estimated proportion of maximum consumption (p) differed between the sub-adult and adult striped bass cohorts and varied throughout the study period for these cohorts. Within the adult striped bass cohorts, values of p were similar for each age cohort in each of the modeled years. Sub-adult cohorts were found to have a greater p than adults for each of the modeled years and p was correlated to sub-adult annual growth ($r = 0.53$). Significant correlations of p to annual average water temperatures, striped bass weight or adult annual growth (i.e., other factors that can influence p) were not observed.

Individual Total Consumption per Striped Bass

Individual total consumption increased with cohort age and varied among years for both sub-adult and adult cohorts (Figures 4 and 5). For age-1 cohorts, individual total consumption varied between a maximum of 2.09 kilograms of prey per striped bass in 1987 and a minimum of 1.07 kilograms of prey per striped bass in 1993 (Figure 4), with no apparent long-term trend. Conversely, there was an apparent long-term increase in individual total consumption by the age-2 striped bass cohort, as after 1994 consumption by this cohort remained higher than in the majority of previous years. Additionally, there were substantial fluctuations in individual total consumption by this cohort (Figure 4), ranging between a maximum of 8.41 kilograms of prey per striped bass in 1997 and a minimum of 5.35 kilograms of prey per striped bass in 1994. For the adult striped bass cohorts, there was a long-term decrease in individual total consumption from 1969 through 2004 (Figure 5).

The correlation of individual total consumption to striped bass weight was significant for adults ($r = 0.98$) but not for sub-adults. Additionally, the individual total consumption by adults and sub-adults were not statistically correlated to the average annual water temperature, the proportion of maximum consumption or annual growth over the respective time periods (1969-2004 for adults, 1981-2003 for sub-adults).

Individual Prey Fish Consumption per Striped Bass

Individual prey fish consumption by striped bass cohorts generally followed temporal trends apparent in individual total consumption. The proportion of prey fish consumed by age-1 striped bass increased starting in 1990, and the consumption rates of prey fish varied from a maximum of 0.25 kilograms of prey fish per striped bass in 1990 to a minimum of 0.03 kilograms of prey fish per striped bass in 1982 (Figure 6). Individual prey fish consumption by the age-2 cohort varied from a maximum of 6.90 kilograms of prey fish per striped bass in 1997 to a minimum of 4.39 kilograms of prey fish per striped bass in 1994. Consistent with the long-term trend in individual total consumption, prey fish consumption by the age-2 cohort increased after 1994. Individual prey fish consumption by adult striped bass closely mirrored the consumption values and trends observed in individual total consumption (Figure 5) by the respective adult cohorts, as prey fish constituted the majority proportion of the adult striped bass diet.

Sub-Adult Striped Bass Population Total Consumption

When summed (age 1 plus age 2), sub-adult population total consumption peaked in 2000 at a value of 41.43×10^6 kg of prey and reached a minimum in 1988 at a value of 8.30×10^6 kg of prey (Figure 7). Sub-adult population total consumption was variable from year to year and was statistically correlated to the sub-adult abundance estimates for age 1 ($r = 0.91$) and age 2 ($r = 0.98$). There was an increase in age-2 population total consumption from 1995 through 2000, likely attributable to the increase in the abundance of this cohort during the same time period.

Adult Striped Bass Population Total Consumption

Adult population total consumption, when summed across all adult cohorts, peaked in 1972 at a value of 30.49×10^6 kg of prey and reached a minimum in 1994 at a value of 8.21×10^6 kg of prey (Figure 8C). Following the adult abundance trends (Figure 2), adult population total consumption declined from 1969 through 1994, and then increased though 2000, where it began to decline thereafter, particularly for females (Figure 8A). Adult population total consumption was statistically correlated to striped bass abundance estimates (*r* = 0.95). Additionally, adult population total consumption by older striped bass cohorts was often less than that of younger cohorts (Figure 8A and Figure 8B), even though older cohorts consume a greater quantity of prey on an individual basis (Figure 5); this result is consistent with the typically lower abundance of older cohorts. Confidence intervals on adult population total consumption (when summed across all adult cohorts) were quite large; on average differing by almost 11×10^6 kg of prey between the lower and upper CIs (Figure 8C), reflective of the large confidence intervals associated with the adult abundance estimates.

Sub-Adult Striped Bass Population Prey Fish Consumption

When summed, sub-adult population prey fish consumption peaked in 2000 at a value of 26.17×10^6 kg of prey fish and reached a minimum in 1988 at a value of 2.60×10^6 kg of prey fish (Figure 9). Sub-adult population prey fish consumption was low for age-1 cohorts due to the small percentage of fish in their diet, and had a step increase starting in 1990 associated with the observed step increase of fish in their diet (Table 2). Population prey fish consumption by the age-1 cohorts was statistically correlated with the age-1 abundances (*r* = 0.85) and with age-1 individual prey fish consumption (*r* = 0.83). For the age-2 cohorts, population prey fish consumption was generally consistent during the 1980s, and steadily increased during the 1990s before significantly declining in 2001. This trend in prey fish consumption by age-2 cohorts was statistically correlated with the trend in age-2 abundance (*r* = 0.98) but was not statistically correlated with age-2 individual prey fish consumption.

Adult Population Prey Fish Consumption

Trends in adult population prey fish consumption followed patterns similar to the trends in adult population level total consumption. When summed, the adult population prey fish consumption across the adult cohorts peaked in 1972 at a value of 30.46×10^6 kg of prey fish and reached a minimum in 1994 at a value of 8.16×10^6 kg of prey fish. Since diets of adult cohorts consist primarily of fish, trends in adult population prey fish consumption closely mirrored the trends in adult population total consumption previously discussed and depicted in Figure 8.

Discussion

The rapid collapse of the pelagic fish community in the SFE (i.e., POD) has been a contributing factor to a major water management crisis in California (Service 2007; Sommer et al. 2007). "Top down" effects from predators are considered one of a suite of possible mechanisms responsible for the decline in pelagic fishes in the SFE (Sommer et al. 2007; Baxter et al. 2008). This hypothesis is consistent with studies from other ecosystems, where top-down effects from striped bass can strongly structure the communities of lower trophic levels (Hartman and Brandt 1995b; Hartman 2003; Vatland et al. 2008). From a long-term perspective, predation effects almost certainly changed with the introduction of striped bass to the Delta in 1879. Indeed, Moyle (2002) proposed that striped bass, a fast-growing and schooling feeder, were likely a much more effective consumer of pelagic prey than native predators. However, because striped bass and other pelagic fishes coexisted for many decades before the POD, predation by striped bass is not the sole cause of recent declines. Moreover, the diet studies analyzed in this study combined with the opportunistic feeding behavior of striped bass and the relatively low abundances of ‘species of concern’ (e.g., delta smelt, longfin smelt, and salmon smolts), also support the notion that predation by striped bass is not the sole cause of the decline of other pelagic fish. Nonetheless, it is possible that established predator-prey relationships have been disrupted by environmental changes or species introductions, a fairly common occurrence in aquatic communities (Brown and Moyle 1991, Carpenter et al. 2001, Frank et al. 2005).

