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

Erik Loboschfsky¹, Gina Benigno², Ted Sommer², Kenneth Rose³, Timothy Ginn¹, Arash Massoudieh⁴, and Frank Loge^{1,*}

ABSTRACT

Striped bass are both a major predator of native fishes and support a recreational fishery in the San Francisco Estuary (the estuary). Quantifying their demands on their prey is important for understanding long-term trends of fish in the estuary. In this study, we: (i) 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 estuary; (ii) developed a method to estimate the abundances of sub-adult striped bass; (iii) evaluated how consumption varied by age and gender; and (iv) identified factors that affect the resulting consumption estimates. On a 'per capita' basis, modeled individual prey fish consumption increased after 1990, and individual total and prey fish consumption by age-2 striped bass increased after 1994. 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 adults. As expected, long-term trends in population consumption (total and prey fish) by all ages of striped bass (ages 1 through 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, largely because of 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 within the estuary; hence, consumption by the relatively abundant sub-adult population may have significant effects upon their estuarine prey species.

KEY WORDS

Bioenergetics model, striped bass, *Morone saxatilis*, consumption, abundance, San Francisco Estuary, pelagic fish

INTRODUCTION

In the San Francisco Estuary (Figure 1; herein referred to as the estuary), 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

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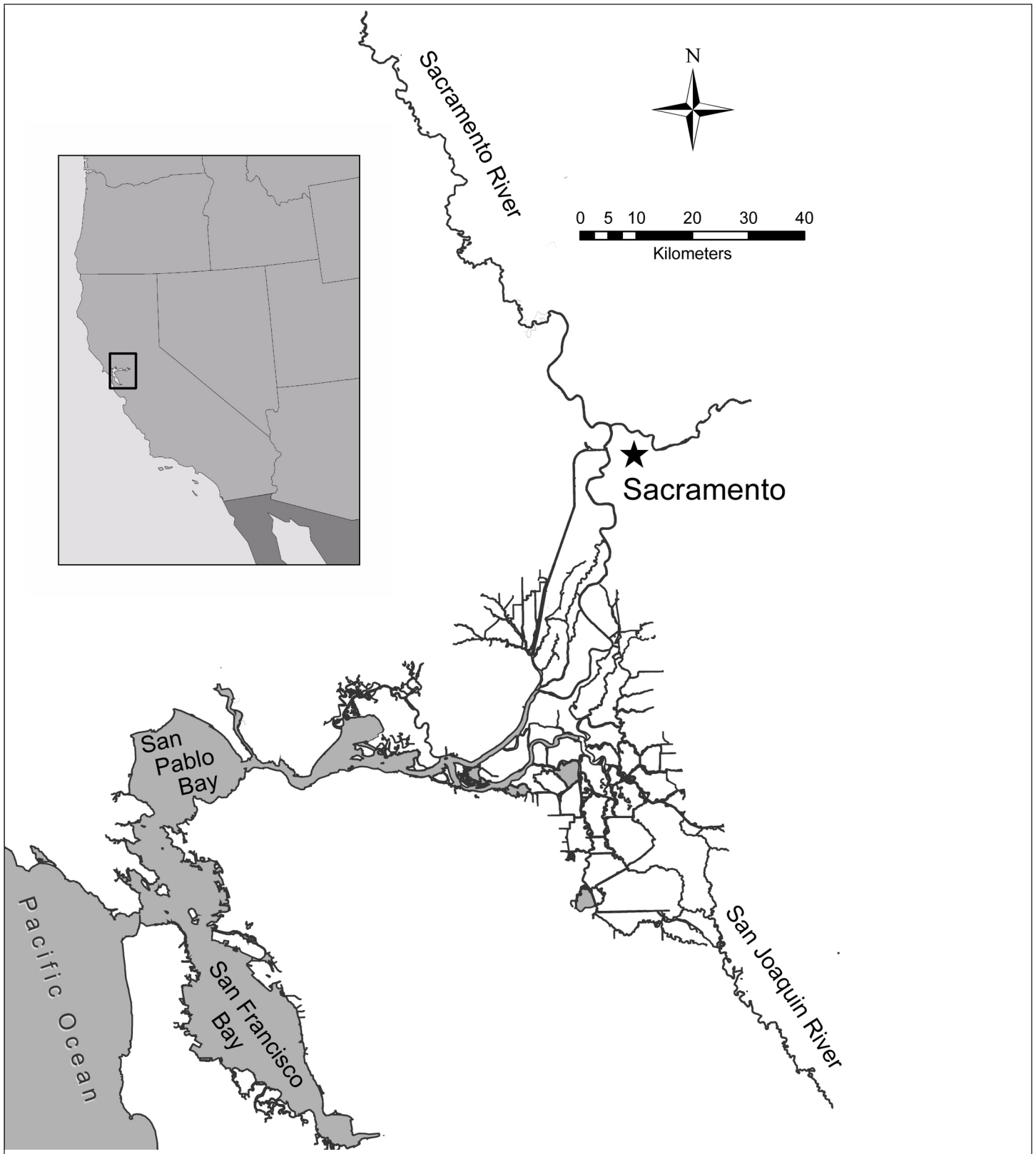


Figure 1 The San Francisco Estuary, inclusive of the San Francisco Bay and Sacramento–San Joaquin River Delta

around 2000, termed the Pelagic Organism Decline (POD) (Feyrer and others 2007; Sommer and others 2007). Numerous factors have been implicated in the POD (Sommer and others 2007), including: (i) effects of reduced stock (Bennett 2005; Feyrer and others 2007; Feyrer and others 2009); (ii) habitat changes (Atwater and others 1979; Nichols and others 1986; Lehman and others 2005; Feyrer and others 2007; Ostrach and others 2008); (iii) water project entrainment (Kimmerer 2008; Kimmerer and Nobriga 2008; Grimaldo and others 2009); (iv) food web effects (Kimmerer 2008); and (v) predation (Nobriga and Feyrer 2007; Sommer and others 2007). The work reported herein specifically focuses on quantifying long-term trends in the consumption by estuary striped bass as a measure of long-term changes in predation on forage fish by striped bass.

Striped bass, inclusive of all ages, are found throughout the estuary, while adults (ages 3+) are additionally found along the California coastline. We refer to striped bass that spawn in the estuary as estuary striped bass. Originally introduced into the estuary over 100 years ago, estuary 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 and others 1985; Hassler 1988; Nobriga and Feyrer 2007). Largely to support this valuable recreational fishery, sub-adult striped bass were stocked into the estuary from 1980 to 2001.

Estuary striped bass exhibit a typical anadromous life cycle and a diet that shifts with age from invertebrates to fish. 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 estuary and into the saltwater/freshwater convergence zone, where they develop into juveniles and then disperse throughout the estuary (Turner and Chadwick 1972; Stevens and others 1985; Hassler 1988). Striped bass are opportunistic predators. Prey selection is largely mouth gape-dependent, ranging from invertebrates (copepods, amphipods, and mysids) to fish (e.g.,

Nobriga and Feyrer 2007, 2008; Kimmerer and others 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 being available for growth (Hartman and Brandt 1995a, 1995b; Hanson and others 1997). For example, adult striped bass in the estuary 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 and others 2003; Nobriga and Feyrer 2007). Conceptually, both the type and quantity of prey consumed are important regulators in striped bass growth. The present study focuses on broad categorical prey types (e.g., fish, decapods, isopods, mysids) and not specific prey species, because of the coarse resolution of the available empirical data.

While other studies have evaluated cumulative annual consumption by striped bass (Hartman and Brandt 1995b; Cyterski and others 2002) and consumption over shorter time-periods (Nelson and others 2006; Tuomikoski and others 2008; Vatland and others 2008), none have evaluated consumption over extended periods of time (i.e., decades). Relationships between striped bass prey consumption, observed growth, abundance, and water temperature have been established through bioenergetics models for stocks in Chesapeake Bay (Hartman and Brandt 1995a, 1995b) and Lake Powell (Vatland and others 2008), but have yet to be established for the Pacific Coast stocks (i.e., fish that spawn in the estuary or Coos Bay, OR). Bioenergetics models, as applied to fish species, use an energy budget approach where the growth of individual fish is typically used to estimate age-class 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 and others 1997).

In this paper, we estimated time-series values of individual and population consumption by estuary striped bass, stratified by age and gender, to address three questions: (i) is there evidence of temporal trends in consumption, (ii) did consumption vary by age-class and gender, and (iii) what factors influenced consumption by the estuary striped bass

population? Given the lack of a bioenergetics model calibrated specifically to estuary 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 applicable the model is to estuary striped bass.

