

BIOENERGETIC MODELING EVIDENCE FOR A CONTEXT-DEPENDENT ROLE OF FOOD LIMITATION IN CALIFORNIA'S SACRAMENTO-SAN JOAQUIN DELTA

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Striped bass, *Morone saxatilis*, and largemouth bass, *Micropterus salmoides*, are two of the top piscivores in California's San Francisco Estuary. The relative abundance of age-0 striped bass has plummeted since the late 1960s, whereas the abundance of largemouth bass has increased since the early 1990s. Major changes to the estuarine food web have made it a likely place for significant striped bass food limitation, and despite their population increase, there is evidence that young largemouth bass might also be chronically food-limited. Food limitation can be thought of as a context-dependent stressor, meaning that population-level consequences of food limitation are discernable only when they are severe enough to override other factors influencing the growth and mortality of young fishes. The purpose of this study was to clarify the role that food limitation plays in the early life history of striped bass and largemouth bass. I used a combination of previously published beach seine data and bioenergetic modeling (BEM) to evaluate the question, which species is likely more food-limited during its first growing season? I hypothesized that age-0 striped bass would show evidence of greater food limitation than largemouth bass (as indexed by realized vs. potential growth). The BEM simulations predicted that largemouth bass would grow larger than striped bass given the water temperature histories these fish experienced in the Sacramento-San Joaquin Delta during summer-autumn 2001 and 2003. However, the striped bass collected during autumn were larger than the largemouth bass and had thus performed better relative to BEM predictions. I conclude that age-0 striped bass were less food limited than age-0 largemouth bass in these recent years. As discussed, the upsurge of largemouth bass is likely the outcome of low survival in an expanding area of suitable habitat, whereas striped bass food limitation covaries in time with high entrainment loss and declining abiotic habitat suitability. This contrast provides a counter-intuitive example of the context-dependence of food

limitation in these sympatric fish populations.**INTRODUCTION**

Striped bass, *Morone saxatilis*, and largemouth bass, *Micropterus salmoides*, are two of the top piscivores in California's San Francisco Estuary (Nobriga and Feyrer 2007). They have overlapping spatial distributions in the tidal freshwater of the Sacramento-San Joaquin Delta (Fig. 1), but are most strongly associated with different habitat types; adult striped bass are anadromous and occur throughout the estuary and sometimes move into the coastal Pacific Ocean (Moyle 2002). However, age-0 striped bass are strongly associated with turbid, low-salinity habitats of the upper estuary and Delta (Nobriga et al. 2005; Feyrer et al. 2007). In contrast, largemouth bass of all ages are most common near the vegetated and relatively unturbid habitats that have proliferated throughout much of the Delta during the past 25 years or so (Nobriga et al. 2005; Brown and Michniuk 2007).

The vegetated habitats used by largemouth bass have encroached on the turbid, open-water habitats more suitable for age-0 striped bass (Brown and Michniuk 2007; Feyrer et al. 2007). This has resulted in a substantial increase in largemouth bass abundance in the Delta (Fig. 2), which now supports an important recreational and tournament fishery (Lee 2000¹). The relative abundance of age-0 striped bass has been monitored intensively by the California Department of Fish and Game in the San Francisco Estuary for decades². This monitoring has documented a substantial long-term decline (Fig. 2). The decline has been attributed to multiple factors; early studies placed a large importance on river flows and water diversions (Stevens 1977; Stevens et al. 1985). Later studies emphasized contaminant effects (Bailey et al. 1994; Bennett et al. 1995). The most recent population dynamics studies have emphasized egg supply reduction due to loss of large adult fish and declining juvenile carrying capacity (Kimmerer et al. 2000; 2001). The latter may be due to a combination of food limitation (Kimmerer et al. 2000; Sommer et al. 2007) and declining abiotic habitat suitability during autumn (Feyrer et al. 2007).