Prior to this study, we could only speculate about how recent predation rates of SFE striped bass correspond to historical levels, including the POD time period. The present study provides an evaluation of how consumption by SFE striped bass may have changed over the past several decades, and possible factors influencing consumption at the individual and population level.

Sub-Adult Striped Bass Abundance Estimates

In this study, we developed estimates of sub-adult population abundance using a combination of relationships with X2, adult abundance, and hatchery fish survival in the SFE. To our knowledge, these are the first published estimates of sub-adult population abundance and survival rates for the SFE striped bass. Two primary observations of biological significance in the SFE arose from estimates of sub-adult population abundance. First, sub-adult striped bass are much more abundant than the adult population. Hence, sub-adult striped bass are the most abundant pelagic predator in the ecosystem. Moreover, their effects are not limited to pelagic habitats, given that sub-adult striped bass are abundant in inshore areas (Nobriga and Feyrer 2007). Second, estimated sub-adult numbers of age-1 and age-2 fish do not show a decline similar to young-of-year striped bass (age-0 fish) observed in the FMWT index (e.g., Feyrer et al. 2007; Sommer et al. 2007; Kimmerer et al. 2000). Hence, if increases in sub-adult survival due to density dependent mechanisms are likely an explanation of an apparent ‘disconnect’ between young-of-year and older striped bass (Kimmerer et al. 2000), the increase in survival rate must have occurred specifically in the young-of-year striped bass. However, given that the population estimates of young-of-year striped bass obtained in this study by applying the method of Newman (2008) to FMWT data resulted in estimates of population numbers generally less than age-3 fish, the FMWT survey may not accurately reflect survival of young-of-year striped bass. Additional explanations for the apparent ‘disconnect’ between population numbers of young-of-year and older striped bass include possible under-sampling of sub-adults in the FMWT because of behavioral changes affecting geographic distribution, stocking of hatchery fish, and probable changes in adult demographics (Baxter et al. 2008). If survival rates of sub-adults changed during our study period as proposed by Kimmerer et al. (2000), our estimates of sub-adult population numbers may not reflect actual population numbers. Unfortunately, there is no empirical data available to reflect otherwise at this time.

Patterns of Individual Striped Bass Consumption

Individual total consumption increased over the study period for the age-2 cohort, while individual prey fish consumption increased over the study period for both sub-adult cohorts (Figures 4, 6). The increase in individual total consumption for the age-2 cohort may be partly attributed to an increase in annual growth of this cohort. In comparing sub-adult SFE striped bass consumption to other ecosystems, individual sub-adult striped bass prey fish consumption rates in the present study were fairly similar to values reported for Chesapeake Bay (Hartman and Brandt 1995b), but more than two times higher than levels reported for Lake Powell (Vatland et al. 2008). The systems studied by Hartman and Brandt (1995a, 1995b) and Vatland et al. (2008) differ vastly from the SFE, so such differences were not surprising.

Adult individual consumption for SFE striped bass were somewhat higher than levels reported for Chesapeake Bay (Hartman and Brandt 1995b), but were markedly higher than Lake Powell (Vatland et al. 2008). As in these other ecosystems, adult individual consumption in the SFE was consistently higher than for sub-adults. Additionally, individual consumption by adult females was higher than adult males at comparable age groups due to: (i) the larger sizes and growth rates of females than males, and (ii) the higher energetic cost of spawning in females then males. Individual consumption by adult striped bass decreased over the period analyzed, apparent mainly in the age 4 and older cohorts, especially males. The main driving factor behind the decline in individual consumption was observed declines in mean length at age from the mark-recapture datasets, and subsequently annual growth for the respective cohorts. The more significant declines in individual consumption (and mean length at age) for the male cohorts (respective to the female cohorts) may be partly explained by characteristics of the mark-recapture length dataset. For example, smaller sample numbers of females (versus male cohorts) could have led to an incorrect estimation of the mean length at age and annual growth of female cohorts and hence a decreasing trend in mean length at age (and individual consumption) was less apparent. Furthermore, spatial and temporal limitations of the water temperature and diet datasets may have also contributed to incorrect estimation of individual consumption. However, given the consistent decreasing trends in individual consumption and mean length at age among the majority of the striped bass cohorts, we believe this trend cannot be fully explained by limitations in the input data.

Patterns of Striped Bass Population Consumption

One of the key findings of the present study is that population total consumption by sub-adult fish was similar to the population total consumption by adult fish. While the individual total consumption by each adult cohort was greater then that of the each sub-adult cohort, the larger sub-adult population abundance resulted in a slightly larger average population total consumption (e.g., mean = 21.9×10^6 kg prey for sub-adults versus 17.9×10^6 kg prey for adults). This finding in the SFE is consistent with other aquatic ecosystems where prey consumption by younger age classes has been observed to represent a substantial contribution of total predatory demand of a given fish species (Cyterski et al. 2002; Hartman 2003; Vatland et al. 2003; Heimbuch 2008). The average population prey fish consumption by sub-adults (mean = 10.3×10^6 kg prey fish) was less than adult average population prey fish consumption (mean = 17.8×10^6 kg prey fish) because prey fish made up a smaller proportion of the sub-adult diet. While both sub-adult population total and prey fish consumption in the SFE increased through 2000, consumption from 2001 through 2003 decreased dramatically.

Adult consumption patterns were closely related to abundance levels, which follow a similar pattern to the Atlantic Coast striped bass stocks (Hartman 2003); this result may seem predetermined since the bioenergetics simulations used population abundance to scale individual consumption estimates. However, changes in fish size and environmental conditions such as water temperature suggest that population numbers alone may not fully reflect the overall pattern. For example, decreasing trends in adult individual consumption (total and prey fish) over the study period likely resulted in smaller population consumption (total and prey fish) estimated during the later years of the study period. As a case in point, the peak in population consumption in 2000 was smaller than the population consumption in 1970, two years where the adult abundance estimates were approximately equal. In general, both adult abundance estimates and the population consumption by each adult cohort declined from 1969 through 1994, then increased though 2000, where they began to decline thereafter. However, when comparing years of similar abundance estimates, population consumption by each adult cohort was lower in recent years, compared to early years in the study, due to the declining trend in adult individual consumption.