METHODS

For sub-adult estuary striped bass (age 1 and age 2), average annual total and prey fish consumption was estimated at the individual and population level from 1981 through 2003. For adult estuary striped bass (age 3 through age 6), average annual total and prey fish consumption was estimated at the individual and population level 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 and others 1997), which is based on physiological and allometric relationships that regulate fish growth. For this study, we obtained previously developed bioenergetics parameters from laboratory studies performed on Chesapeake Bay stocks of striped bass (Table 1; Hartman and Brandt 1995a, 1995b). Historical datasets specific to the estuary, such as striped bass weights, diets, and water temperatures, were used as inputs to the model.

Water Temperature

Water temperature data from the estuary was compiled from three different datasets to span 1969 through 2004. Monthly water temperatures from the United States Geological Survey's (USGS) water quality cruises were used for 1969 through 1975¹. Bi-monthly water temperatures from the California Department of Water Resources' (DWR) discrete monitoring data were used for 1976 through 1982². Averaged daily water temperatures from four DWR

continuous monitoring³ stations in the estuary were used for 1983 through 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.

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 and others 2000; McCloskey 1986) for each year from 1969 to 2004:

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

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 April 1 through March 31, 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 adult estuary striped bass (age 3 through age 7) were obtained from California Department of Fish and Game's (DFG) mark-recapture survey for 1969 through 2004, except for 1995, 1997, 1999 and 2001, when no survey data were collected (Figure 2). 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 age-class. This mark-recapture survey partially includes adult striped bass found in the Pacific Ocean, and hence does not

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)

Table 1 Values of equation parameters used in this study

Parameter	Description (units)	Value		
		Age 1	Age 2	Age 3+
Wisconsin Bioenergetics Model parameters ^a				
CA	Allometric mass function intercept for consumption ($g_{\text{prey}} \cdot g_{\text{bass}}^{-1} \cdot d^{-1}$)	0.3021	0.3021	0.3021
CB	Allometric mass function slope for consumption	-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	0.262	0.255	0.323
K ₂ and K ₃	Proportion of C _{max} at q ₂ and q ₃	0.98	0.98	0.98
K ₄	Proportion of C _{max} at q ₄	0.850	0.900	0.850
RA	Allometric mass function intercept for standard metabolism ($g_{O_2} \cdot g_{\text{bass}}^{-1} \cdot d^{-1}$)	0.0028	0.0028	0.0028
RB	Allometric mass function slope for standard metabolism	-0.218	-0.218	-0.218
RQ	Temperature-dependent coefficient for standard metabolism (°C ⁻¹)	0.076	0.076	0.076
OXY	Oxycalorific coefficient ($J \cdot g_{O_2}^{-1}$)	13560	13560	13560
SDA	Specific dynamic action	0.172	0.172	0.172
ACT	Multiplier of metabolism	1.649	1.649	1.649
F	Egestion ($g_{\text{prey}} \cdot g_{\text{bass}}^{-1} \cdot d^{-1}$)	0.104	0.104	0.104
E	Excretion ($g_{\text{prey}} \cdot g_{\text{bass}}^{-1} \cdot d^{-1}$)	0.068	0.068	0.068
Striped bass and striped bass prey energy density parameters				
k	Equations 3 and 4 ($J \cdot g_{\text{bass}}^{-1} \cdot yr^{-1}$)	123.00 ^b	928 ^c	193 ^d
l	Equations 3 and 4 ($J \cdot g_{\text{bass}}^{-1} \cdot yr^{-1}$)	5659.50 ^b	6860 ^c	7681 ^d
m	Equation 4 ($J \cdot g_{\text{bass}}^{-1} \cdot yr^{-1}$)	--	-402 ^c	-220 ^d
Striped bass reproduction parameters				
		Males		Females
r _c	Equation 6	0.056		0.111
r _i	Equation 6	-13.08		-72.04

^a Hartman and Brandt (1995a, 1995b).

^b Valid for striped bass between 365 and 690 days of age.

^c Valid for striped bass between 691 and 1,216 days of age.

^d Valid for striped bass between 1,216+ days of age.

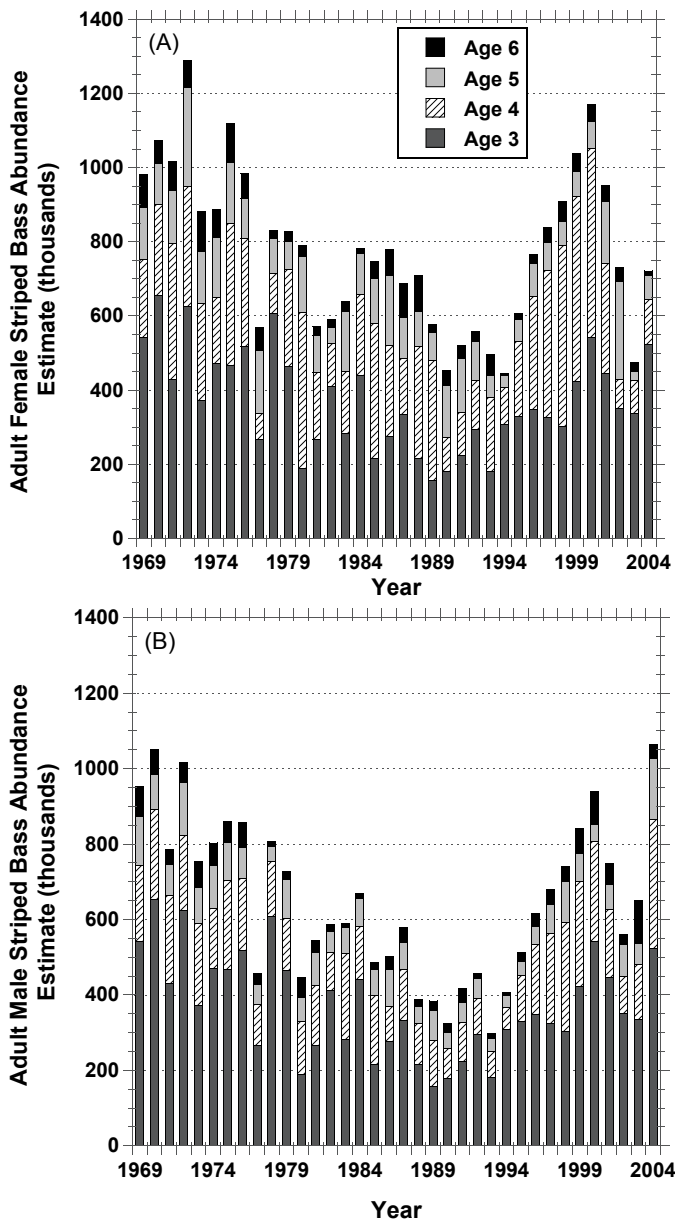


Figure 2 Population abundance estimates of adult striped bass (A) females and (B) males by age from 1969 to 2004

entirely represent year-round population abundances found within the estuary.

Sub-Adult Striped Bass Abundance Estimates

The population abundance of sub-adult estuary 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) Survey, Summer Towntnet 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. Because of 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 the numbers of age-3 fish with survival estimates of age-1 to age-3 hatchery striped bass stocked into the estuary 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 estuarine-dependent fish in the estuary (Jassby and others 1995). Both Delta outflow and the position of X2 were obtained from Interagency Ecological Program's (IEP) Dayflow program⁴. A stepwise linear regression 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 3-year span (e.g., for a survival estimate in year y , we used $X2_y + X2_{y+1} + X2_{y+2}$) 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 estuary between 1981 and 1990.

⁴ <http://www.water.ca.gov/dayflow>

Other researchers have shown statistical relationships between X_2 and striped bass survival (Kimmerer and others 2001). The regression model was then used to estimate the survival of age-1 to age-3 striped bass for each year from 1991 to 2003 based upon the corresponding values of X_2 . 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 2 years later. 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 here to estimate age-1 to age-3 survival rates.

We approximated annual age-2 striped bass population abundance from age-3 population abundance estimates using annual 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. We 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-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 and others 1985; White 1986; Kohlhorst unpublished, 1999). For the years when natural mortality rates could not be calculated because of the lack of tagging (1994 through 2001), we either estimated rates from DFG's creel surveys (1995, 1997, 1999, and 2001), or averaged the rates from the prior and subsequent years (1994, 1996, 1998, and 2000).