Major changes to the estuarine food web have made it a likely place for significant striped bass food limitation. Over the past 4 decades, there has been a long-term decline in the productivity of several lower trophic level organisms that historically helped fuel pelagic fish production, including striped bass. In particular, the steep decline in mysid shrimp density and dominance of a smaller introduced species that followed the introduction of the overbite clam, *Corbula amurensis*, in 1986 is likely the most significant contributor to food limitation of young striped bass (Feyrer et al. 2003; Nobriga and Feyrer 2008). Note that diet composition studies have also been used to suggest that the *C. amurensis* invasion did not affect juvenile striped

¹Lee, D. P. 2000. The Sacramento-San Joaquin Delta largemouth bass fishery. Interagency Ecological Program for the San Francisco Estuary Newsletter 13(3): 37-40. (available online at <http://iep.water.ca.gov/report/newsletter/>)

²<http://www.delta.dfg.ca.gov/>

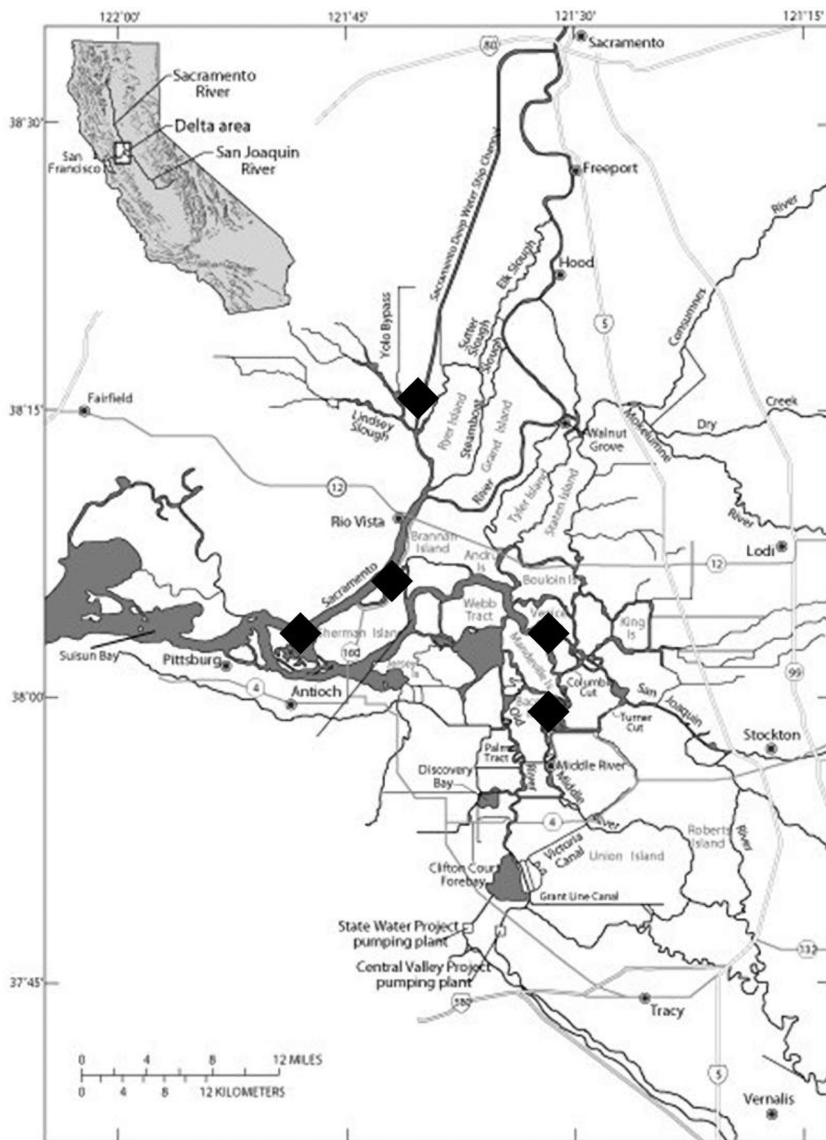


Figure 1. Map of the San Francisco Estuary, California showing the locations of the beach seine sampling sites used by Nobriga et al. (2005).

bass feeding success (Bryant and Arnold 2007), but analyses of available abundance indices provide compelling evidence for a *C. amurensis* impact on young striped bass carrying capacity (Kimmerer et al. 2000; Sommer et al. 2007).