The consumption estimates in this study were influenced by: (1) abundance estimates of sub-adults and adults, (2) unknown ocean migration behavior, (3) limited number of diet studies, and (4) the bioenergetics model itself. First, since population consumption and population abundances are highly correlated, under or over estimates of population numbers (resulting from the mark-recapture dataset itself and/or the method used to estimate sub-adult abundance) can lead to significant changes in estimates of population consumption. Uncertainty associated with adult abundance estimates likely dominates uncertainty associated with population consumption estimates (Figure 8C). Second, the proportion of the adult striped bass population that leaves the SFE and enters the Pacific Ocean is unknown. Hence, an unknown proportion of adult consumption estimated in this study may have occurred in the Pacific Ocean. Third, relatively few diet studies were available over the modeled time-period, and the available data may not fully represent spatial and temporal variation in prey type consumed by striped bass. Finally, the overall bioenergetics model used in this study was not comprehensively validated for the SFE.

Independent estimates of model parameters were used whenever possible. Nevertheless further testing of the model is necessary to identify and quantify key sources of uncertainty.

Management Implications

An evaluation of long-term consumption trends of striped bass in the SFE may provide critical information to resource agencies on the relevance, or lack thereof, of management actions related to striped bass, and the broader SFE as a whole. Three primary sets of findings from this study may have management implications in the SFE.

First, predation rates increased recently (ca. 1990 to 2001) coincident with higher population numbers of adult striped bass and age-2 sub-adults. The management significance for this finding to key threatened species such as delta smelt and longfin smelt is less clear. The regional diet data were inadequate to estimate consumption of individual prey species over the entire study period. In our study, the limited diet data only allowed us to evaluate consumption of fishes as a generalized prey category. Because striped bass predation tends to reflect the “prey field”, it is likely that these increasingly rare osmerids represented a minor proportion of the striped bass diet during recent years (Nobriga and Feyrer 2008; Nobriga and Feyrer 2007). However, this does not necessarily imply that predation rates by SFE striped bass on the populations of such species is negligible, as even low predation rates on a rare species can have a significant impacts to the prey population. In any case, the recognition of recent increases in the predation rates by the SFE striped bass may warrant the re-evaluation of current management strategies.

Second, findings from this study suggest a possible recent shift in the established striped bass predator-prey relationship in the SFE. Individual total consumption has declined in the adult population from 1969 to 2004. Additionally, individual total consumption has remained fairly constant in the age-1 cohort over the period of available data (1981-2003). In defining what an established striped bass predator-prey relationship might look like in the SFE, it would be reasonable to assume that individual total consumption by the age-2 cohort would follow either the trend of adults or the age-1 cohort. However, individual total consumption by the age-2 cohort increased over the period of available data (1981-2003), with the most significant change occurring in the early 1990s. Additionally, based on diet studies, sub-adults became more piscivorous in the early 1990s. Hence, established predator-prey relationships of the striped bass population in the SFE may have recently changed (ca. early- to mid-1990s). The significance of such a change on the proportions of specific prey species in the striped bass diet is unclear, but likely has a negligible effect on the proportions of species of concern (e.g., delta smelt, longfin smelt, and Chinook salmon smolts) in the striped bass diet due to the: (i) opportunistic feeding behavior of striped bass combined with the low abundances of such species, making feeding encounters rare, and (ii) supporting diet studies which show very little, if any, consumption of such species (Stevens 1966; Feyrer et al. 2003). However, this does not imply that possible changes in the established SFE striped bass predator-prey relationships had no effect upon the populations of species of concern, and as such, the evaluation of adaptive management strategies that target sub-adult striped bass is advisable.

Third, striped bass can spend large periods of time in the ocean, effectively providing a marine prey subsidy for the SFE striped bass population (Moyle 2002; Baxter et al. 2008). Prey outside of the SFE represent an unknown percentage of the total prey estimated for adults. By contrast, since sub-adults primarily reside in the SFE and since our simulations showed that this demographic frequently consumes more than adults, sub-adults have a particularly large consumption demand within the SFE. Sub-adult striped bass can be highly abundant in shallow water habitat (Nobriga and Feyrer 2007), and hence, an unknown but perhaps high percentage of prey may originate inshore, not in pelagic habitat generally associated with delta smelt and longfin smelt. In any case, recognition of the magnitude and localization of sub-adult consumption within the SFE may warrant further evaluation of adaptive management strategies targeted at sub-adult striped bass.

Overall, current management actions related to SFE striped bass have largely targeted adult population numbers to sustain the fishery. Findings from this study support the continued evaluation of the management of adult population numbers, as well as the inclusion of sub-adults, particularly age-2 fish. Any changes to current management practices should be continually evaluated given the potential for detrimental effects to the striped bass population as well as to other populations in the SFE. For example, reduction of sub-adult populations could lead to an increase in the abundances of other species (e.g., silversides and large mouth bass), that may in turn have a much more significant impact upon species of concern (i.e, delta smelt, longfin smelt, and Chinook salmon smolts) than striped bass. Additionally, while this study represents the synthesis of a comprehensive set of existing data, key data gaps still exist, particularly related to the spatial and temporal distribution of population demographics.

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Table 1.

Values of equation parameters used in this study.