Striped Bass Weight and Annual Growth

Two long-term monitoring programs collected fork length data of estuary striped bass: (i) Bay Study, which sampled mainly age-1 fish from 1980 through 2004 (Armor and Herrgesell 1985), and; (ii) 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 and others 2000). Both programs collected data dur-

ing 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 and others 2005):

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

where L is fork length in millimeters and W is fish weight in grams. Individual weights were then grouped by age-class for each study year to determine an average weight. Annual growth was then calculated in a given year (Y) by subtracting the average weight of an older age-class ($X+1$) in the subsequent year ($Y+1$) from the average weight of a younger age-class (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, and 2001. In both situations, the lack of data necessitated the calculation of annual growth over 2 years, rather than 1 year. Moreover, lengths, and subsequently weights, were skewed for age-3 and age-4 striped bass because of a legal 'take size' restriction in the mark-recapture dataset of 42-cm fork length and larger. To account for the effect of the take size restriction on calculated mean weights, a normal distribution was fit through the histogram of weights for age 3 and age 4. The mean of the normal distribution was then used as the mean weight for age-3 and age-4 striped bass in the bioenergetics model. Because the DFG's mark-recapture survey is partially inclusive of adult striped bass that have migrated to and from (or were found in) the Pacific Ocean and upstream tributaries, annual growth calculated from this dataset may not fully represent the growth patterns of striped bass residing solely within the estuary.

Striped Bass Diet

The diet composition of estuary striped bass was compiled from a variety of sources (i.e., Stevens 1966; Feyrer and others 2003; DFG unpublished data) to span the period from 1969 to 2004 (Table 2). In each of the datasets, the proportions of different prey

Table 2 Striped bass diet composition and prey energy density values

Year	Age	% Diet of prey type (energy density) ^a				Average energy density ^b (J · 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 ^f	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 ^f	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 and others (2001), Chipps and Bennett (2002), and Vatland and others (2008) (J · g_{prey}⁻¹).

^b Values calculated by Equation 5.

^c Stevens 1966

^d Feyrer and others 2003

^e DFG, unpublished data

^f 4.2% of age-2 diet was unspecified “debris;” a zero energy density was assigned to that proportion of age-2 diet (not shown in table).

consumed were determined from analyses of striped bass stomach contents. Largely because of the coarseness of the diet composition data, prey types were combined into several broad prey categories (i.e., fish, decapods/isopods, mysids, and others) to simplify the bioenergetics modeling. 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 estuary striped bass and their prey were obtained from several literature sources. We approximated striped bass energy densities 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 · 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 · g_{bass}⁻¹ · 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 than 690 days of age. Energy densities of different striped bass prey types were obtained from the literature (Steimle and Terranova 1985; Pope and others 2001; Chipps and Bennett 2002; Vatland and others 2008). Because striped bass consume multiple prey types with different energy densities, we took a weighted average of energy density (\bar{e}_p) based upon the proportions of each different prey type consumed:

$$\bar{e}_p = \sum_{z=1}^{z=n} (\alpha_z \cdot e_{p,z}) \tag{5}$$

where n 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 ($J \cdot g_{\text{prey}}^{-1}$) (Table 2).

Striped Bass Reproduction

Adult male and female striped bass energy losses associated with reproduction (i.e., gonad development and gamete production) were accounted for in the bioenergetics model. Two empirical relationships were developed that relate the gonad weights of both males and females to fish body weight using empirical field data from age-4 through age-7 fish collected by DFG in 2008 and 2009 (DFG unpublished data):

$$W_g = r_c \cdot W_{ts} + r_i \quad (6)$$

where W_g is gonad 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. 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. We did not consider reproductive losses for striped bass younger than age 4 because of: (i) the limitations of the empirical gonad dataset, and (ii) the unknown fraction of age-3 striped bass that are sexually mature.

Bioenergetics Model Simulation

The bioenergetics model, as described by Hartman and Brandt (1995a, 1995b), is based upon an energy balance whereby net growth is defined as the change in weight (in grams) per day by an individual fish:

$$\text{Growth} = \frac{e_p}{e_b} \cdot (\text{Consumption} - \text{Metabolism} - \text{Egestion} - \text{Excretion}) \cdot W \quad (7)$$

where *Consumption*, *Metabolism*, *Egestion*, and *Excretion* have units of $g_{\text{prey}} \cdot g_{\text{bass}}^{-1} \cdot d^{-1}$ and W is the initial striped bass weight (grams). In the present study, we modified Equation 7 to include an additional term that reflects 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 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, which varies based on numerous physiological variables such as age, body weight, gender, and ambient temperature. The maximum consumption rate (C_{max}) in the model is computed as:

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

where C_{max} has units of ($g_{\text{prey}} \cdot g_{\text{bass}}^{-1} \cdot d^{-1}$), and CA and CB are the intercept and slope of the allometric mass function for consumption, respectively (Table 1; Hartman and Brandt 1995a; Hanson and others 1997). The function $f(T)$ in Equation 8 describes how the maximum consumption rate changes as a function of water temperature, using 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:

$$C = p \cdot C_{\text{max}} \quad (9)$$

where C has units of ($g_{\text{prey}} \cdot g_{\text{bass}}^{-1} \cdot d^{-1}$) and the proportion of the maximum consumption (p) has values between zero and one. The proportion of maximum consumption can be viewed as a measure of prey availability; when prey is 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) depends upon fish weight, age, water temperature, and activity:

$$R = RA \cdot W^{RB} \cdot e^{(RQ \cdot T)} \cdot ACT \cdot \left(OXY \cdot e_p^{-1} \right) \quad (10)$$

where R has units of ($g_{\text{prey}} \cdot g_{\text{bass}}^{-1} \cdot d^{-1}$), RA and RB are the intercept and slope of the allometric mass function for standard metabolism, respectively, RQ is the temperature-dependent coefficient for standard metabolism, and ACT is the activity multiplier of metabolism (Table 1; Hartman and Brandt 1995a; Hanson and others 1997). The oxycaloric coefficient (OXY) in Equation 10 relates to the energy density of typical prey (Elliott and Davison 1975). Specific dynamic action (SDA) is calculated as a proportion of consumption minus egestion (Table 1; Hartman and Brandt 1995a; Hanson and others 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 ($t = \text{day } 1$): (i) we obtained the initial fish weight from the historical empirical field data, (ii) we obtained the average water temperature from the temperature model (Equation 1), and (iii) we assumed a value for the proportion of maximum consumption (p). The combination of this information then allowed us to calculate 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 we obtained a new water temperature from the temperature model (Equation 1). Unlike the other terms of Equation 7, we applied the reproductive term only on a single day (i.e., April 30, the selected spawning day) for sexually mature adult striped bass. At the end of the simulation year ($t = 365$ or 366 days), we subtracted the final fish weight (W_{final}) from the initial fish weight (W_{initial}) to obtain the annual growth (G) in grams for that year. We compared the modeled annual growth to the observed annual growth obtained from empirical field data. We adjusted values of the proportion of maximum consumption (p) iteratively in the above simulation for each age in each year until a 0.5% difference (or less) was achieved between the values of modeled and observed annual growth increments. Thus, values of p were specific to each age and year.

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

$$C_T = \sum_{t=1}^{t=t_{\text{max}}} (C \cdot W) \quad (11)$$

where t is time (days), t_{max} is 365 or 366 days (depending upon leap year), and C_T is annual consumption ($g_{\text{prey}} \cdot \text{yr}^{-1}$), 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. We calculated individual prey fish consumption 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, we calculated growth over a 2-year period. Accordingly, we ran the bioenergetics model over a 2-year period to determine the proportion of maximum consumption (p), and applied the resulting p over the respective 2-year period to estimate individual total consumption.

Striped Bass Population Consumption

We calculated population total consumption and population prey fish consumption by estuary striped bass by incorporating the sub-adult and adult population abundance estimates. Population total consumption reflects the total amount of all prey types consumed (in a given year by a specific age). We calculated it by multiplying the individual total consumption by the corresponding population numbers (for the given year and age). Similarly, population prey fish consumption reflects the total amount of prey fish consumed in a given year, and we calculated it by multiplying the individual prey fish consumption by the corresponding population numbers. Confidence intervals (CI) on the total adult abundances (summed across all adult ages), as reported by the DFG, were multiplied by the total population consumption (summed across all adult ages) to determine confidence levels associated with the total population consumption. We did not consider intra-annual mortality of striped bass in this study, because seasonal estimates of sub-adult or adult abundance were not available. The inclusion of intra-annual mortality would have led to declining abundances throughout a

year, resulting in lower estimates of population total and prey fish consumption, thus the population consumption estimates reported herein are likely maximal estimates of actual values.

Statistical Analyses

We used Pearson's correlation coefficients (r) to investigate relationships among the proportion of maximum consumption (p), 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 ($r > 0.50$) and having a probability of < 0.05 .

