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Journal

San Francisco Estuary and Watershed Science, 7(1)

Authors

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Publication Date

2009

DOI

https://doi.org/10.15447/sfews.2009v7iss1art3

SEPTEMBER 2009

SAN FRANCISCO ESTUARY & WATERSHED SCIENCE

Published by the California Bay-Delta Authority Science Program and the John Muir Institute of the Environment

Old School vs. New School: Status of Threadfin Shad (*Dorosoma petenense*) Five Decades After Its Introduction to the Sacramento–San Joaquin Delta

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ABSTRACT

Threadfin shad (*Dorosoma petenense*) is a schooling pelagic forage fish native to watersheds of the Gulf Coast of North America. Around 1962 it invaded the Sacramento-San Joaquin Delta from upstream reservoirs, where it was stocked to support sport fisheries. It quickly became, and continues to be, one of the most abundant fishes collected by ongoing monitoring programs in the delta. A substantial portion of the delta provides suitable abiotic habitat and so the species is widely distributed. However, in routine sampling it is most commonly collected and most abundant in the southeastern delta, where suitable abiotic habitat (relatively deep, clear water with low flow) coincides with high prey abundance. Apparent growth rate appears to be relatively fast with summer-spawned age-0 fish attaining fork lengths of 70-90 mm by the onset of winter. During fall months (September-December) the apparent growth rate of age-0 fish is negatively related to abundance, although there is no long-term trend. This suggests that density-dependent factors may be important to the population. Although abundance has fluctuated since its introduction almost five decades ago, it has recently dropped to persistent near-record lows since 2002, which has been coincident with similar declines for other pelagic species in the delta. The recent decline is apparent in two long-term monitoring programs, fish salvaged from the diversions of the State and Federal Water Projects, and commercial fishing harvest. It appears that the decline is, at least in part, a function of fewer and smaller schools of threadfin shad encountered relative to the past. There was little evidence from the data examined for consistent stock-recruit or stage-recruit effects on the population. It is likely that a combination of abiotic and biotic factors have a large effect on abundance. These appear to be regionally-focused where threadfin shad are most abundant, and are episodic in nature. More focused studies and more effective sampling of threadfin shad are necessary in order to better understand population dynamics in the delta.

KEYWORDS

Dorosoma petenense, baitfish, Clupeidae, San Francisco Estuary, pelagic organism decline

SUGGESTED CITATION

Feyrer F, Sommer T, 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://repositories.cdlib.org/jmie/sfews/vol7/iss1/art3

INTRODUCTION

Threadfin shad (*Dorosoma petenense*) is a key forage fish native to North and Central America in watersheds draining into the Gulf of Mexico. Fisheries managers have commonly manipulated threadfin shad populations in an attempt to enhance sport fisheries, although the results associated with these manipulations have been inconsistent for predator and competitor species (DeVries and Stein 1990). Because of the importance of this species as a forage fish, its biology and interactions with other species have been studied. However, relatively little appears to be known about its long-term population dynamics.

A member of the herring family (Clupeidae) that rarely exceeds 100 mm in length, threadfin shad is typically found in open water habitats of lakes, reservoirs, and backwaters of rivers. It can tolerate low salinities but typically requires freshwater for successful reproduction. Threadfin shad usually spawn from April to August in California (Feyrer 2004; Grimaldo and others 2004). Spawning is typically associated with floating or partially submerged objects, especially submerged aquatic vegetation in the Sacramento-San Joaquin Delta (Grimaldo and others 2004). Threadfin shad at all life stages are typically planktonic feeders (Turner 1966; Feyrer and others 2003), focusing on crustacean zooplankton, although it has the ability to switch feeding modes in response to prey availability (Ingram and Ziebell 1983).

Threadfin shad was intentionally introduced into California in 1953 by the California Department of Fish and Game (CDFG) to provide forage for sport fishes in reservoirs (Dill and Cordone 1997). It was stocked into reservoirs in watersheds of the Sacramento and San Joaquin rivers in 1959, and invaded the Sacramento-San Joaquin Delta by 1962, when it was first detected by the CDFG's Summer Townet Survey. The effect of threadfin shad on the delta ecosystem is largely unknown because there is virtually no pre-invasion fish community data with which to compare. Moreover, there have been relatively few studies on threadfin shad since its introduction almost five decades ago. Nonetheless, it is clear that threadfin shad irreversibly altered the fish community because it quickly became one of the most abundant pelagic fishes in the system. Due to its relatively high abundance, it serves as a primary forage fish for the largest striped bass (*Morone saxatilis*) fishery in western North America and one of the premier largemouth bass (*Micropterus salmoides*) fisheries in the world (Stevens 1966; Feyrer and others 2003; Nobriga and Feyrer 2007).

The abundance of threadfin shad, as measured by indices calculated annually by the CDFG from their Fall Midwater Trawl Survey (FMT), has fluctuated over time but has dropped to persistent near-record lows since 2002 (Feyrer and others 2007; Sommer and others 2007). Although there have been previous periods with similarly low abundance, the current decline has persisted and is coincident with similar declines for several other native and introduced pelagic fishes in the upper San Francisco Estuary over the same time period (Feyrer and others 2007; Sommer and others 2007). This decline in the primary components of the pelagic fish community has prompted unprecedented efforts to compile and synthesize data on the affected species (Sommer and others 2007). The goal of our study was to describe life history aspects of threadfin shad from data available from existing monitoring programs of the Interagency Ecological Program (IEP). The IEP is a cooperative monitoring and research effort led by State and Federal agencies plus university and private partners. It has numerous fish monitoring programs that together take place year-round across the system (Honey and others 2004). Based on extensive previous history working with these data sets (e.g., Feyrer and others 2004; Feyrer and others 2007) and further exploratory analyses, we determined that the IEP data sets would be suitable for a retrospective analysis of abundance, distribution, habitat associations, and apparent growth rate of age-0 fish in the delta.

STUDY AREA

San Francisco Bay (Figure 1) is the entrance to the largest estuary on the Pacific coast of the United States. The estuary is fed by California's two largest rivers – Sacramento (from the north) and San Joaquin (from the south) – which drain a 100,000-km^2 watershed encompassing 40% of California's surface area. The delta is a 3,000-km^2 network of tidal freshwater channels formed by the confluence of the two rivers. From the delta, water flows west into Suisun Bay, through the Carquinez Strait, and enters San Pablo Bay before reaching San Francisco Bay and ultimately the Pacific Ocean. Freshwater flow entering the estuary varies seasonally, with most coming in late winter through spring. Anthropogenic modifications to the estuary include the loss of wetlands, channel modifications for flood control and navigation, and a variety of water reclamation activities including storage, conveyance, and large water diversions by the State Water Project (SWP) and Central Valley Project (CVP) (Nichols and others 1986). Dams on the Sacramento and San Joaquin rivers, including most of their major tributaries, control estuarine inflow. The fish community of the delta is dominated by introduced species (Feyrer and Healey 2003; Nobriga and others 2005; Sommer and others 2007) and has been called the most highly invaded in the world (Cohen and Carlton 1998).