			Value	
Parameter	**Description (units)**	**Age 1**	**Age 2**	**Age 3+**
Wisconsin Bioenergetics Model Parameters[a]				
CA	Allometric mass function intercept ($g_{prey}\cdot g_{bass}^{-2}\cdot d^{-1}$)	0.3021	0.3021	0.3021
CB	Allometric mass function slope (unitless)	-0.2523	-0.2523	-0.2523
q_1	Temperature for K_1 (°C)	6.6	6.6	7.4
q_2	Temperature for K_2 (°C)	19.0	18.0	15.0
q_3	Temperature for K_3 (°C)	28.0	29.0	28.0
q_4	Temperature for K_4 (°C)	30.0	32.0	30.0
K_1	Proportion of C_{max} at q_1 (unitless)	0.262	0.255	0.323
K_2 and K_3	Proportion of C_{max} at q_2 and q_3 (unitless)	0.98	0.98	0.98
K_4	Proportion of C_{max} at q_4 (unitless)	0.850	0.900	0.850
RA	Allometric mass function intercept ($g_{O2}\cdot g_{bass}^{-2}\cdot d^{-1}$)	0.0028	0.0028	0.0028
RB	Allometric mass function slope (unitless)	-0.218	-0.218	-0.218
RQ	Coefficient of metabolism temperature function (unitless)	0.076	0.076	0.076
OXY	Oxycalorific coefficient ($J\cdot g_{O2}^{-1}$)	13560	13560	13560
SDA	Specific dynamic action (unitless)	0.172	0.172	0.172
ACT	Multiplier of metabolism (unitless)	1.649	1.649	1.649
F	Egestion ($g_{prey}\cdot g_{bass}^{-1}\cdot d^{-1}$)	0.104	0.104	0.104
E	Excretion ($g_{prey}\cdot g_{bass}^{-1}\cdot d^{-1}$)	0.068	0.068	0.068
Striped Bass and Striped Bass Prey Energy Density Parameters				
k	Equations 3 and 4 ($J\cdot g_{bass}^{-1}\cdot yr^{-1}$)	123.00[b]	928[c]	193[d]
l	Equations 3 and 4 ($J\cdot g_{bass}^{-1}\cdot yr^{-1}$)	5659.50[b]	6860[c]	7681[d]
m	Equation 4 ($J\cdot g_{bass}^{-1}\cdot yr^{-1}$)	--	-402[c]	-220[d]
Striped Bass Reproduction Parameters				
		Males		**Females**
r_c	Equation 6 (unitless)	0.056		0.111
r_i	Equation 6 (unitless)	-13.08		-72.04

[a] Hartman and Brandt (1995a, 1995b).

[b] Valid for striped bass between 365-690 days of age.

[c] Valid for striped bass between 691-1216 days of age.

[d] Valid for striped bass between 1216+ days of age.

Table 2.

Striped bass diet composition and prey energy density values.

Year	**Age**	**% Diet by weight of prey type (*Energy Density*)[a]**				**Average Energy Density[b] ($J \cdot g_{prey}^{-1}$)**
		Fish (*4800*)	**Decapods, Isopods (*4181*)**	**Mysids (*3140*)**	**Other (*2025*)**	
1969-1979[c]	3+	99.9	0.1	--	--	4799
1980-1989[d]	1	2.5	--	95.9	1.6	3164
	2	78.5	1.1	18.4	2.0	4432
	3+	98.9	0.9	0.2	--	4791
1990-1999[d,e]	1	12.2	3.1	58.5	26.2	3083
	2	82.1	1.1	8.4	4.2	4336
	3+	99.3	0.4	0.3	--	4793
2000-2004[d,e]	1	12.2	3.1	58.5	26.2	3083
	2	82.1	1.1	8.4	4.2	4336
	3+	98.7	0.6	0.7	--	4785

[a] Energy densities expressed parenthetically, from Steimle and Terranova (1985), Pope et al. (2001), Chipps and Bennett (2002), and Vatland et al. (2008) ($J \cdot g_{prey}^{-1}$).

[b] Values calculated by Equation 5.

[c] Stevens 1966

[d] Feyrer at al. 2003

[e] *DFG, unpublished data*

List of Figures

Figure	Title
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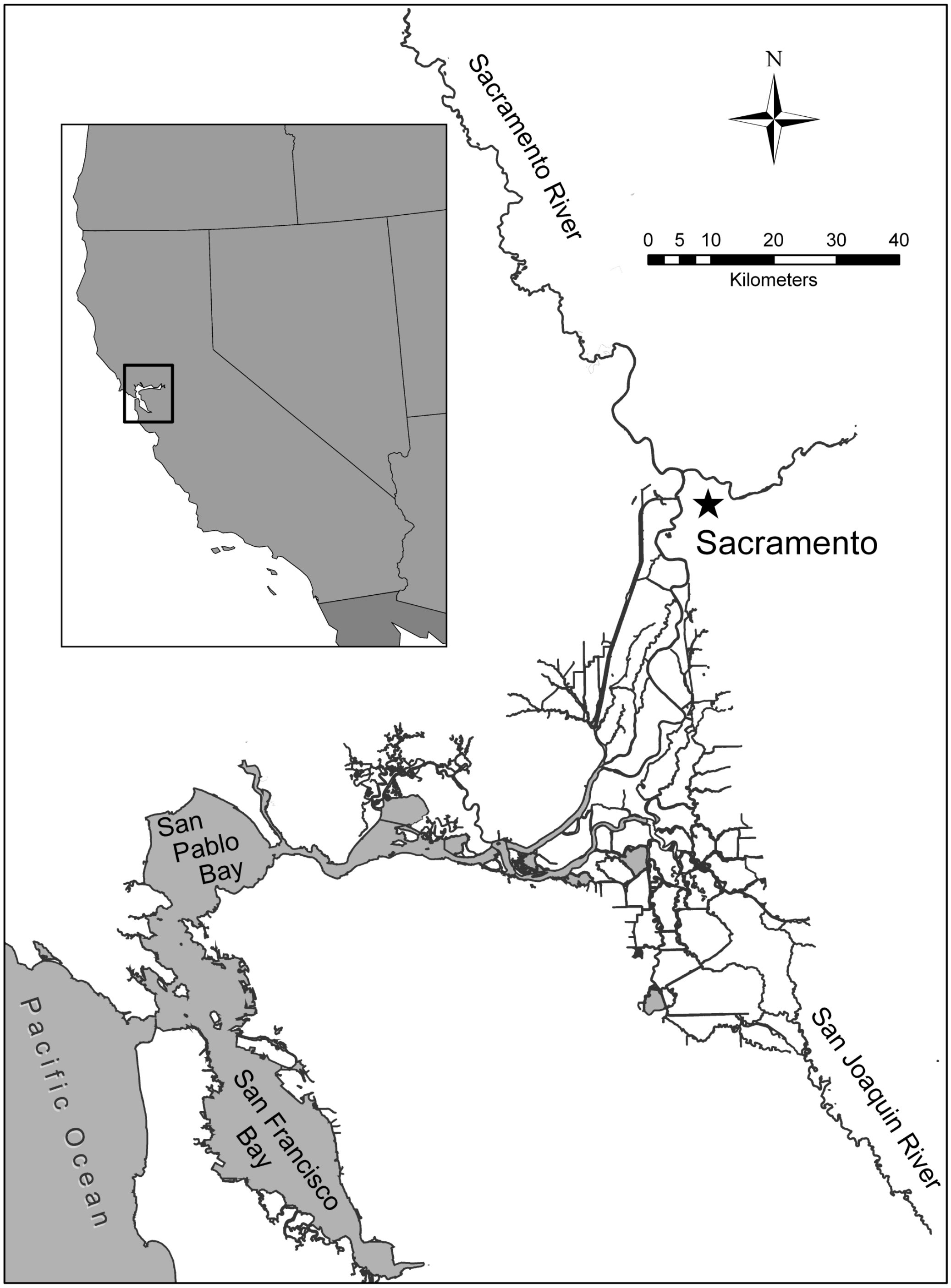
9	Population prey fish consumption by sub-adult striped bass. Consumption by each age cohort is reflected in the length of each respective bar.