Despite their population increase, there is evidence that young largemouth bass

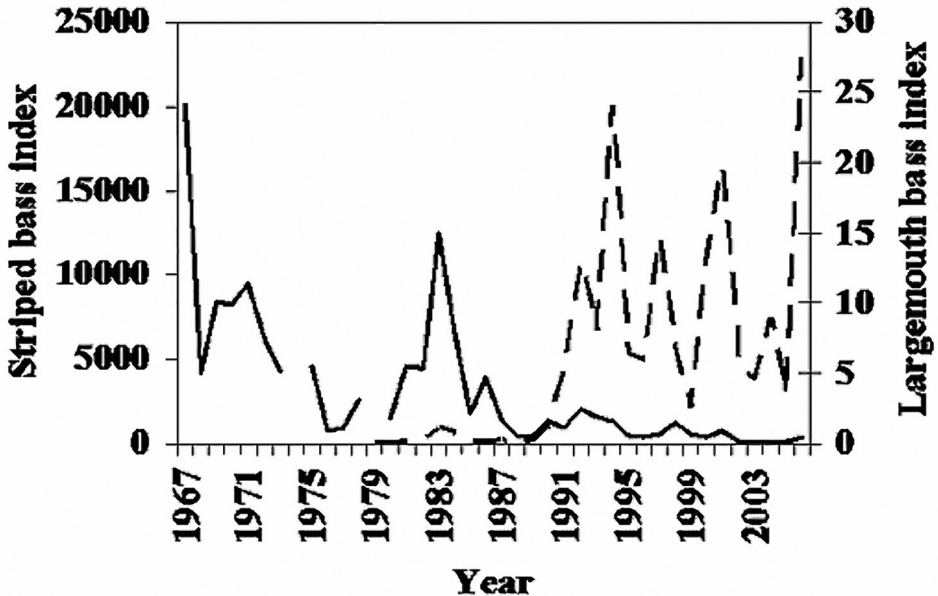


Figure 2. Relative abundance trends for age-0 striped bass (1967-2006; solid line) and largemouth bass (1979-2006; dashed line) in the San Francisco Estuary, California. The striped bass abundance indices are based on the California Department of Fish and Game Fall Midwater Trawl (<http://www.delta.dfg.ca.gov/data/mwt/>). The largemouth bass abundance indices are summed daily salvage \cdot acre feet⁻¹ of water diverted by the State Water Project and Central Valley Project in the Sacramento-San Joaquin Delta (<http://www.delta.dfg.ca.gov/Data/Salvage/>). Note that these data series do not depict relative abundance among species.

might also be chronically food-limited. Schaffter (1998³) provided length-at-age data for largemouth bass collected from the Delta during 1980-1984 and again in 1995 and 1997. During both time periods, average lengths at age-1 were < 90 mm. In contrast, length at age-1 in native Atlantic coastal river systems typically averages > 120 mm (Meador and Kelso 1990).

Food limitation in fishes can be tested directly. For instance, histopathological evaluations of fish liver tissue have been used to evaluate food limitation in larval striped bass (Bennett et al. 1995). Bioenergetics modeling (BEM) can also provide insights into food limitation. BEMs are mathematical simulation tools that predict fish growth or consumption as functions of time, water temperature, and ration; the latter is a function of two components, proportion of maximum ration (Pmax) and prey energy density (PED). For instance, Rand et al. (1994) used BEMs to determine how well the forage fish base in Lake Ontario was meeting the predatory demand of Chinook salmon, *Oncorhynchus tshawytscha*. Hartman and Brandt (1995) con-

³Schaffter, R. G. 1998. Growth of largemouth bass in the Sacramento-San Joaquin Delta. Interagency Ecological Program for the San Francisco Estuary Newsletter 11(3): 27-30. (available online at <http://iep.water.ca.gov/report/newsletter/>)

ducted a similar BEM-based analysis of striped bass, bluefish, *Pomatomus saltatrix*, and weakfish, *Cynoscion regalis* in Chesapeake Bay. Locally, Sommer et al. (2001) used bioenergetic modeling to demonstrate that tagged groups of Chinook salmon released into a highly channelized reach of the Sacramento River were food-limited relative to groups released into the Yolo Bypass.

The purpose of the present study was to clarify the role(s) that food limitation plays in the early life history of striped bass and largemouth bass in the San Francisco Estuary. I used a bioenergetic modeling approach to evaluate food limitation in these fishes. The approach involved the use of BEMs to evaluate the question, which species is likely more food-limited during its first growing season? I hypothesized that age-0 striped bass would show evidence of greater food limitation than largemouth bass (as indexed by realized vs. potential growth).

METHODS

I used field data collected by Nobriga et al. (2005) to provide empirical inputs to the BEMs. Nobriga et al. (2005) sampled fishes monthly (March–October 2001 and March–November 2003) using 30 m X 1.8 m, 3.2-mm mesh beach seines deployed from small-draft boats at five shoreline sites in the Delta (Fig. 1). Eighty-seven percent of the 5,704 striped bass, and 99% of the 1,301 largemouth bass collected were measured for fork length (FL; to the nearest 1 mm) in the field. These data provided robust and concurrent monthly length frequencies for both species based on a single gear type, which provided consistent time series for estimating age-0 striped bass and largemouth bass growth rates. Age-0 individuals remained vulnerable to the sampling gear and clearly separable from older conspecifics throughout the sampled periods.