Sensitivity Analysis

We assessed the sensitivity of the bioenergetics model to variation in striped bass diet, energy density, and the proportion of maximum consumption (p) by varying these model inputs by $\pm 10\%$ one at a time. Diet was varied by increasing the proportion of fish in the diet by $\pm 10\%$, and then adjusting the dietary proportions of non-fish categories (decapods/isopods, mysids, and others) to ensure proportions summed as observed. For ages 3+, the baseline diet proportion of fish was greater than 0.9, so rather than increasing the proportion of fish 10%, we set the proportion to 1.0 and adjusted the non-fish prey categories to zero. We varied energy density by applying $\pm 10\%$ to the ratio used in Equation 7. Energy density ratio could vary because of variability in the prey energy densities, striped bass energy densities, or both. We varied the proportion of maximum consumption (p) for each age and year by $\pm 10\%$ all together; we applied $+10\%$ to all values of p and then applied -10% to all values of p . Varying p captures the potential sensitivity of the bioenergetics model to growth. Previous sensitivity of bioenergetics models to individual parameters related to consumption, respiration, excretion, egestion, and SDA showed that predicted growth was highly sensitive to p (Bartell and others 1986).

The output variable used in assessing model sensitivity was the percent change in individual prey fish

consumption. We summed daily individual prey fish consumption over days to obtain age- and year-specific values of individual prey fish consumption. We then computed the percent change from baseline individual prey fish consumption to each of these values (i.e., by age and year). We reported the average and a standard deviation of these percent changes for age 1, age 2, and age 3+ stratified by gender to provide information on the variability in the annual percent changes.

RESULTS

Historical Datasets Summary

Average annual water temperatures over the study area ranged from 14 °C 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 observed to change significantly over time. Sub-adult striped bass became more piscivorous during the study period beginning in 1990, with a commensurate decline in the proportion of mysids in their diet. Prey fish increased from 2.5% to 12.2% in the diet of age 1 and from 78.5% to 82.1% in the diet of age 2 between 1980 and 1990 (Table 2), and mysids in the diets decreased from 95.9% to 58.5% and from 18.4% to 8.4%. 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 Striped Bass Abundance Estimates

Population abundance estimates of sub-adults varied 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 of sub-adults was apparent. Annual survival rate esti-

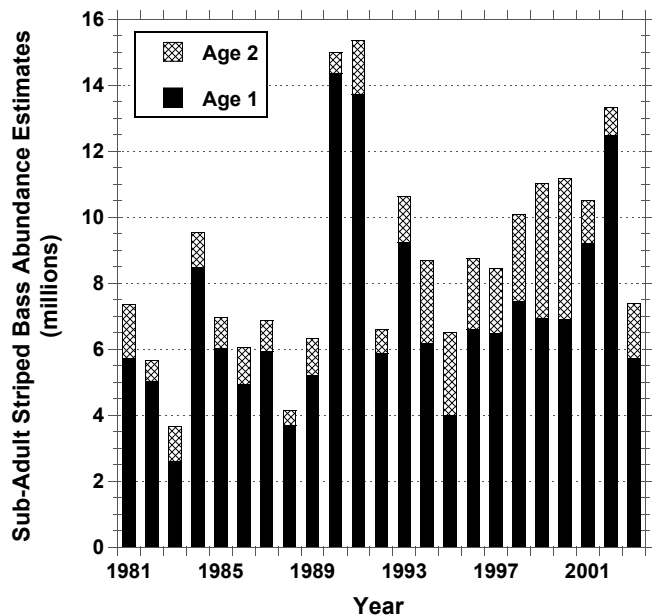


Figure 3 Population abundance estimates of sub-adult striped bass (ages 1 and 2)

mates 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 Striped Bass Consumption

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

Individual Total Consumption per Striped Bass

Individual total consumption increased with age and varied among years for both sub-adults and adults (Figures 4 and 5). Age-1 individual total consumption varied between a maximum of 2.10 kg of prey per striped bass in 1987 and a minimum of 0.92 kg of prey per striped bass in 1993 (Figure 4), with no apparent long-term trend. Conversely, there was an apparent long-term increase in age-2 individual total consumption, because after 1994 consumption remained higher than in the majority of previous years. Additionally, there were substantial fluctuations in age-2 individual total consumption (Figure 4), ranging between a maximum of 6.08 kg of prey per striped bass in 1996 and a minimum of 3.93 kg of prey per striped bass in 1994. For the adult striped bass, 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 was not statistically correlated to the aver-

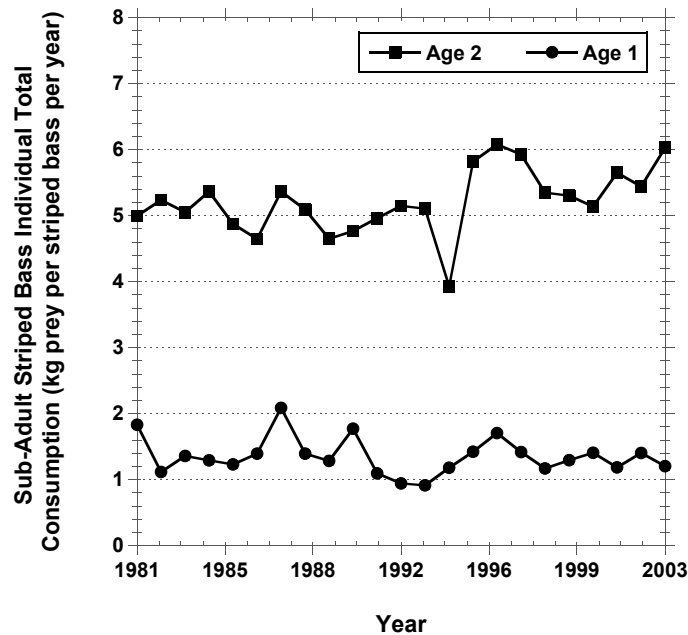


Figure 4 Individual total consumption by sub-adult striped bass (ages 1 and 2)

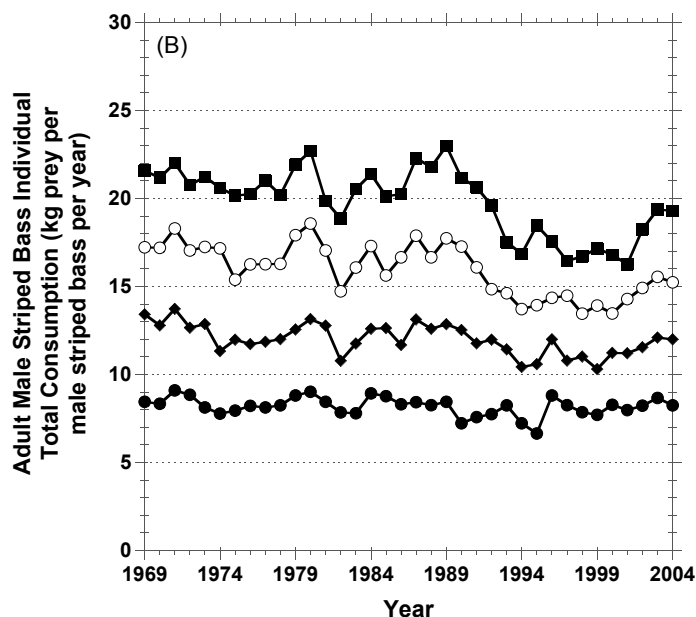
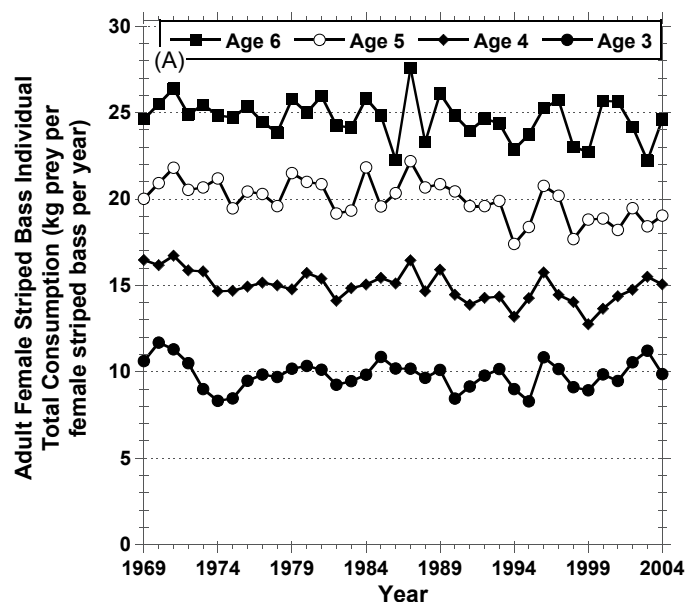


Figure 5 Individual total consumption by adult striped bass, subdivided by (A) females and (B) males

age 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 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 0.22 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). Age-2 individual prey fish consumption varied from a maximum of 4.99 kilograms of prey fish per striped bass in 1996 to a minimum of 3.22 kilograms of prey fish per striped bass in 1994. Consistent with the long-term trend in individual total consumption by age-2 striped bass, individual prey fish consumption increased after 1994. Individual prey fish consumption by adult striped bass closely mirrored the values and trends observed in adult individual total consumption (Figure 5), because prey fish constituted the majority proportion of the adult striped bass diet.