887

888 Figure 1

889

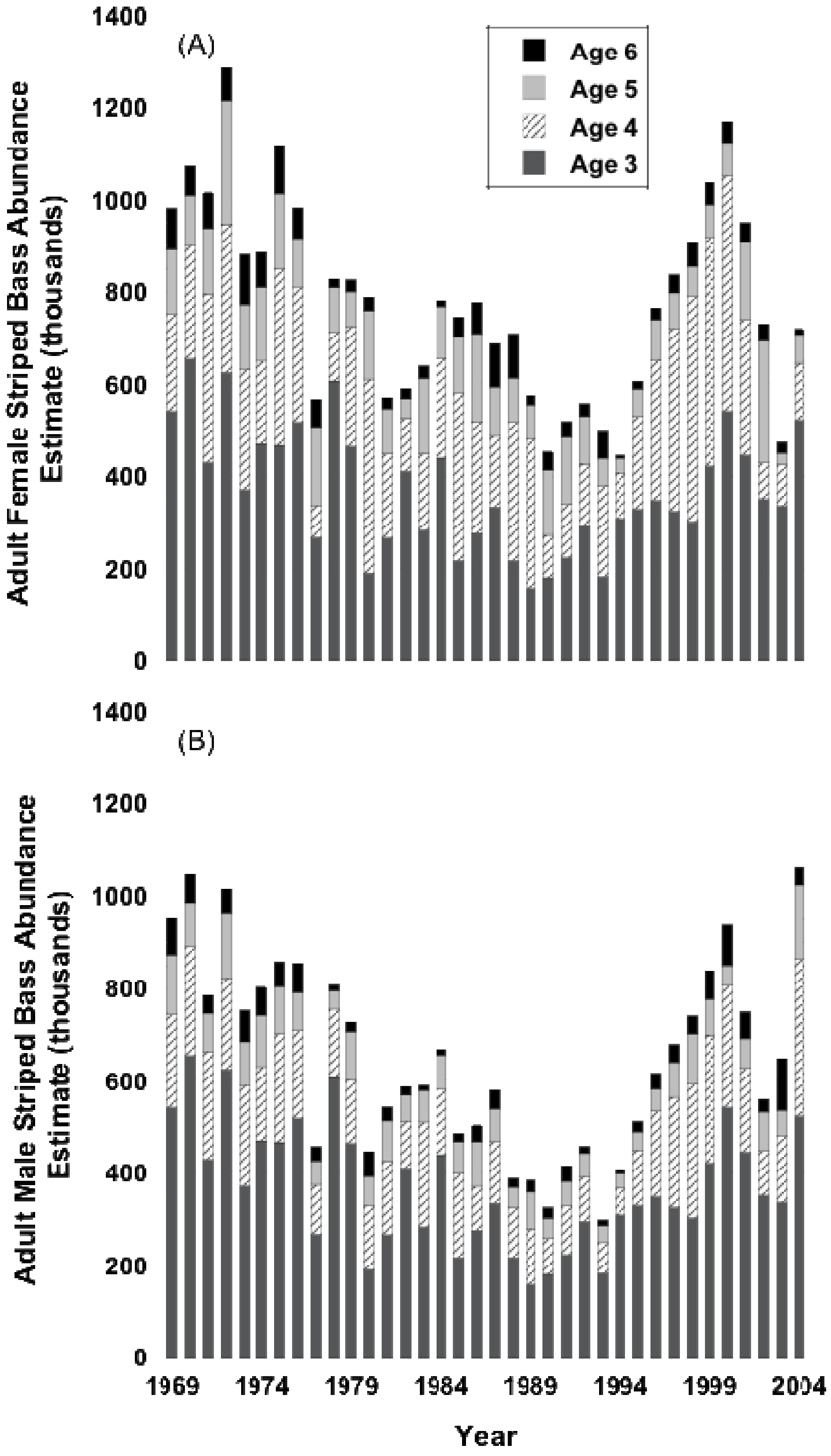

(A)
Adult Female Striped Bass Abundance Estimate (thousands)
1400
1200
1000
800
600
400
200
0
Age 6
Age 5
Age 4
Age 3
(B)
Adult Male Striped Bass Abundance Estimate (thousands)
1400
1200
1000
800
600
400
200
0
1969
1974
1979
1984
1989
1994
1999
2004
Year