METHODS

Data Sources

The primary data we examined originate from trawl surveys conducted during spring (20-mm Survey) and fall (FMT). We also evaluated data from other sampling programs for this project but ultimately focused on these two data sets because they provided the most comprehensive spatial and temporal coverage for analyses. For example, we excluded the IEP's San Francisco Bay Study because, although it collects threadfin shad, the majority of its samples are collected in saltwater habitats of the lower estuary where threadfin shad are rare or absent. For further information we refer readers to Honey and others (2004), who provide detailed descriptions for all IEP fish monitoring programs.

The 20-mm Survey targets young age-0 fish during spring-summer while the FMT targets older age-0 fish during fall. Although neither of these programs was designed to specifically target threadfin shad, the programs were designed to sample pelagic fishes; threadfin shad is one of the most abundant species encountered in terms of the number of individuals captured (Dege and Brown 2004). The efficiency of these sampling gears for threadfin shad is unknown. However, published studies examining threadfin shad in other systems have used nets with larger mesh sizes, which would presumably be less efficient (e.g., Allen and DeVries 1993; Van Den Avyle and others 1995). Further, data from these programs have been used extensively in prior studies of pelagic fish abundance and distribution in the system (e.g., Stevens and Miller 1983; Moyle and others 1992; Jassby and others 1995; Dege and Brown 2004; Feyrer and others 2007). Both monitoring programs encompass the full distribution of threadfin shad in the system; they extend beyond its downstream distribution into marine-influenced habitats and upstream to the margin of the major freshwater tributaries.

The FMT (Stevens and Miller 1983) has been conducted each year since 1967, except that no sampling was done in 1974 or 1979. Samples (12-minute tows) are collected at 100 sites each month from September to December throughout the upper estuary. Net dimensions are as follows: 17.6-m long with a mouth opening of 13.7 m^2, and nine tapered panels of stretch mesh from 20.3 cm to 1.3 cm in the cod-end. Water temperature (°C), Secchi depth (m), and specific conductance ($\mu s \cdot cm^{-1}$) were measured with each tow.

The 20-mm Survey (Dege and Brown 2004) has been conducted each year since 1995. The survey collects three replicate samples (10-minute tows) at a subset of 48 of the 100 FMT sites. A complete set of samples from each site is termed a survey: five to nine sur-

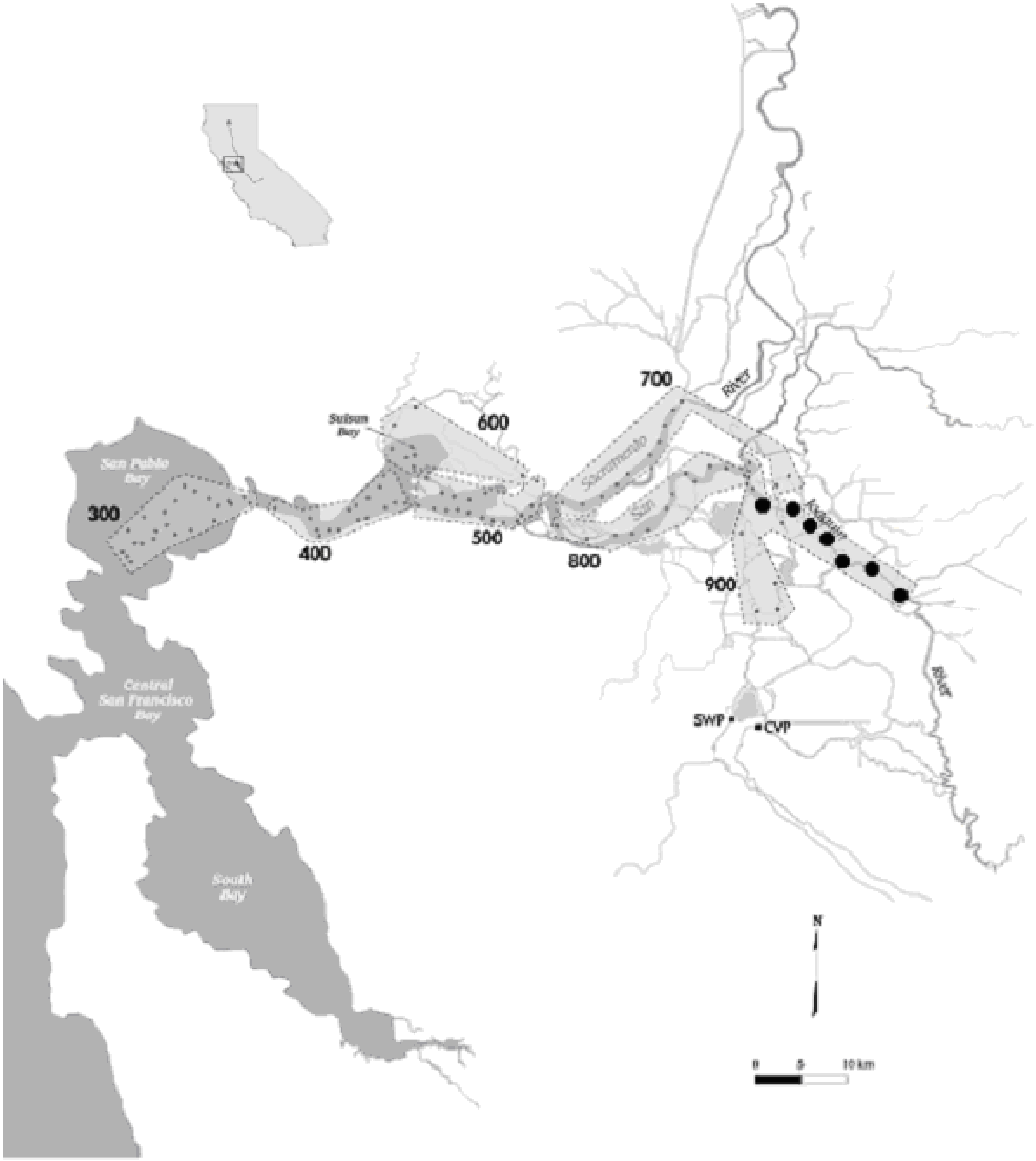

Figure 1 Sampling sites in the Sacramento-San Joaquin Delta. Sites (in bold text) along the San Joaquin River are, from west to east: stations 906, 907, 908, 909, 910, 911, and 912

veys are completed each year from approximately March though June. The conical plankton net used for the survey is 5.1 m long with a mouth opening of 1.5 m^2. The net is constructed of 1,600-µm knotless nylon delta mesh and is mounted on a weighted tow frame with skids. As with the FMT, water temperature, Secchi depth, and specific conductance are measured at each site visit. This survey also simultaneously samples zooplankton during one of the three tows at each site. Zooplankton is sampled with a Clarke-Bumpus net that is attached to the metal frame of the fish net. This net consists of 160 µm knotless nylon mesh and measures 78 cm long with a 12 cm mouth diameter.