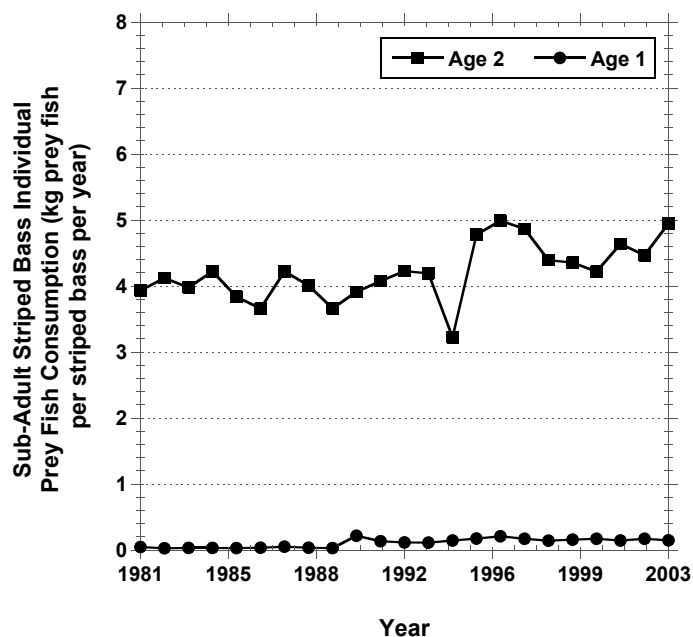


Figure 6 Individual prey fish consumption by sub-adult striped bass (ages 1 and 2)

Sub-Adult Striped Bass Population Total Consumption

Sub-adult population total consumption, when summed (age 1 plus age 2), reached a maximum of 31.63×10^6 kg of prey in 2000, and a minimum of 7.38×10^6 kg of prey in 1988 (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 ($r = 0.88$) 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 during the same time-period.

Adult Striped Bass Population Total Consumption

Adult population total consumption, when summed across all adult ages, 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 through 2000, where it began to decline thereafter, particu-

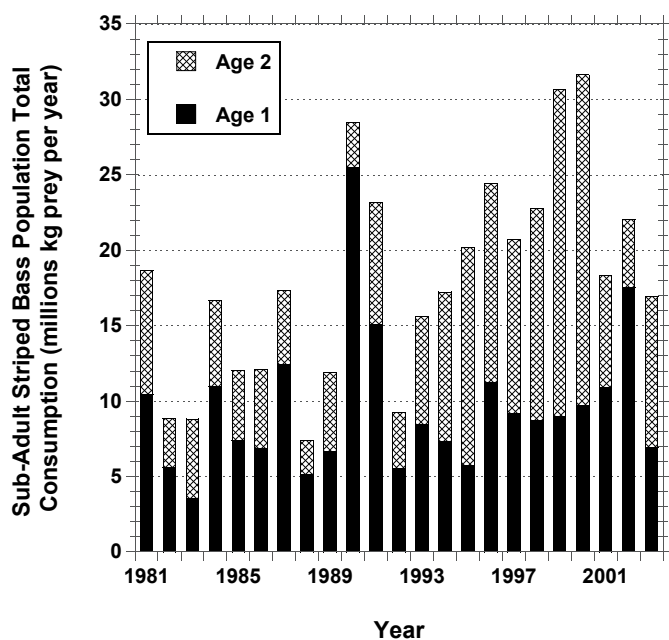


Figure 7 Population total consumption by sub-adult striped bass. Consumption by age is reflected in the length of each respective bar.

larly 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 was often less than that of younger fish (Figure 8A and Figure 8B), even though older fish consume a greater quantity of prey on an individual basis (Figure 5); this result is consistent with the typically lower abundance of older fish. Confidence intervals (CIs) on adult population total consumption were quite large, on average differing by almost 11×10^6 kg of prey between the lower and upper CIs (Figure 8C), which reflects the large CIs associated with the age-specific adult abundance estimates.

Sub-Adult Striped Bass Population Prey Fish Consumption

Sub-adult population prey fish consumption, when summed (age 1 plus age 2) peaked in 2000 at a value of 19.18×10^6 kg of prey fish, and reached a minimum in 1988 at a value of 1.87×10^6 kg of prey fish (Figure 9). Age-1 population prey fish consumption was low because of the small percentage of fish in their diet, and had a step increase beginning in 1990 that correlated to the observed step increase of fish in their diet (Table 2). Age-1 population prey fish consumption was statistically correlated with the age-1 abundances ($r = 0.86$) and with age-1 individual prey fish consumption ($r = 0.83$). Age-2 population prey fish consumption was generally constant during the 1980s, and steadily increased during the 1990s before declining in 2001. This trend in age-2 population prey fish consumption 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 Striped Bass Population Prey Fish Consumption

Trends in adult striped bass population prey fish consumption followed patterns similar to the trends in adult population total consumption. When summed across adult age-classes, the adult population prey fish consumption peaked in 1972 at a value of

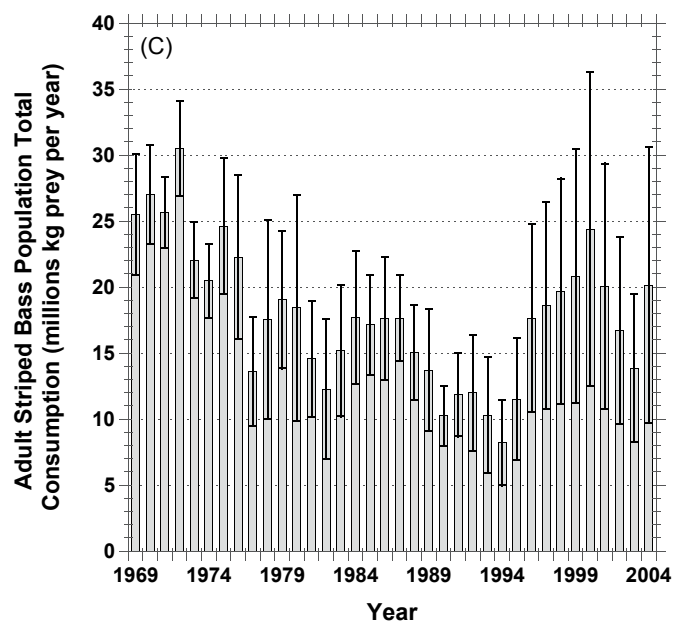
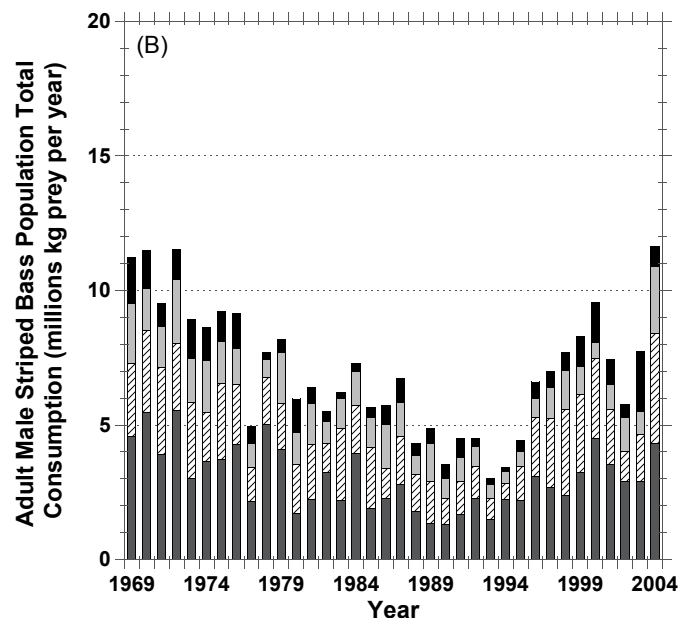
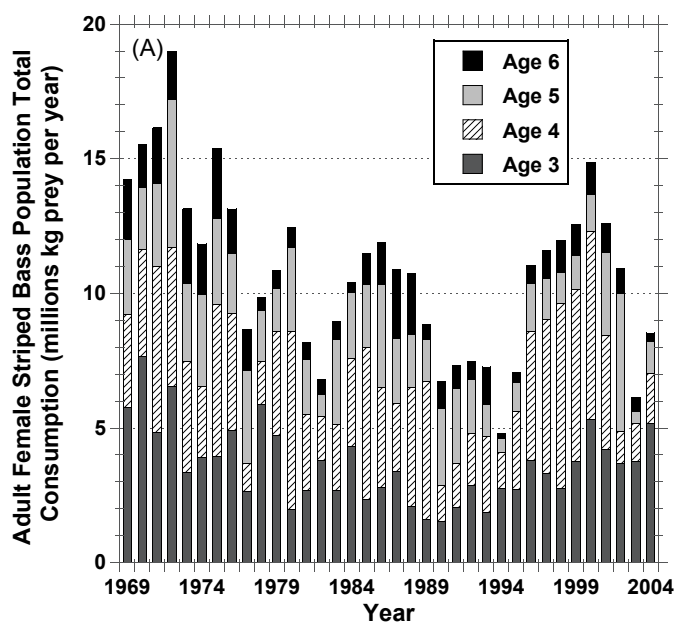


Figure 8 Population total consumption by adult striped bass subdivided by (A) females and (B) males. Consumption by age is reflected in the length of each respective bar. Combined population total consumption by male and female adult striped bass along with 95% confidence intervals (C).