Figure 2

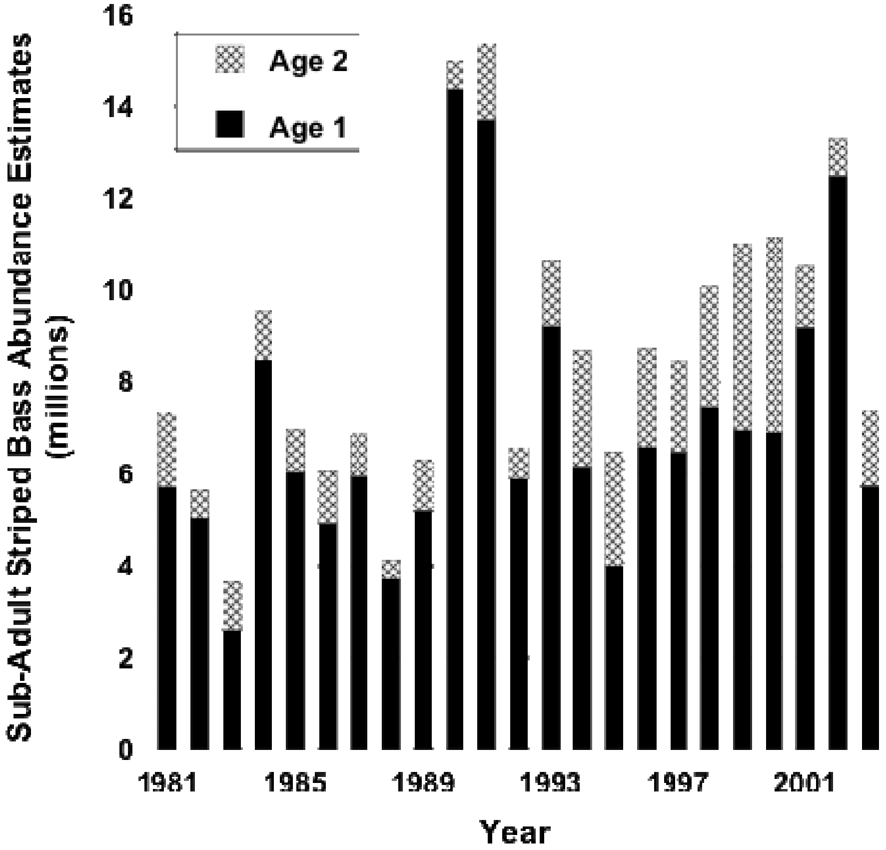
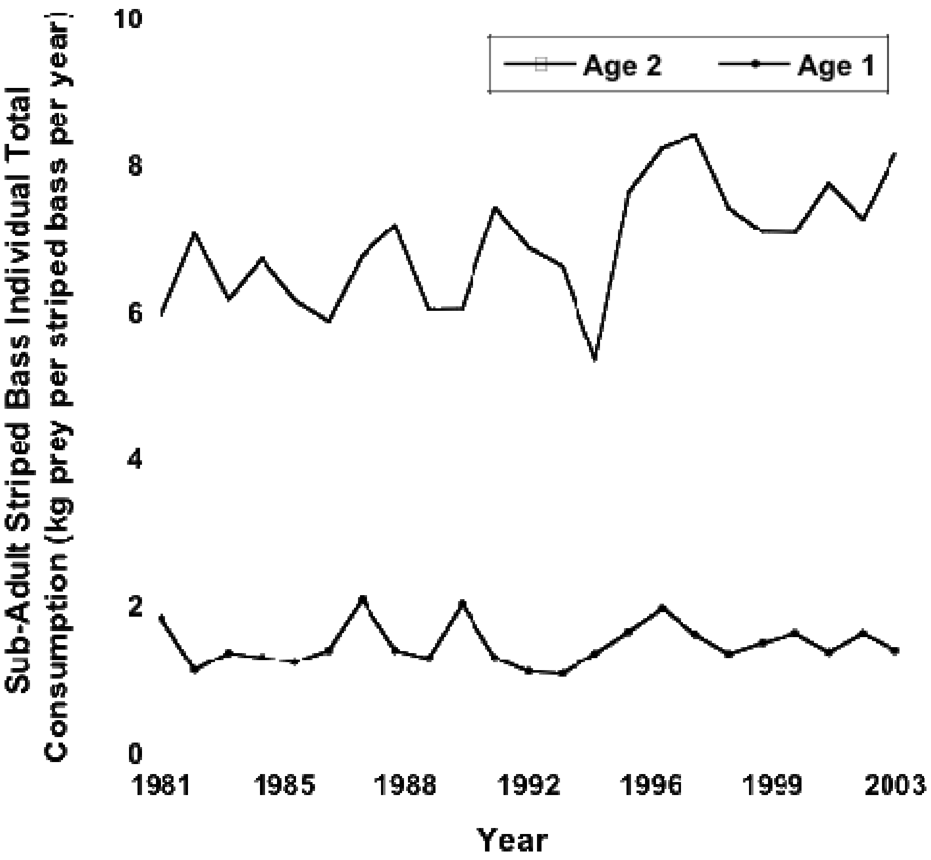

Age 2
Age 1
Sub-Adult Striped Bass Abundance Estimates (millions)
0
2
4
6
8
10
12
14
16
1981
1985
1989
1993
1997
2001
Year