We also summarized two other sets of data, salvage of fish at SWP and CVP water projects and harvest by the commercial fishery. The intakes to the south delta diversion facilities of the SWP and CVP (Figure 1) are screened with fish-behavioral louvers designed to separate fish from diverted water before they enter the pumps (Brown and others 1996; Kimmerer 2008). In general, this salvage process consists of fish capture, identification and measurement, transport, and ultimately release at distant locations where the fish are presumed safe from the pumps. However, it is commonly accepted that the majority of threadfin shad probably do not survive the salvage process because of either handling stress or predation at the release sites. Although data from the salvage facilities do not cover the geographic scope of the other surveys, sample size (numbers of fish captured) for the salvage data sets are dramatically larger than the trawl data sets because of the substantial volumes of water diverted, presently more than 6 km^3 per year (Kimmerer 2002). We summarized the salvage data seasonally (spring = March-May, summer = June-August, fall = September-November, winter = December-February) for each year as the total number of threadfin shad combined for both facilities standardized by the total amount of water exported (salvage density). Similar methods have been successfully used to examine abundance trends in other delta fishes (Stevens and Miller 1983; Sommer and others 1997).

Commercial harvest data were provided to us directly from the CDFG. Of the 360 records for threadfin shad from 1977 to 2007, 327 were for the southeast region of the delta ("CDFG's accounting block 306") from approximately Stockton to Franks Tract. The remaining 21 records were for other regions of the delta and were excluded from analyses because they were sparse and represented less than one half of one percent of the total biomass harvested. The data were provided in units of pounds with an associated dollar value ($), which we converted to metric units and then ultimately to an estimated number of individual fish using the length-weight regression from Kimmerer and others (2005) and an average size fish of 80 mm fork length (FL).

Data Analyses

While we examined all of the data sets for interannual trends, the FMT and 20-mm data were the most useful to identify the habitat associations and geographic distribution of threadfin shad. Data from the FMT were also suitable to estimate apparent growth rates.

To identify habitat associations, we used principal components analysis (PCA) to examine distribution along environmental gradients. First, the environmental data from each tow were standardized by subtracting the mean and dividing by the standard deviation, and principal components were extracted from the covariance matrix. Next, we plotted the PCA scores for each sampling station and scaled the size of the points by abundance (average catch per trawl [CPT] for the FMT and average density (fish per 10,000 m^3 for the 20-mm Survey). A key benefit of this approach versus other possible regression-type analyses is that these plots allowed us to interpret how threadfin shad was distributed spatially along environmental gradients in multivariate space coincident with geography as represented by the sampling stations.

We conducted several additional data summaries to better understand patterns of distribution and abundance. First, based upon the results of the PCA, we examined FMT CPT and 20-mm Survey density across stations. Because threadfin shad is a strongly schooling species, we reasoned that simpler measurements of fish presence in trawls might help to reduce the effects of a patchy distribution on the catch data. We plotted time series for the fraction of samples with threadfin shad present, fraction of samples with values above the long-term median and third quartile, and the largest sample. Finally, we constructed several plots - with data from FMT CPT, 20-mm density, and summer salvage density - to examine stock-recruit and stage-recruit effects on the population.

We used a length-frequency method of estimating apparent growth rate. In the FMT, the number of threadfin shad collected during each tow was recorded throughout the survey, but length measurements on individuals were not made until 1975. Initial inspection of the data suggested that most of the fish collected in the FMT were age-0. We systematically identified age-0 cohorts by means of length-frequency histograms created for each month and year from size data based on class intervals of 5.0 mm FL. From the length-frequency histograms, we used the modal progression routine of the FiSAT software program (version 1.2.2; Food and Agriculture Organization–International Center for Living Aquatic Resources Management stock assessment tools; Gayanilo and others 2002) to identify age-0 cohorts. FiSAT applies Bhattacharya's (1967) method to fit normal components to mode means in the length-frequency histograms and then employs NORMSEP (Hasselblad 1966) to refine parameter estimates. This includes an iterative process of the maximum likelihood concept to decompose complex size-frequency distributions into normal curves that represent each cohort within the data set. Modes were accepted as distinct cohorts only when differentiated by a separation index above the critical value of 2 (Gayanilo and others 2002). We estimated the abundance of age-0 threadfin shad in each month from the total number of fish belonging to the age-0 cohort, as determined by FiSAT, divided by the total number of trawls. Apparent growth rates of the age-0 cohort were estimated as the slope of the FiSAT-estimated average fork lengths from September to December. We used regression analysis to determine if apparent growth rate was related to a few key factors that commonly affect bioenergetics: initial abundance (average catch per trawl in September); initial size (average FL in September); overall average water temperature during the sampling period (September-December); or the slope of the average water temperatures for September-December.

RESULTS

Average CPT in the FMT was variable and exhibited no long-term trend (Figure 2). Intra-annual variation in CPT was proportional to average CPT (Pearson correlation coefficient $r = 0.91$, $P < 0.001$). Average CPT peaked at over 80 in 2000 and 2001, and then in 2002 dropped to below 20 and has remained at that level. The CPT time series was significantly correlated with the indices of abundance calculated by CDFG (Figure 2; Pearson correlation coefficient $r = 0.87$, $P < 0.001$).

Average density (number of fish per 10,000 m^3) in the 20-mm Survey was also variable and exhibited no long-term trend (Figure 3). Just as with the FMT, intra-annual variation in density was proportional to average density (Pearson correlation coefficient $r = 0.97$, $P < 0.001$). Average density peaked at over 1,000 from 2001-2003, and then in 2004 dropped to below 500 and has continued to decline.