I also used striped bass and largemouth bass collected by Nobriga et al. (2005) to develop length–weight conversions. Individuals of both species were subsampled (striped bass $n = 521$; 28–322 mm; largemouth bass $n = 311$; 27–310 mm), preserved in 10% formaldehyde, and returned to the laboratory where the fish were re-measured and weighed to the nearest 0.01 g using an electronic balance. The resulting equations were: $\ln(\text{wt}) = 2.93\ln(\text{FL}) - 11.0$, and $\ln(\text{wt}) = 3.10\ln(\text{FL}) - 11.7$, for striped bass and largemouth bass, respectively. I used these equations to convert observed fish fork lengths (FL; mm) to weight estimates (g) to input into bioenergetic model (BEM) simulations and to convert BEM-predicted weights into length estimates (Table 1).

I used the striped bass and largemouth bass BEMs of Hanson et al. (1997⁴). I used the models heuristically to produce standardized arrays of plausible growth end points based on initial average sizes of age-0 striped bass and largemouth bass given the water temperatures they occupied during their first summer–autumn of life (Table 1). Then I evaluated the relative degree of food limitation among these species by comparing their observed autumn FLs to these standardized arrays of potentially achievable FLs. Note that a key assumption is that differences in observed growth

⁴Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish bioenergetics 3.0. Center for Limnology, University of Wisconsin, Madison.

Table 1. Summary data for age-0 striped bass (StrBas) and largemouth bass (LarBas) used in bioenergetic modeling simulations. The fish were collected in the Sacramento-San Joaquin Delta, California, Jun-Oct 2001 and Jul-Nov 2003. The mean fork lengths are based on beach seine collections (Nobriga et al. 2005); the mean weights were estimated from length-weight regression relationships.

	StrBas 2001	StrBas 2003	LarBas 2001	LarBas 2003
Sample size, 26-29 June 2001	440		464	
Sample size, 14-18 July 2003		598		47
Mean FL (mm) \pm SD	47 \pm 14	47 \pm 11	43 \pm 8	45 \pm 9
Mean wt (g) \pm SD	1.7 \pm 1.4	1.6 \pm 1.2	1.2 \pm 0.77	1.3 \pm 0.88
Sample size, 4-11 Oct 2001	771		9	
Sample size, 23 Oct-5 Nov 2003		53		18
Mean FL (mm) \pm SD	93 \pm 16	91 \pm 14	80 \pm 16	78 \pm 15
Mean wt (g) \pm SD	11 \pm 5.9	9.7 \pm 4.4	7.7 \pm 5.3	7.0 \pm 4.5
Water temperature range ($^{\circ}$ C)	20-23	18-25	21-25	19-26
Model simulation duration (days)	104	101	101	113

relative to BEM predictions reflects food limitation, possibly including contaminant effects on food supply, but not differences in direct contaminant effects on fish growth. This assumption seems reasonable since both species feed at similar trophic levels on similar prey taxa (Nobriga and Feyrer 2007) and water throughout the Delta is dominated by water originating from the Sacramento River (Kimmerer 2002).

To develop autumn size predictions, I converted the Nobriga et al. (2005) sampling dates to days of the year (1-365); each simulation started on the average collection day that a cohort fully recruited to the beach seine and ended on each cohort's average final day of collection. Note that the term cohort in this paper refers to an age-0 year class of a species in a given year. Simulation start dates ranged from 27 June through 18 July and end dates ranged from 6 October through 5 November. The simulation start and end dates were shifted about 3-4 weeks later in 2003 due to differences in sample collection dates among years. In both years for both species, age-0 fish were fully recruited to the beach seine during the same series of sampling events. This suggests that striped bass and largemouth bass had considerable temporal overlap in spawn timing, so the BEM simulation durations were also very similar, ranging from 101-113 days (Table 1).

Water temperature data were collected by Nobriga et al. (2005) during each site visit using a hand-held thermometer. Based on different spatial distributions of young striped bass and largemouth bass inhabiting the Delta, I used average water temperature at the three Sacramento River sampling sites (Fig. 2) for the striped bass simulations and average water temperature at the two San Joaquin River sampling sites for the largemouth bass simulations. Summer-fall water temperatures ranged from 26 $^{\circ}$ -18 $^{\circ}$ C and were typically 1-2 $^{\circ}$ C higher in the San Joaquin River (Table 1). The BEMs linearly interpolated water temperatures between months.