Figure 3



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897 Figure 4

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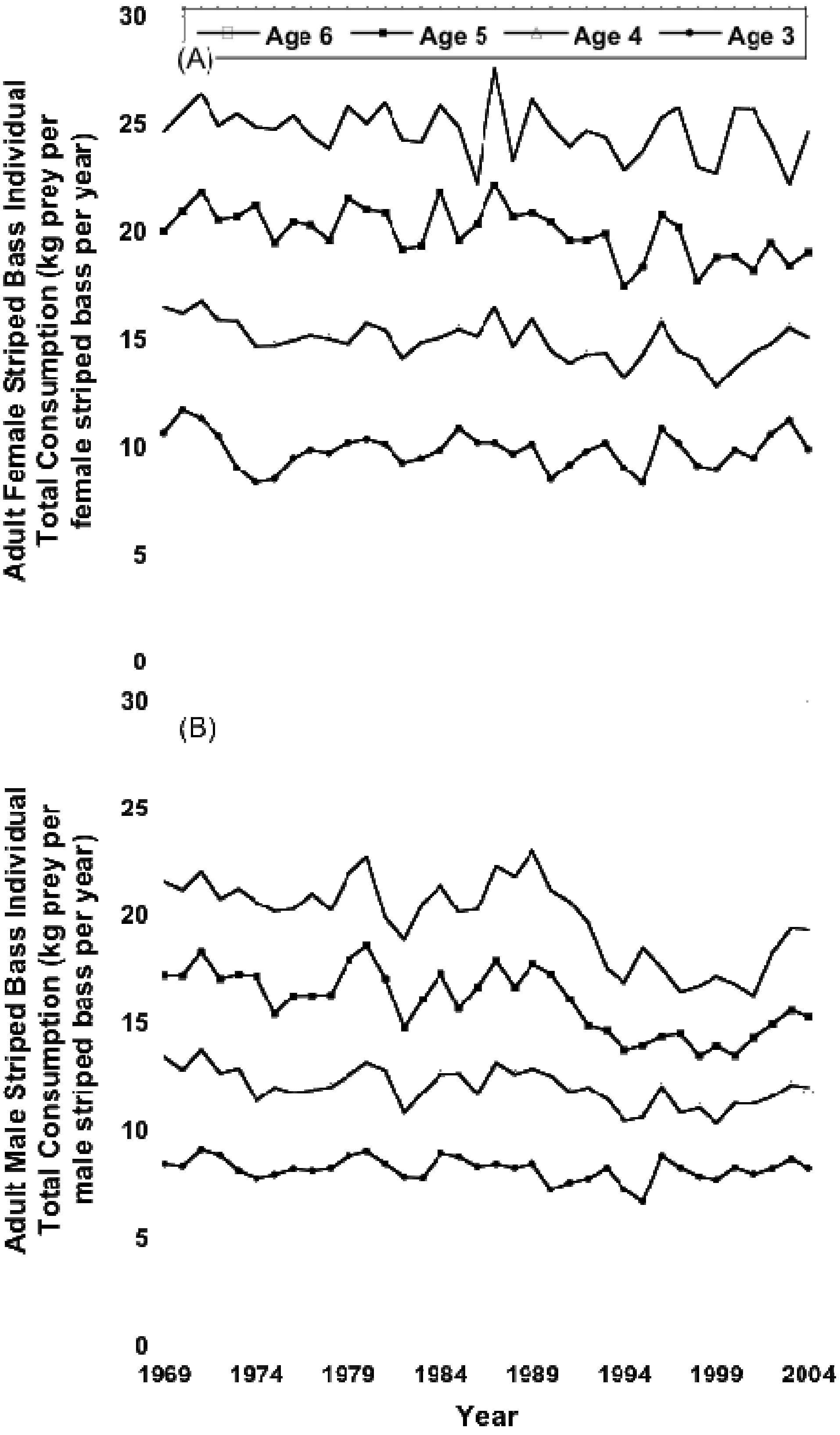
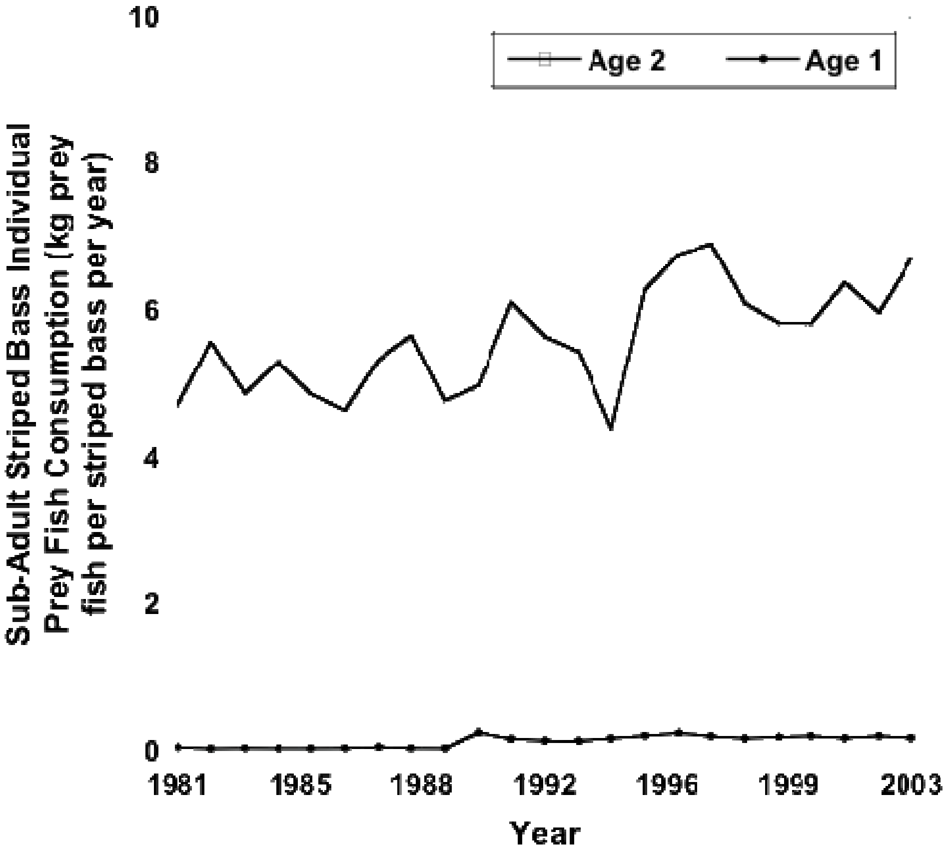

Age 6
Age 5
Age 4
Age 3
(A)
Adult Female Striped Bass Individual Total Consumption (kg prey per female striped bass per year)
30
25
20
15
10
5
0
(B)
Adult Male Striped Bass Individual Total Consumption (kg prey per male striped bass per year)
30
25
20
15
10
5
0
1969
1974
1979
1984
1989
1994
1999
2004
Year

Figure 5



10
8
6
4
2
0
Age 2
Age 1
Sub-Adult Striped Bass Individual Prey Fish Consumption (kg prey fish per striped bass per year)
1981
1985
1988
1992
1996
1999
2003
Year

Figure 6

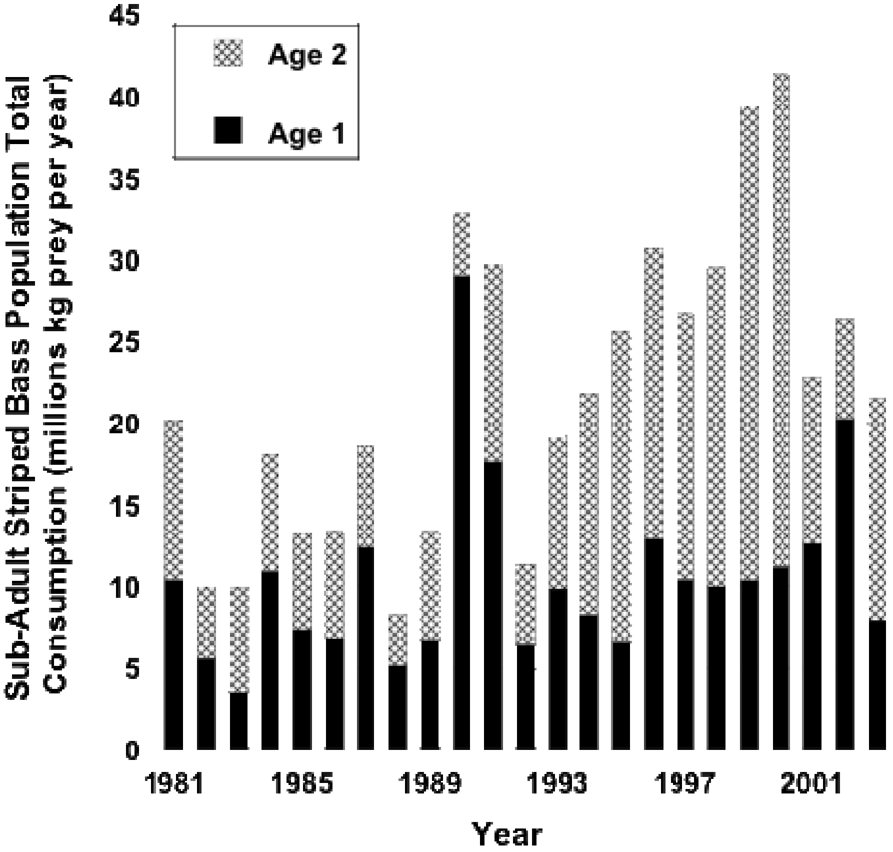

Sub-Adult Striped Bass Population Total Consumption (millions kg prey per year)
Age 2
Age 1
0
5
10
15
20
25
30
35
40
45
1981
1985
1989
1993
1997
2001
Year