Salvage density was also variable and has exhibited no long-term trend across seasons (Figure 4). Overall, salvage density in all seasons has been relatively low in recent years. Salvage densities were highest and most variable during summer when spawning occurs and new fish are recruited to the population. Salvage density was lowest during spring, where it has remained relatively low after peaking in the early 1980s. Salvage density during fall was highest in the late 1990s and early 2000s, and has been relatively low since 2003. Winter salvage density peaked in 2003 and has since remained relatively low.

Commercially harvested biomass (kg) and its associated dollar value were also variable over the course of their time series, but exhibited a steady decline after peaking in 2003 (Figure 5). Overall, harvested biomass of threadfin shad ranged from a low of 16 kg in 1977 to a high of 45,067 kg in 2003. The associated dollar values were $45 and $102,810, respectively. By

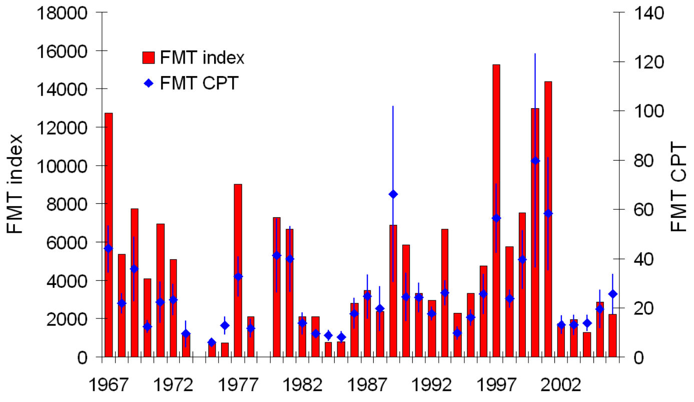

Figure 2 Time series of threadfin shad abundance indices calculated by CDFG and average catch per trawl (+ one standard error; CPT) in the Fall Midwater Trawl Survey (FMT)

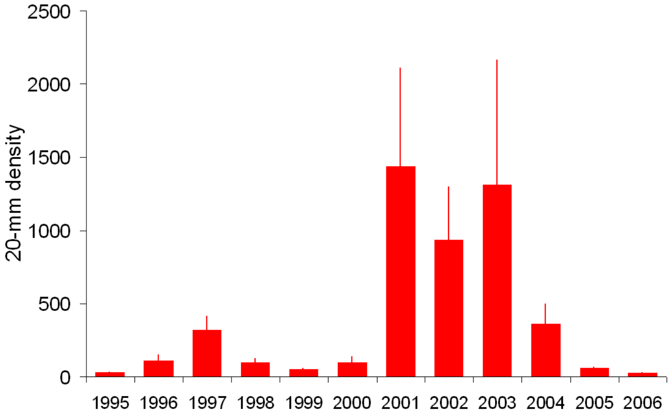

Figure 3 Time series of average (+ one standard error) threadfin shad density (fish per 10,000 m^3) in the 20-mm Survey

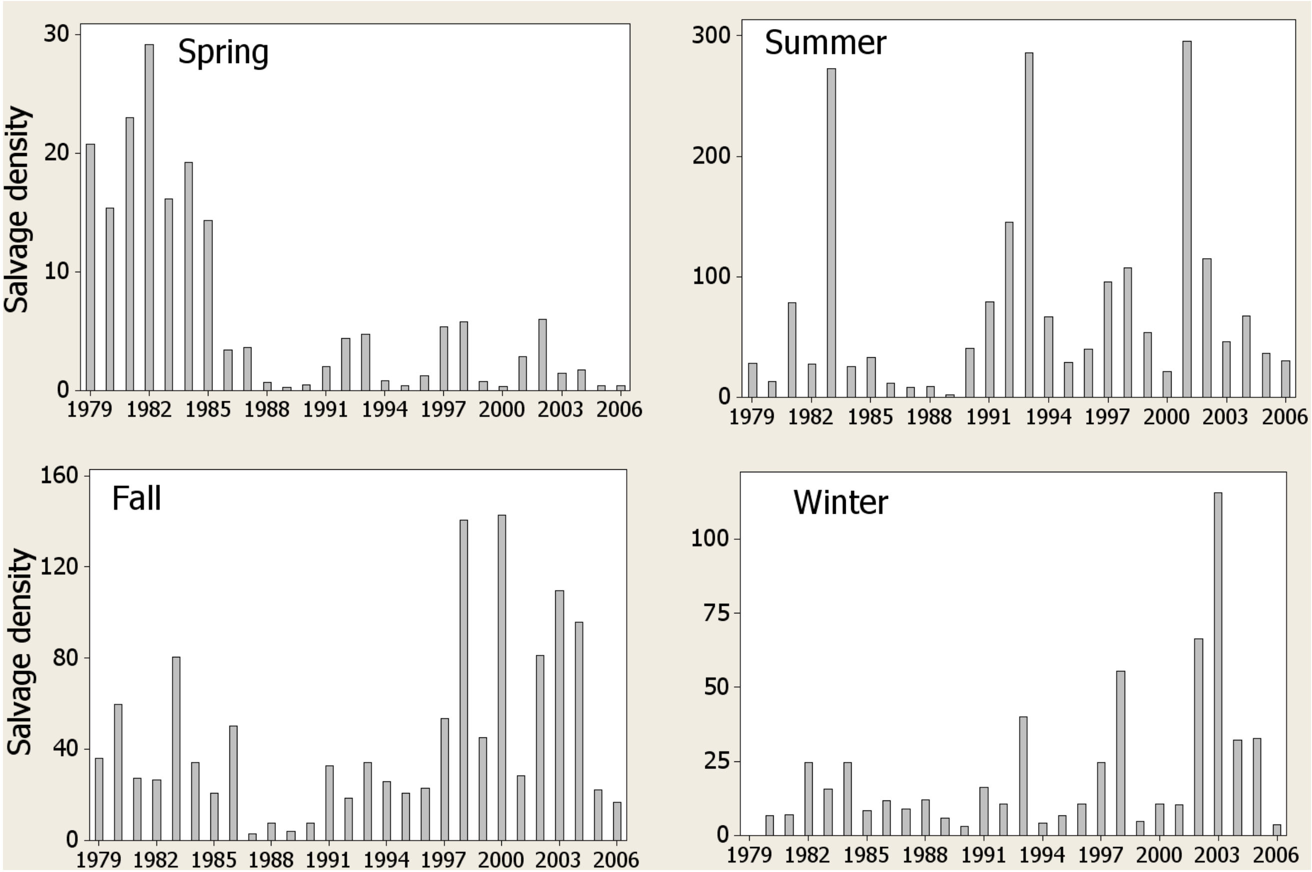

Figure 4 Time series of total combined threadfin salvage density by season. Spring = March – May, Summer = June – August, Fall = September – November, and Winter = December – February.