I generated variability in predicted autumn FLs by varying Pmax and PED, both

of which likely vary considerably in nature (Hartman and Brandt 1995; Lawson et al. 1998). For each cohort, I produced nine potentially achievable autumn sizes by assuming an average PED of $3,000 \text{ J} \cdot \text{g}^{-1}$ and solving for end weights that produced Pmax of 50%, 60%, 70%, and 80% ($\pm 0.1\%$) and for an average PED of $4,000 \text{ J} \cdot \text{g}^{-1}$ and solving for end weights that produced Pmax of 40%, 50%, 60%, 70%, and 80% ($\pm 0.1\%$). These Pmax and PED combinations were chosen because they produced growth predictions that fully encompassed the observed autumn FLs at the observed water temperatures using PEDs in the range of typical striped bass and largemouth bass prey (Hanson et al. 1997⁵). The percentages of fishes in each cohort that equalled or exceeded the various BEM-based autumn FL projections were calculated and then evaluated graphically.

RESULTS

The BEM simulations predicted minimal growth differences among years for both species (Table 2). The simulations also predicted that all else equal, largemouth bass would grow larger than striped bass by autumn given their observed initial sizes and the water temperatures each species inhabited. Largemouth bass were predicted to be 1-15 mm larger than striped bass depending on year and the Pmax/PED combination that was modeled.

In the field however, the striped bass grew larger relative to their growth predictions than largemouth bass. Most of the striped bass collected in the Delta during autumn 2001 and 2003 had attained sizes that the striped bass BEM indicated represented about 60% of Pmax at a PED of $3,000 \text{ J} \cdot \text{g}^{-1}$ or 40%-50% of Pmax at a PED of $4,000 \text{ J} \cdot \text{g}^{-1}$, while most of the largemouth bass had only attained sizes that the largemouth

Table 2. Predicted autumn FLs (mm) of age-0 striped bass (SB) and largemouth bass (LB) in California's Sacramento-San Joaquin Delta, 2001 and 2003. Results are presented for various model input assumptions about combinations of proportion of maximum ration (Pmax) attained and average prey energy density (PED in $\text{J} \cdot \text{g}^{-1}$).

Pmax (%)	PED	SB2001	SB2003	LB2001	LB2003
50	3000	47	46	54	56
60	3000	67	66	76	79
70	3000	89	87	97	102
80	3000	112	109	119	124
40	4000	54	53	61	64
50	4000	82	80	90	94
60	4000	112	109	119	124
70	4000	145	140	146	153
80	4000	179	173	174	182

⁵Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish bioenergetics 3.0. Center for Limnology, University of Wisconsin, Madison.

bass BEM indicated represented 50% of P_{max} at a PED of $3,000 \text{ J} \cdot \text{g}^{-1}$ or 40% of P_{max} at a PED of $4,000 \text{ J} \cdot \text{g}^{-1}$ (Fig. 3).

DISCUSSION

I hypothesized that age-0 largemouth bass would show less evidence of food limitation than age-0 striped bass. However, the comparison of field collections with BEM simulations did not support this hypothesis. The BEM simulations predicted that largemouth bass would grow larger than the striped bass given the water temperature histories these fish experienced in the Sacramento-San Joaquin Delta during summer-autumn 2001 and 2003. However, the striped bass collected during autumn were larger than the largemouth bass (Table 1) and had thus performed better relative to BEM predictions (Fig. 3).