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 the adult diets 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.

Sensitivity Analysis

Individual prey fish consumption was most sensitive to variation in p , and relatively insensitive to changes in the diet composition and energy densities (Table 3). The small standard deviation confirmed that the percent changes were consistent, and thus close to the overall average, among years and ages. A 10% change in the striped bass diet or energy density ratio resulted, on average, in less than a 10% change in individual prey fish consumption. In contrast, variation in p resulted in an average change of -31.7% to 74.5% for sub-adults and -17.9% to 20.7% for adults.

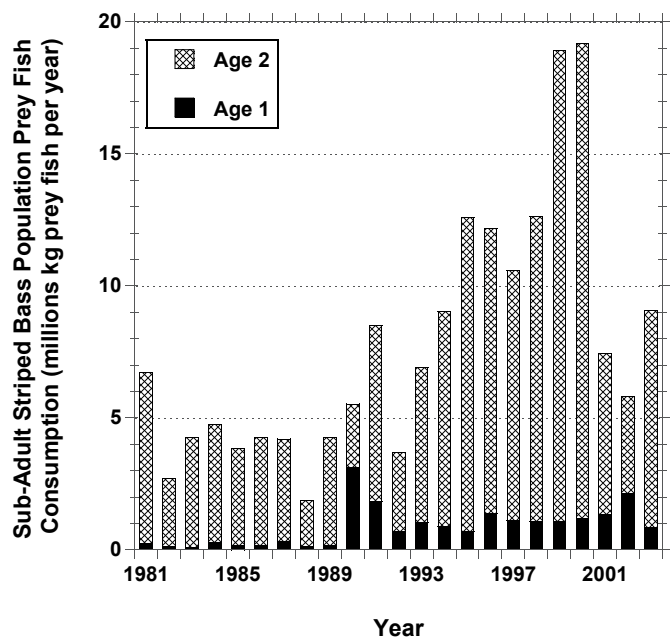


Figure 9 Population prey fish consumption by sub-adult striped bass. Consumption by age is reflected in the length of each respective bar.

DISCUSSION

Striped bass are major piscivorous predators in numerous aquatic systems. The rapid collapse of the pelagic fish community in the estuary (i.e., pelagic organism decline or POD) has been a contributing factor to a major water-management crisis in California (Service 2007; Sommer and others 2007). “Top down” effects from predators are considered one of a suite of possible mechanisms responsible for the decline in pelagic fishes in the estuary (Sommer and others 2007; Baxter and others 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 and others 2008). As a first step towards understanding the effect of predation by striped bass on fish in the estuary, we quantified the individual and population-level consumption by striped bass in this paper. Prior to this study, we could only speculate about how recent predation rates of estuary striped bass correspond to historical levels, including during the POD time-period. The present study evaluates how consumption by estuary striped bass may have changed over the past several decades, and possible factors influencing their consumption of prey fish species at the individual and population level.

Table 3 Average percent change (Avg) and standard deviation (SD) of individual prey fish consumption relative to baseline values for sub-adult and adult striped bass due to variation ($\pm 10\%$) in diet composition, energy density ratio, and the proportion of maximum consumption (ρ)

Factor varied	Sub-Adults				Adults			
	Age 1		Age 2		Females		Males	
	Avg ^a	SD	Avg ^a	SD	Avg ^a	SD	Avg ^a	SD
- 10% prey fish in diet	-7.3	0.5	-8.0	0.2	-7.0	1.5	-7.1	1.4
+ 10% prey fish in diet	6.9	0.5	7.7	0.2	-2.0	1.7	-1.9	1.6
- 10% energy density ratio	9.4	0.9	6.4	0.3	3.1	0.5	3.0	0.4
+ 10% energy density ratio	-8.2	0.8	-5.5	0.2	-2.6	0.4	-2.6	0.3
- 10% ρ	-31.7	2.1	-47.5	1.3	-17.9	1.3	-18.1	1.0
+ 10% ρ	43.1	3.9	74.5	3.1	20.4	1.8	20.7	1.5

^a Percent change was computed for each age and year as $[100 \cdot (Y_b - Y / Y_b)]$ where Y_b is the consumption under baseline and Y is the consumption with a factor varied.

From a long-term perspective, predation effects almost certainly changed with the introduction of striped bass to the Sacramento–San Joaquin 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 co-existed for many decades before the POD, predation by striped bass is not likely 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 the POD species. 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 and others 2001; Frank and others 2005).

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 estuary. To our knowledge, these are the first published estimates of sub-adult population abundance and survival rates for the estuary striped bass. The sub-adults are much more abundant than the adult population, making them the most abundant pelagic predator in the estuary ecosystem. Additionally, unlike adults, the effects of sub-adults are not limited to pelagic habitats, since they are known to be abundant in inshore areas (Nobriga and Feyrer 2007). The estimated sub-adult abundances did not reveal a declining trend similar to the trend observed in the young-of-year striped bass (age-0 fish) as inferred from the FMWT Index (e.g., Feyrer and others 2007; Sommer and others 2007; Kimmerer and others 2000). Thus, if increases in sub-adult survival resulting from density-dependent mechanisms explain of the apparent ‘disconnect’ between young-of-year and older striped bass (Kimmerer and others 2000), the increase in survival rate must have

occurred specifically in the young-of-year striped bass. However, the FMWT Survey may not accurately reflect survival of young-of-year striped bass since the population estimates of young-of-year striped bass obtained by applying the method of Newman (2008) to FMWT data generally resulted in estimates of population numbers less than that of age-3 fish. 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 that affect geographic distribution, stocking of hatchery fish, and probable changes in adult demographics (Baxter and others 2008). If survival rates of sub-adults changed during our study period as proposed by Kimmerer and others (2000), our estimates of sub-adult population numbers may not accurately reflect actual population numbers. Unfortunately, there is no empirical data available to reflect otherwise at this time.

Patterns of Individual Striped Bass Consumption

Age-2 individual total consumption increased over the study period, while individual prey fish consumption increased over the study period for both age 1 and age 2 (Figures 4, 6). The increase in observed age-2 annual growth may be partly attributed to the increase in individual total consumption. In comparing sub-adult estuary striped bass consumption to other ecosystems, sub-adult individual 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 and others 2008). The systems studied by Hartman and Brandt (1995a, 1995b) and Vatland and others (2008) differ vastly from the estuary, so such differences were not surprising.

Adult individual consumption for estuary striped bass were somewhat higher than levels reported for Chesapeake Bay (Hartman and Brandt 1995b), but were markedly higher than levels for Lake Powell (Vatland and others 2008). As in these other ecosystems, adult individual consumption in the estuary was consistently higher than for sub-adults.

Additionally, individual consumption by adult females was higher than adult males at comparable age-classes because of: (i) the larger sizes and growth rates of females than of males, and (ii) the higher energetic cost of spawning in females than in males. Individual consumption by adult striped bass decreased over the period analyzed, apparent mainly for male striped bass, age 4 and older. Observed declines in mean length at age, and subsequent declines in annual growth, likely led to the decline in individual consumption for these age-classes. The larger declines in individual consumption (and mean length at age) for striped bass males (relative to females) may be partly explained by characteristics of the mark-recapture length dataset. For example, smaller sample numbers of females (vs. males) could have led to a less accurate estimation of the mean length at age and annual growth, thereby resulting in errors of individual consumption. Spatial and temporal limitations of the water temperature and diet datasets may have also decreased the accuracy of individual consumption for all ages. However, given the consistent decreasing trends in mean length at age, and, subsequently, individual consumption among the majority of the adult striped bass, 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 this paper is that population total consumption by sub-adult striped bass was similar to the population total consumption by adults. While the individual total consumption by adults was greater than that of the sub-adults, the larger sub-adult population abundance resulted in very similar total consumption (e.g., mean = 18.1×10^6 kg prey for sub-adults versus 17.9×10^6 kg prey for adults). This finding in the estuary 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 and others 2002; Hartman 2003; Vatland and others 2003; Heimbuch 2008). The average population prey fish consumption by sub-adults (mean = 7.8×10^6 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 estuary increased through 2000, consumption from 2001 through 2003 decreased dramatically.