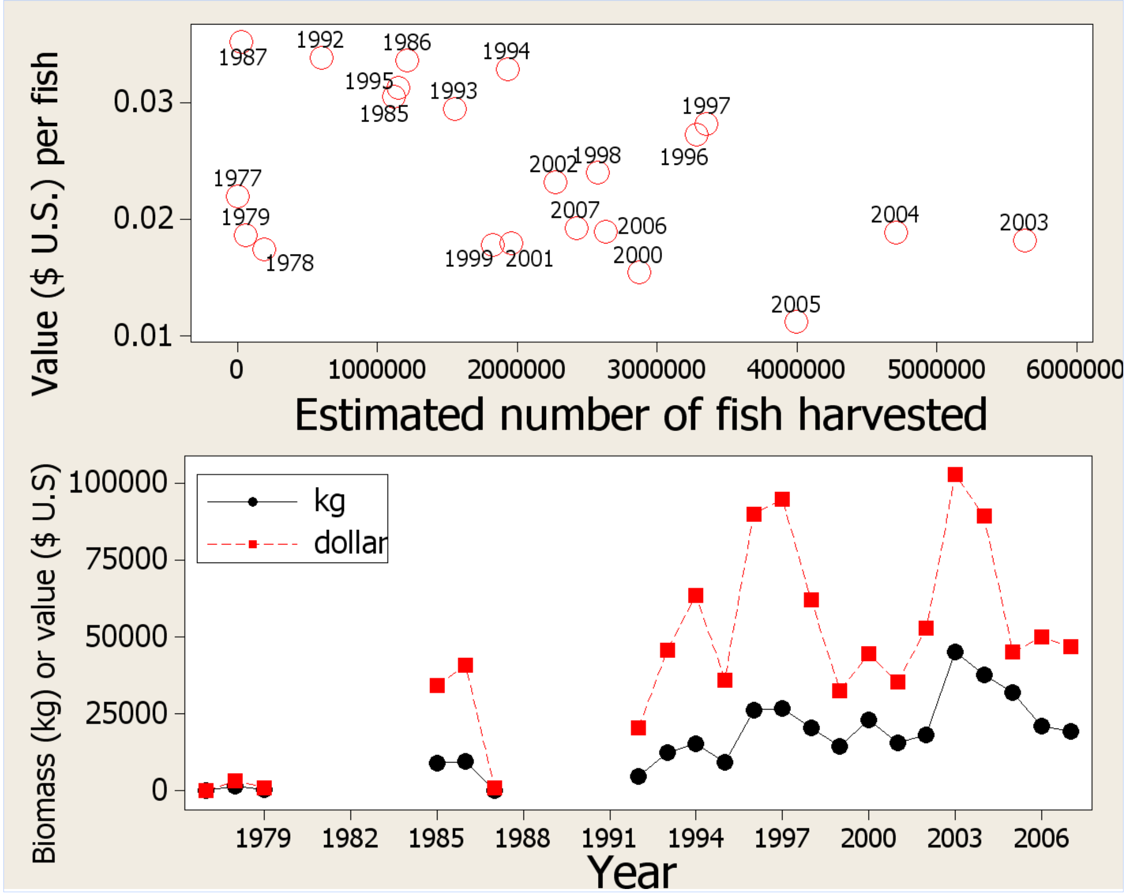

Figure 5 Upper panel: estimated dollar value of commercially harvested individuals plotted against the total number of individuals harvested. Lower panel: time series of commercially harvested biomass (kg) and its associated dollar value of threadfin shad.

2007 harvested biomass and its dollar value dropped to 19,377 kg and $46,816, respectively. Data were not available to determine if this was a function of smaller catches, decreasing effort, or a combination of both. The approximated dollar value per individual fish typically centered around $0.02, but hovered near or above $0.03 for a period from the late 1980s to the mid 1990s (Figure 5). Seasonally, commercially harvested biomass (kg) was highest during fall and winter and lowest in spring and summer (Figure 6).

The results of the PCAs with the FMT and 20-mm data sets showed that both younger and older age-0 threadfin shad was primarily distributed in the southeastern region of the delta under similar environmental conditions (Figure 7). The first two axes of the PCA on the FMT data set were significant eigenvectors as indicated by values > 1.0 (1.19 and 1.05, respectively), which explained 57.6% (30.7 and 26.9, respectively) of the variation (see Figure 2). Axis one was characterized by a strong positive loading for water depth and a negative loading for specific conductance. Axis two was characterized by strong positive loadings for water depth and Secchi depth. The plot of scores on these two axes, scaled by average CPT, demonstrated that threadfin shad were most abundant at sites along the San Joaquin River and the south delta in association with deep, clear, fresh water.

The first two axes of the PCA on the 20-mm data set were significant eigenvectors as indicated by values > 1.0 (1.40 and 1.06, respectively), which explained 49.3% (28.0 and 21.3, respectively) of the variation in the data set (Figure 7). Axis one was characterized by strong positive loadings for water depth and Secchi depth, and a negative loading for specific conductance. Axis two was characterized by strong positive loadings for water temperature, Secchi depth, and zooplankton abundance. The plot of site scores on these two axes scaled by average threadfin shad density demonstrated that younger age-0 threadfin shad were also most abundant at sites along the San Joaquin River and the south delta in association with deep, clear, fresh water with high zooplankton abundance.