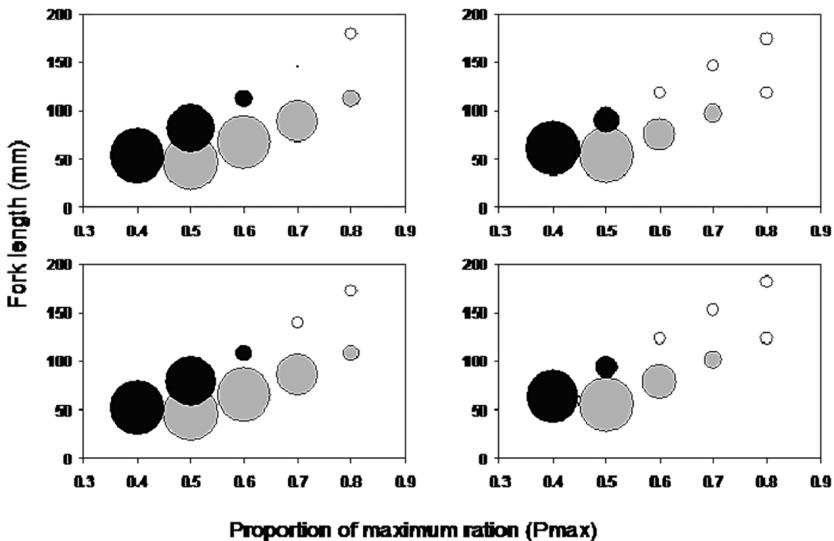


Figure 3. Scatterplots showing the influence of proportion of maximum ration on bioenergetics model-predicted autumn fork lengths of age-0 striped bass and largemouth bass: a) striped bass 2001, b) striped bass 2003, c) largemouth bass 2001, and d) largemouth bass 2003. Results are shown for two prey energy densities: $3000 \text{ J} \cdot \text{g}^{-1}$ shown as light grey symbols, and $4000 \text{ J} \cdot \text{g}^{-1}$ shown as black symbols. Each weight prediction is sized to reflect the percentage of field-collected age-0 striped bass and largemouth bass that equalled or exceeded it (maximum bubble size = 100% exceedance). Open symbols depict 0% exceedance.

It is unlikely that my use of length frequency distributions from beach seine sampling greatly influenced the results. The mean autumn fork lengths of largemouth bass in this study (78–80 mm; Table 1), are in close agreement with previous estimates of length at age-1 based on analysis of scale annuli from specimens collected by elec-

trofishing (78-86 mm; Schaffter 1998⁶). Further, the mean October fork lengths of age-0 striped bass from the California Department of Fish and Game's Fall Midwater Trawl Survey have ranged from 73-98 mm (California Department of Fish and Game, unpublished data). The beach seine estimates of mean autumn striped bass fork lengths in 2001 (93 mm) and 2003 (91 mm) were likewise in agreement with CDFG data. Thus, the appropriate conclusion appears to be that age-0 striped bass were less food limited than age-0 largemouth bass in these recent years. I acknowledge that although 2 years of data allows for some contrast, it may not have been sufficient to capture the full range of recent feeding and growth variability experienced by these fishes. Nonetheless, as discussed below, this result has implications for how food limitation is conceptualized as a stressor on fish population dynamics in the San Francisco Estuary.

The universal importance of first-year growth to fish recruitment is a subject of scientific debate (e.g., Houde 1987; Leggett and DeBlois 1994). However, studies of young striped bass and largemouth bass in other systems have demonstrated that slow first-year growth can lead to poor survival (Hurst and Conover 1998; Ludsin and DeVries 1997). Further, as stated above, statistical explorations of juvenile striped bass population dynamics have provided strong circumstantial evidence for food limitation following the *C. amurensis* invasion of the San Francisco Estuary (Kimmerer et al. 2000; Sommer et al. 2007). Thus, the notion that largemouth bass food limitation may be worse than striped bass is counter-intuitive based on recent abundance trends (Fig. 1).

Striped bass food limitation, to the extent it is occurring, covaries with high entrainment loss to water diversions (Stevens et al. 1985; Kimmerer et al. 2001) and declining abiotic habitat suitability (Feyrer et al. 2007). Thus, food limitation of age-0 striped bass occurs as a stressor interacting with other persistent stressors that all contribute to decreased habitat suitability (Rose 2000). This contrasts the situation for largemouth bass. For largemouth bass, there is strong evidence that rapid increases in habitat have facilitated population growth (Nobriga et al. 2005; Brown and Michniuk 2007). Specifically, the rapid expansion of aquatic weeds and associated increase in water clarity in the Delta has improved habitat suitability for largemouth bass. The present study suggests that this alteration is much more important to largemouth bass' recent success than patterns of growth during the first year of life. There have been no studies to determine the influence of first-year growth rate or size-at-age on survival of largemouth bass in the Delta, but based on studies elsewhere, small size is expected to result in low survival (Ludsin and DeVries 1997). Thus, the upsurge of largemouth bass is likely the outcome of low survival in an expanding area of suitable habitat. This contrast provides a counter-intuitive example of the context-dependence of food limitation in these sympatric fish populations.

6 Schaffter, R. G. 1998. Growth of largemouth bass in the Sacramento-San Joaquin Delta. Interagency Ecological Program for the San Francisco Estuary Newsletter 11(3): 27-30. (available online at <http://iep.water.ca.gov/report/newsletter/>)

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