Adult consumption patterns were closely related to abundance levels, which follow a pattern similar to the Atlantic Coast striped bass stocks (Hartman 2003); this result may seem pre-determined 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) being estimated during the later years of the study period. As a case in point, the peak in adult population total consumption in 2000 was smaller than the population consumption in 1970, 2 years where the adult abundance estimates were approximately equal. In general, both adult abundance estimates and adult population consumption declined from 1969 through 1994, then increased through 2000, then began to decline again thereafter. However, when comparing years of similar abundance estimates, adult population consumption was lower in recent years, compared to early years in the study, because of the declining trend in adult individual consumption.

The proportion of maximum consumption (p) was the most sensitive factor we examined in affecting individual prey fish consumption. Variation of striped bass diet and energy density ratios only produced a change in individual prey fish consumption equal to or less than the factor's variation (Table 3). While a relatively small change (i.e., 10%) in p produced a relatively large change in individual prey fish consumption (i.e., ~20% to 75%), this small change in p resulted in a 75% average change in annual growth across all age-classes (assuming all other factors were equal). Since it is unlikely that annual growth was measured with a 75% error in the input datasets, a $\pm 10\%$ variation in p likely represents the extreme upper and lower bounds of error in the bioenerget-

ics model associated with p . The larger response to variation in p also partially results from how change in p was applied to all ages. Our results illustrate the importance of evaluating systematic biases in the bioenergetics model that apply across multiple ages and years, which could lead to errors in estimating the consumption required for simulated growth to match observed growth.

Consumption estimates in this study were influenced by: (i) abundance estimates of sub-adults and adults, (ii) unknown ocean migration behavior, (iii) limited number of diet studies, and (iv) 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 dominated uncertainty associated with population consumption estimates, among all factors assessed in the sensitivity analysis (i.e., striped bass diet, energy density ratio, p , and adult abundance estimates; see [Figure 8C](#)). Second, the proportion of the adult striped bass population that leaves the estuary 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 variations in prey types consumed by striped bass. Finally, the overall bioenergetics model used in this study was not comprehensively validated for the estuary. Independent estimates of model parameters were used whenever possible. Nevertheless further testing of the model is advisable to identify and quantify key sources of uncertainty outside of the factors identified in the above sensitivity analysis.

FUTURE RESEARCH AND MANAGEMENT IMPLICATIONS

An evaluation of long-term consumption trends of striped bass in the estuary may provide critical information to resource agencies on the relevance, or lack

thereof, of future research studies and management actions related to striped bass, and the broader estuary as a whole. Three primary sets of findings from this study may help guide research studies and have management implications in the estuary.

First, predation rates increased recently (ca. 1990 to 2001) coincident with higher population numbers of adult striped bass and sub-adults. The management significance of this finding, especially to threatened species, such as delta smelt and longfin smelt, is less clear, yet the recognition of recent increases in the predation rates by estuary striped bass may warrant the re-evaluation of current management strategies. Likewise, the regional diet data was inadequate to estimate consumption of individual prey species over the entire study period, only allowing us to evaluate consumption of fishes as a generalized prey category. Future research studies that target regional estuary striped bass diet analysis would be helpful to refine consumption estimates into better-defined prey categories.

Second, findings from this study suggest a possible recent shift in established striped bass predator-prey relationships in the estuary. Individual total consumption declined from 1969 to 2004 for adults, while remaining fairly constant for age 1 from 1981 to 2003. In defining what an established striped bass predator-prey relationship might look like in the estuary, it would be reasonable to assume that age-2 individual total consumption would follow either the consumption trend of adults or age 1. However, age-2 individual total consumption 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 estuary may have changed beginning in the early 1990s. The significance of such a change on specific prey species in the striped bass diet is unclear and complicated, but predation by a major piscivore is known to have influenced trends in prey species in other systems (Hartman and Brandt 1995b; Hartman 2003; Vatland and others 2008). The implementation of research studies that aim to evaluate predator-prey relationships in the

estuary striped bass population, especially in sub-adult striped bass populations, may help to clarify the role that estuary striped bass have upon influencing trends in estuary prey species.

Third, striped bass can spend large periods of time in the ocean, effectively providing a marine prey subsidy for the estuary striped bass population (Moyle 2002; Baxter and others 2008). Prey located outside of the estuary represents an unknown percentage of the estimated total prey consumed by adults. By contrast, since sub-adults primarily reside in the estuary, and since our simulations showed that this demographic frequently consumes more than adults, sub-adults have a particularly large consumption demand within the estuary. 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 consumed may originate inshore rather than in pelagic habitat. Future research studies focused upon the population distributions of sub-adult striped bass in addition to the ocean-migrating fraction of adult striped bass would help to clarify the spatial extent of striped bass consumption within the estuary.

Overall, current management actions related to estuary 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 estuary. For example, reduction of sub-adult populations could lead to an increase in the abundances of other piscivorous species that may in turn have a much more significant effect upon estuary prey species 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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REFERENCES

- Armor C, Herrgesell PL. 1985. Distribution and abundance of fishes in the San Francisco Bay Estuary between 1980 and 1982. *Hydrobiologia* 129:211–227.
- Atwater BF, Conard SG, Dowden JN, Hedel CW, MacDonald RL, Savage W. 1979. History, landforms, and vegetation of the estuary's tidal marshes. In: Conomos TJ, editor. *San Francisco Bay: the ecosystem*. San Francisco (CA): Pacific Division, AAAS. p 347–385.
- Bartell SM, Breck JE, Gardner RH, Brenkert AL. 1986. Individual parameter perturbation and error analysis of fish bioenergetics models. *Canadian Journal of Fisheries and Aquatic Sciences* 43(1):160–168.

- Baxter R, Breuer R, Brown L, Chotkowski M, Feyrer F, Gingras M, Herbold B, Mueller-Solger A, Nobriga M, Sommer T, Souza K. 2008. Pelagic organism decline progress report: 2007 synthesis of results. Interagency Ecological Program for the San Francisco Estuary. Sacramento (CA): California Dept. of Water Resources. Available from: http://wwdwr.water.ca.gov/iep/docs/pod/synthesis_report_031408.pdf
- Bennett WA. 2005. Critical assessment of the delta smelt population in the San Francisco Estuary, California. *San Francisco Estuary and Watershed Science* [internet]. Available from: <http://www.escholarship.org/uc/item/0725n5vk>.
- Brown LR, Moyle PB. 1991. Changes in habitat and microhabitat use of an assemblage of stream fishes in response to predation by Sacramento squawfish (*Ptychocheilus grandis*). *Canadian Journal of Fisheries and Aquatic Sciences* 48:849–856.
- Carpenter SR, Cole JJ, Hodgson JR, Kitchell JF, Pace ML, Bade D, Cottingham KL, Essington TE, Houser JN, Schindler DE. 2001. Trophic cascades, nutrients, and lake productivity: whole-lake experiments. *Ecological Monographs* 71:163–186.
- Chadwick HK. 1968. Mortality rates in the California striped bass population. *California Fish and Game* 54(4):228–246.
- Chippis SR, Bennett DH. 2002. Evaluation of a mysis bioenergetics model. *Journal of Plankton Research* 24:77–82.
- Cyterski M, Ney J, Duval M. 2002. Predator demand for clupeid prey in Smith Mountain Lake, Virginia. *Fisheries Research* 59:1–16.
- [DFG] Department of Fish and Game. 1999. Conservation plan for the California Department of Fish and Game striped bass management program. Available from: ftp://ftp.delta.dfg.ca.gov/Adult_Sturgeon_and_Striped_Bass/
- Elliot JM, Davison W. 1975. Energy equivalents of oxygen consumption in animal energetics. *Oecologia* 19:195–201.
- Feyrer F, Herbold B, Matern SA, Moyle PB. 2003. Dietary shifts in a stressed fish assemblage: consequences of a bivalve invasion in the San Francisco Estuary. *Environmental Biology of Fishes* 67:277–288.
- Feyrer F, Nobriga ML, Sommer TR. 2007. Multidecadal trends for three declining fish species: habitat patterns and mechanisms in the San Francisco Estuary, California, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 64:723–734.
- Feyrer F, Sommer TR, Slater SB. 2009. Old school vs. new school: status of threadfin shad (*Dorosoma petenense*) five decades after its introduction to the Sacramento–San Joaquin Delta. *San Francisco Estuary and Watershed Science* [internet]. Available from: <http://www.escholarship.org/uc/item/4dt6p4bv>.
- Frank KT, Petrie B, Choi JS, Leggett WC. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308:1621–1623.
- Grimaldo LF, Sommer T, Van Ark N, Jones G, Holland E, Moyle PB, Herbold B, Smith P. 2009. Factors affecting fish entrainment into massive water diversions in a freshwater tidal estuary: Can fish losses be managed? *North American Journal of Fisheries Management* 29:1259–1270.
- Hanson PC, Johnson TB, Schindler DE, Kitchell JF. 1997. *Fish bioenergetics 3.0*. Madison (WI): University of Wisconsin Sea Grant Institute, Technical Report WIS-CU-T-97-001.
- Harris MD, Kohlhorst DW. 2002. Survival and contribution of hatchery-reared striped bass stocked in the Sacramento–San Joaquin Estuary. Draft. California Department of Fish and Game. ????
- Hartman KJ, Brandt SB. 1995a. Comparative energetics and the development of bioenergetics models for sympatric estuarine piscivores. *Canadian Journal of Fisheries and Aquatic Sciences* 52:1647–1666.
- Hartman KJ, Brandt SB. 1995b. Predatory demand and impact of striped bass, bluefish, and weakfish in the Chesapeake Bay: applications of bioenergetics models. *Canadian Journal of Fisheries and Aquatic Sciences* 52:1667–1686.