As suggested by the variability in the time series data and the distribution patterns in the PCAs, we found that threadfin shad exhibited a contagious distribution such that the majority of the catch occurred in a small geographic area and interannual variation in abundance was highly influenced by large individual catches. In the FMT, a suite of seven adjacent stations (906, 907, 908, 909, 910, 911, and 912; see bold text in Figure 1) in the San Joaquin River dominated the catch relative to all other stations, including average catch per trawl (140 versus 11) and the fraction of samples with threadfin shad present (0.76 vs. 0.27). The average CPT across these stations was highly correlated with the annual abundance indices calculated by CDFG (Pearson correlation coefficient *r* = 0.84, P < 0.001), suggesting these stations have

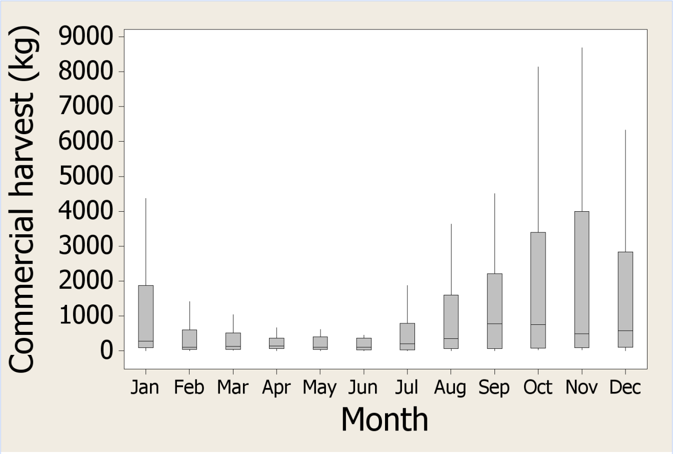

Figure 6 Box plot representation of commercially harvested biomass (kg) of threadfin shad by month

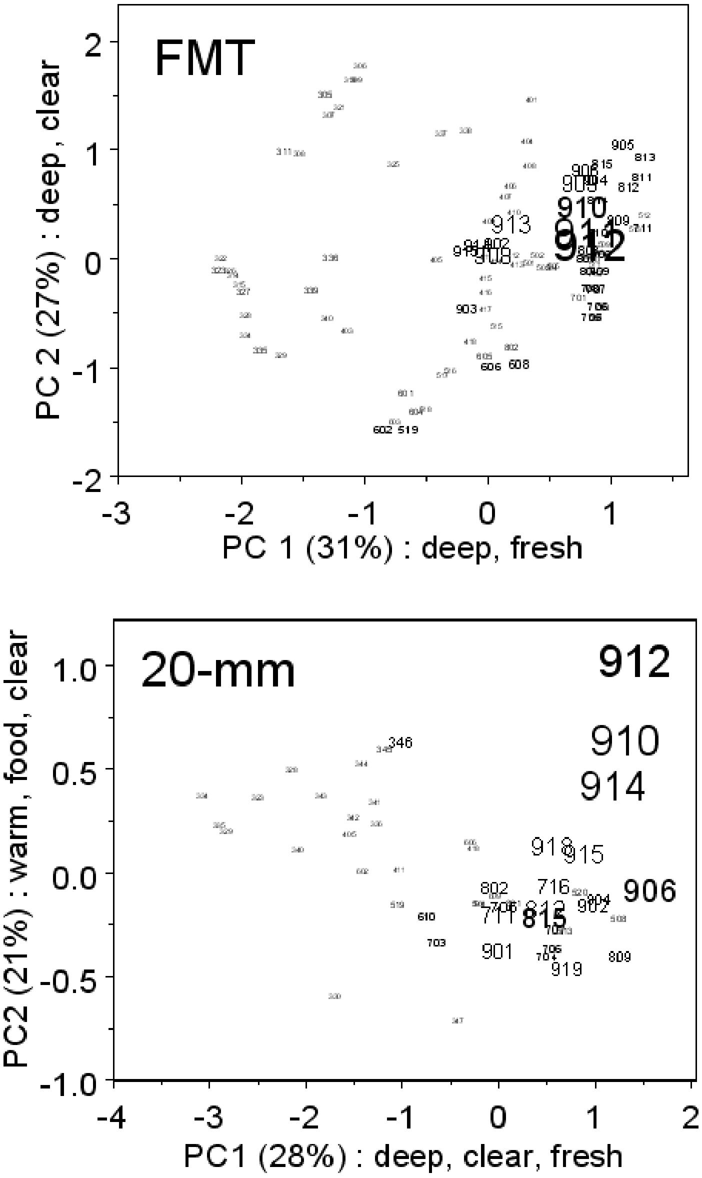

Figure 7 Plots of scores for the first two axes of principal components analyses conducted with data from the Fall Midwater Trawl Survey (top panel) and the 20-mm Survey (lower panel). Sample scores are labeled for the sampling stations and are scaled by average abundance. The general location of the stations is given in Figure 1. Values in parentheses in the axis labels indicate the explained amount of variance.

been driving the long-term trends observed in the abundance indices. At these stations there has been a substantial recent decline in the fraction of samples with threadfin shad present, the fraction of samples with counts of threadfin shad above the long-term median and third quartile, and the maximum count of threadfin shad in a sample (Figure 8).

The 20-mm Survey data set is also dominated by catches from the same geographic region (stations 910 and 912) in terms of the fraction of samples with threadfin shad present (0.61 vs. 0.30) and average density of threadfin shad (2,275 vs. 107 fish per 10,000 m^3). However, unlike the FMT, there were no trends across these stations in the fraction of samples with threadfin shad present, fraction of samples with densities above the long-term median and third quartile, and the maximum density (Figure 9).

We constructed three candidate stock-recruit relationships and two candidate stage-recruit relationships (Figure 10). The stock-recruit models were FMT CPT, 20-mm density, and summer salvage density all plotted against the previous year's FMT CPT. The stage-recruit models were summer salvage density plotted against 20-mm density and FMT CPT plotted against summer salvage density. Although none of the models provided particularly strong evidence of consistent stock- or stage-recruit effects, all response variables exhibited at least some positive response to the prediction variables, with the exception of the FMT CPT-summer salvage density model which had no response.

Using the FiSAT software we were able to identify an age-0 cohort for each month (September-December) in 24 of the 28 years; data were insufficient in 1984, 1986, 1991, and 1997. In total, 85% of the fish mea-