Figure 7

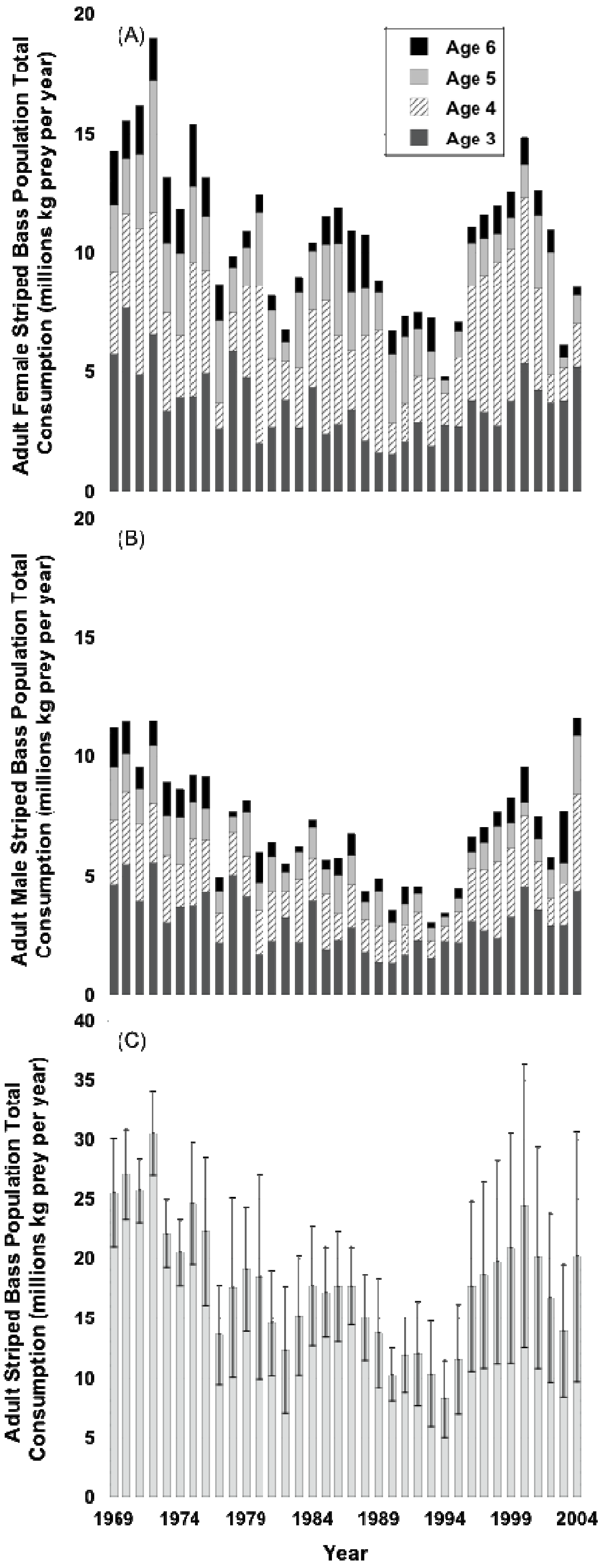
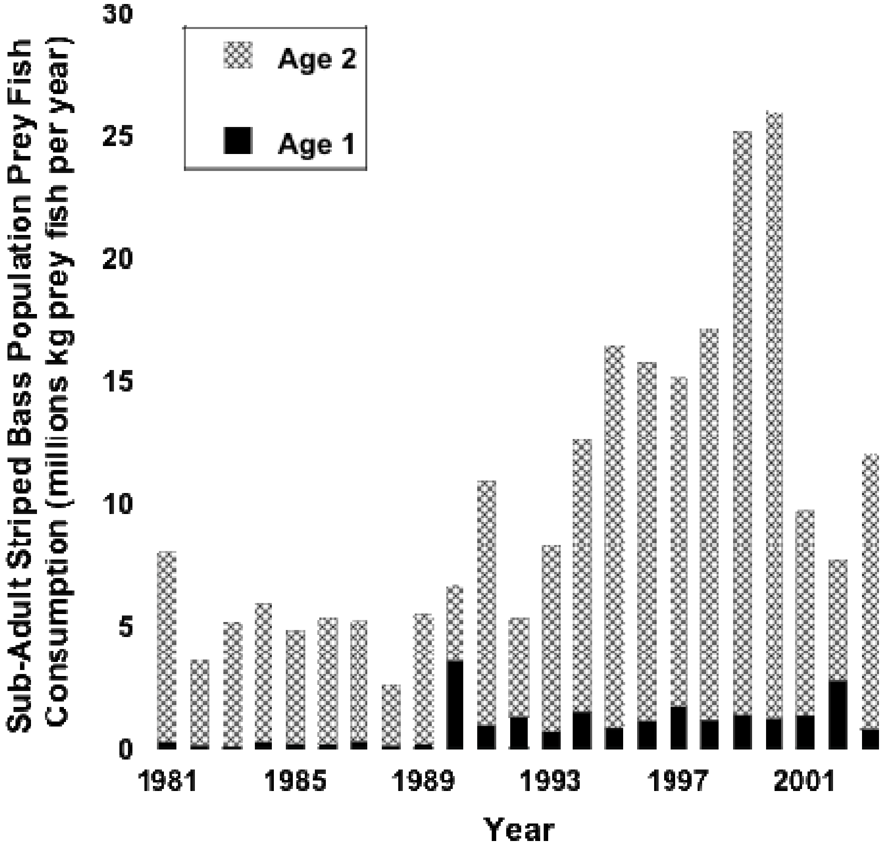

(A)
Age 6
Age 5
Age 4
Age 3
Adult Female Striped Bass Population Total Consumption (millions kg prey per year)
0
5
10
15
20
(B)
Adult Male Striped Bass Population Total Consumption (millions kg prey per year)
0
5
10
15
20
(C)
Adult Striped Bass Population Total Consumption (millions kg prey per year)
0
5
10
15
20
25
30
35
40
1969
1974
1979
1984
1989
1994
1999
2004
Year

Figure 8



912

913 Figure 9