SAN FRANCISCO ESTUARY & WATERSHED SCIENCE

- Hartman KJ. 2003. Population-level consumption by Atlantic coastal striped bass and the influence of population recovery upon prey communities. *Fisheries Management and Ecology* 10:281–288.
- Hassler TJ. 1988. Species profiles: life history and environmental requirements of coastal fishes and invertebrates (Pacific Southwest) – striped bass. Washington (DC): U.S. Fish and Wildlife Service Biological Report 82(11.82).
- Heimbuch DG. 2008. Potential effects of striped bass predation on juvenile fish in the Hudson River. *Transactions of the American Fisheries Society* 137:1591–1605.
- Hogg EH, Price DT, Black, TA. 2000. Postulated feedbacks of deciduous forest phenology on seasonal climate patterns in the Western Canadian Interior. *Journal of Climate* 13:4229–4243.
- Jassby AD, Kimmerer WJ, Monismith SG, Armor C, Cloern JE, Powell TM, Schubel JR, Vendlinski TJ. 1995. Isohaline position as a habitat indicator for estuarine populations. *Ecological Applications* 5(1):272–289.
- Kimmerer WJ. 2008. Losses of Sacramento River Chinook salmon and delta smelt to entrainment in water diversions in the Sacramento–San Joaquin Delta. *San Francisco Estuary and Watershed Science* [Internet]. Available from: <http://www.escholarship.org/uc/item/7v92h6fs>.
- Kimmerer WJ, Nobriga ML. 2008. Investigating particle transport and fate in the Sacramento–San Joaquin Delta using a particle tracking model. *San Francisco Estuary and Watershed Science* [Internet]. Available from: <http://www.escholarship.org/uc/item/547917gn>.
- Kimmerer WJ, Avent S, Bollens SM, Feyrer F, Grimaldo L, Moyle PB, Nobriga M, Visintainer T. 2005. Variability in length–weight relationships used to estimate biomass of estuarine fishes from survey data. *Transactions of the American Fisheries Society* 134:481–495.
- Kimmerer WJ, Cowan JH, Miller LW, Rose KA. 2001. Analysis of an estuarine striped bass population: effects of environmental conditions during early life. *Estuaries* 24(4):557–575.
- Kimmerer WJ, Cowan JH, Miller LW, Rose KA. 2000. Analysis of an estuarine striped bass (*Morone saxatilis*) population: influence of density-dependent mortality between metamorphosis and recruitment. *Canadian Journal of Fisheries and Aquatic Sciences* 57:478–486.
- Kohlhorst DW. Unpublished. 2007 striped bass harvest and survival rate estimation.
- Kohlhorst DW. 1999. Status of striped bass in the Sacramento–San Joaquin Estuary. *California Department of Fish and Game* 85:31–36.
- Lehman PW, Boyer G, Hall C, Waller S, Gehrts K. 2005. Distribution and toxicity of a new colonial *Microcystis aeruginosa* bloom in the San Francisco Bay Estuary, California. *Hydrobiologia* 541:87–99.
- McCloskey JW. 1986. Seasonal temperature patterns of selected cities in and around Ohio. *Ohio Journal of Science* 86(1):8–10.
- Miller LW. 1974. Mortality Rates for California Striped Bass (*Morone saxatilis*) from 1965–1971. *California Department of Fish and Game* 60(4):157–171.
- Moyle PB. 2002. *Inland fishes of California*. Berkeley (CA): University of California Press. 517 p.
- Nelson GA, Chase BC, Stockwell JD. 2006. Population consumption of fish and invertebrate prey by striped bass (*Morone saxatilis*) from coastal waters of Northern Massachusetts, USA. *Journal of Northwest Atlantic Fishery Science* 36:111–126.
- Newman KB. 2008. Sample design-based methodology for estimating delta smelt abundance. *San Francisco Estuary and Watershed Science* [Internet]. Available from: <http://www.escholarship.org/uc/item/99p428z6>.
- Nobriga ML, Feyrer F. 2008. Diet composition in San Francisco Estuary striped bass: does trophic adaptability have its limits? *Environmental Biology of Fishes* 83(4):495–503.

- Nobriga ML, Feyrer F. 2007. Shallow-water piscivore-prey dynamics in California's Sacramento-San Joaquin Delta. San Francisco Estuary and Watershed Science [Internet]. Available from: <http://www.escholarship.org/uc/item/387603c0>.
- Nichols FH, Cloern JE, Luoma SN, Peterson DH. 1986. The modification of an estuary. *Science* 231:567-573.
- Ostrach DJ, Low-Carchelli JM, Eder KJ, Whiteman SJ, Zinki JG. 2008. Maternal transfer of xenobiotics and effects on larval striped bass in the San Francisco Estuary. *Proceedings of the National Academy of Sciences* 105:19354-19359.
- Pope KL, Brown ML, Duffy WG, Michaletz PH. 2001. A caloric-based evaluation of diet indices for largemouth bass. *Environmental Biology of Fishes* 61:329-339.
- Service R. 2007. Delta blues, California style. *Science* 317:442-445.
- Sommer T, Armor C, Baxter R, Breuer R, Brown L, Chotkowski M, Culberson S, Feyrer F, Gingras M, Herbold B, Kimmerer W, Mueller-Solger A, Nobriga M, Souza K. 2007. The collapse of pelagic fishes in the upper San Francisco Estuary. *Fisheries* 32:270-277.
- Steimle FW, Terranova RJ. 1985. Energy equivalents of marine organisms from the continental shelf of the temperate northwest Atlantic. *Journal of Northwest Atlantic Fishery Science* 6:117-124.
- Stevens DE. 1966. Food habits of striped bass, *Morone saxatilis*, in the Sacramento-San Joaquin Delta. In: *Fish Bulletin 136. Ecological studies of the Sacramento-San Joaquin Delta. Part II: Fishes of the Delta*. Sacramento (CA): California Department of Fish and Game. p 68-96.
- Stevens DE. 1977. Striped bass (*Morone saxatilis*) monitoring techniques in the Sacramento-San Joaquin Estuary. *Proceedings of the conference on assessing the effects of power-plant-induced mortality on fish populations*; 1977 May 3-6; Gatlinburg. New York (NY): Pergamon Press. p 91-109.
- Stevens DE. 1980. Factors affecting striped bass fisheries on the West Coast. In: Clepper H, editor. *Marine recreational fisheries 5. Proceedings of the Fifth Annual Marine Recreational Fisheries Symposium*; 1980 March 27-28; Boston. Washington (DC): Sport Fishing Institute. p 15-28.
- Stevens DE, Kohlhorst DW, Miller LW, Kelly DW. 1985. The decline of striped bass in the Sacramento-San Joaquin Estuary, California. *Transactions of the American Fisheries Society* 114:12-30.
- Thornton KW, Lessem AS. 1978. A temperature algorithm for modifying biological rates. *Transactions of the American Fisheries Society* 107:284-287.
- Tuomikoski JE, Rudershausen PJ, Buckel JA, Hightower JE. 2008. Effects of age-1 striped bass predation on juvenile fish in western Albermarle Sound. *Transactions of the American Fisheries Society* 137:324-339.
- Turner J, Chadwick HK. 1972. Distribution and abundance of young-of-the-year striped bass, *Morone saxatilis*, in relation to river flow in the Sacramento-San Joaquin Estuary. *Transactions of the American Fisheries Society* 101:442-452.
- Vatland S, Budy P, Thiede GP. 2008. A bioenergetics approach to modeling striped bass and threadfin shad predator-prey dynamics in Lake Powell, Utah-Arizona. *Transactions of the American Fisheries Society* 137:262-277.
- White, JR. 1986. The striped bass sport fishery in the Sacramento-San Joaquin Estuary, 1969-1979. *California Fish and Game* 72(1):17-37.