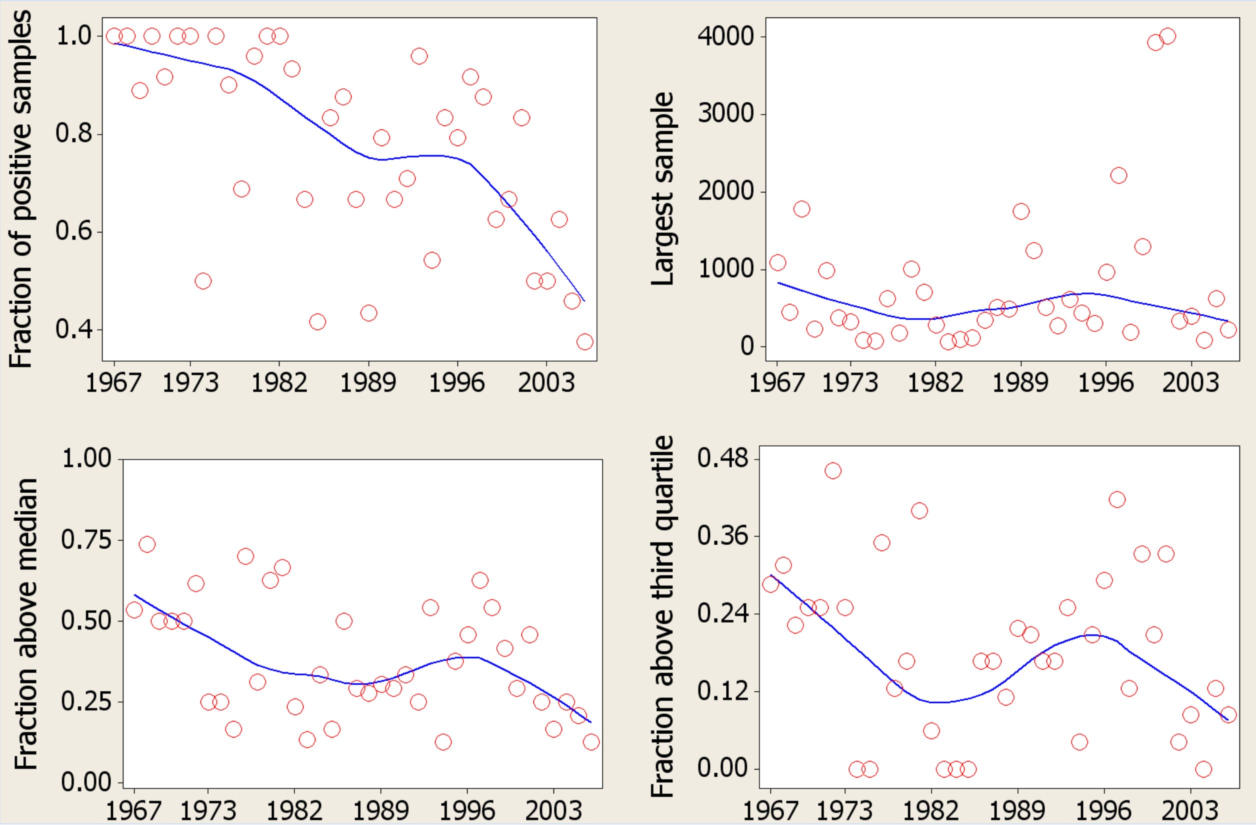

Figure 8 Time series for various factors summarized across key stations (906-912) of the Fall Midwater Trawl Survey. Curves are LOESS smooths.

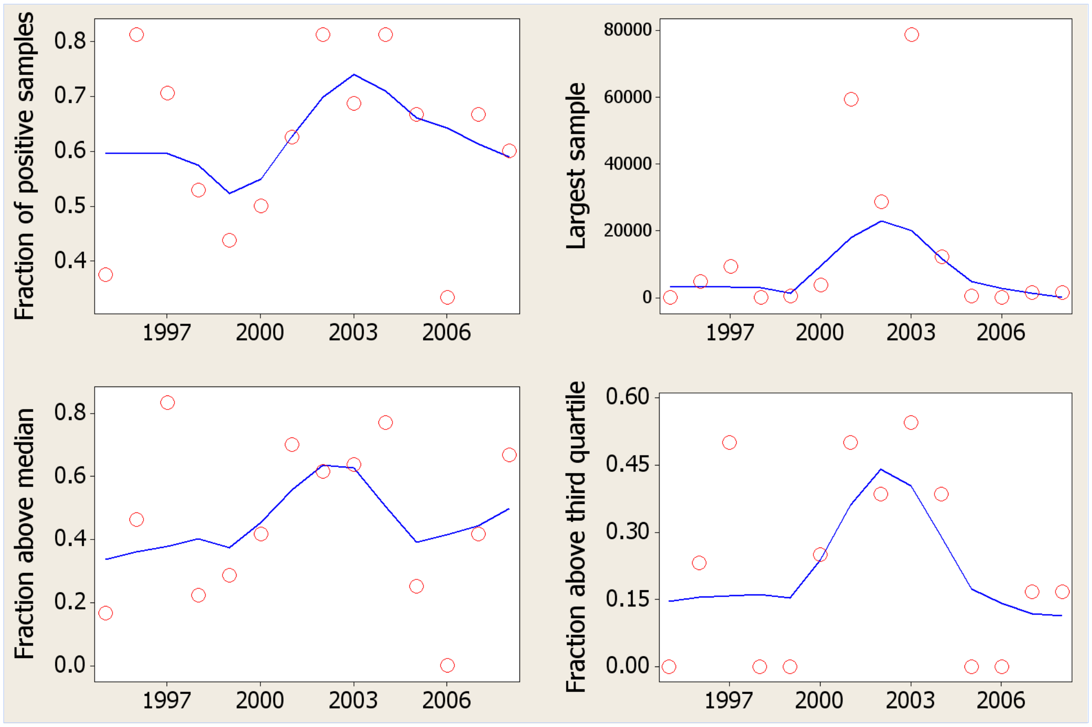

Figure 9 Time series for various factors summarized across key stations (910 and 912) of the 20-mm Survey. Curves are LOESS smooths.

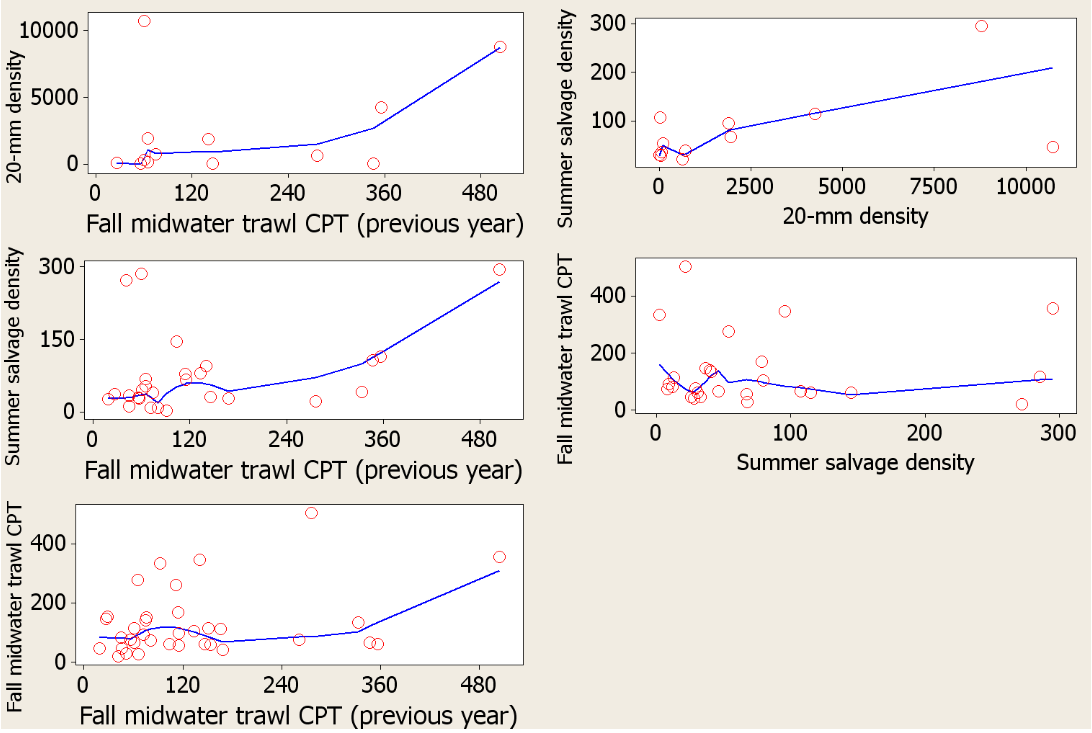

Figure 10 Candidate stock-recruit and stage-recruit plots for threadfin shad. Curves are LOESS smooths.

sured during the FMT belonged to an age-0 cohort as estimated by FiSAT. Across the full 24 years, average catch per trawl of threadfin shad estimated to belong to the age-0 cohort was significantly correlated with total threadfin shad catch per trawl, suggesting age-0 fish indeed dominate the FMT samples (Pearson correlation coefficient $r = 0.99$; $P < 0.001$).

Average apparent growth rate of the age-0 cohorts during September-December was 8.5 mm FL/month (standard deviation = 2.3, minimum = 5.4, maximum = 13.5), and exhibited no apparent long-term trend. Apparent growth rate was only significantly related, and negatively so, to initial abundance (apparent growth rate = 10.3 – 0.207 (initial abundance); r^2 = 26%; $P = 0.036$).

DISCUSSION

Since most aquatic species introductions generally fail (Moyle and Light 1996), why has threadfin shad persisted during the many decades since its initial introduction? Moyle and Light (1996) propose that several attributes can contribute to the success or population growth of introduced species. Of particular relevance for this case are that success usually comes in disturbed environments, disturbed (e.g., non co-evolved) communities, and where existing species numbers are low. Relative to other fish species in the delta, threadfin shad exhibits traits that conform to an opportunistic life history strategy (Winemiller and Rose 1992; Nobriga and others 2005). These general traits (small, short-lived, high reproductive effort) combined with favorable conditions to foster the successful integration of threadfin shad into the delta fish community. The physical environment of the delta is suitable for threadfin shad across the entire system based on salinity, water temperature, and water clarity (Feyrer and others 2007). Thus, while we observed substantial variability in the abundance of different life stages, the fish is found throughout this tidal freshwater system. This suggests that the delta has been physiologically accommodating for threadfin shad. However, the availability of resources (food abundance) appears to have a particularly strong effect on where threadfin shad are most abundant. Thus, the invasion success of threadfin shad in the delta could be a model for the ‘niche opportunity’ concept (Shea and Chesson 2002), and conforms to many of the empirical rules of biological invasions proposed by Moyle and Light (1996).

In the delta threadfin shad is widely distributed. However it is most commonly encountered and abundant in the southeastern region where suitable abiotic habitat coincides with high prey abundance. These regions also have a relatively high density of submerged aquatic vegetation in shallow flooded islands and littoral zones (Brown and Michniuk 2007), which provides important spawning and larval rearing habitat (Grimaldo and others 2004). Historic studies conducted in 1963-1964 (Turner 1966), and those more recently (Feyrer 2004; Grimaldo and others 2004), identified a similar distribution for threadfin shad. Turner (1966) also found that threadfin shad was relatively abundant in dead-end sloughs of the northeast delta, areas which are not sampled by the current monitoring programs but provide functionally similar habitat.

Threadfin shad appear to grow relatively fast in the delta and reach 70-90 mm by the onset of winter. This growth rate is generally consistent with that reported for Lake Powell, Utah and Arizona, U.S.A. (Blommer and Gustaveson 2002). However, it is faster than that observed in central Arizona, U.S.A., reservoirs (Johnson 1970). Sources of growth rate variation in fish populations can often be difficult to detect. Our results indicated that apparent growth rate during fall declined with increasing abundance. The negative relationship with abundance suggests density-dependent effects may be important. Density dependence is consistent with previous research indicating that intraspecific competition for food can be a major factor limiting growth of threadfin shad in reservoirs (Johnson 1970). Other studies have also found that the condition of young shad is sensitive to prey abundance (Kashuba and Matthews 1984). We could not detect an effect of overall average temperature or the rate at which temperatures decrease into winter. However, Betsill and Van Den Avyle (1997) found that interactions between food availability and water temperature explained a substantial portion of the variability in growth rates and cohort survival of young threadfin shad.

Catches at just seven of the 100 sampling sites have driven long-term patterns in the CDFG-calculated abundance indices. The general pattern at these stations can be characterized as having variable periods of high and low abundance with no overall long-term trend. The recent period of near-record low abundance in the FMT is not unprecedented but is especially noteworthy because it has persisted. Low abundance is also apparent in the 20-mm Survey, in salvage density during all seasons, and also in commercially harvested biomass trends. It is coincident with similar declines for other pelagic fishes (Feyrer and others 2007; Sommer and others 2007). The persistence of low abundance is also noteworthy because of the documented ability of threadfin shad to rapidly recover from low abundance levels. These so-called population explosions occur in part because of synchronous spawning behavior, which maximizes reproductive fitness (Kimsey and others 1957; McLean and others 1982). The contagious distribution of threadfin shad necessitates examining factors other than simple abundance to better understand the context of the current period. The observed lower fraction of samples with threadfin shad present and smaller-sized catches suggest that the recent decline in abundance may be driven by the FMT encountering fewer and smaller-sized schools of threadfin shad. There have been similar periods of smaller-sized catches in the past, especially around the mid 1980s. However, the persistently low fraction of samples with fish present is unprecedented in the time series.

There may be a number of factors affecting threadfin shad abundance in the delta. Recent studies suggest that there are no measurable effects of disease on the population (Baxter and others 2008). There is also no evidence that abiotic habitat – measured as the combination of water temperature, clarity, and salinity – has declined in recent years (Feyrer and others 2007). Traditional stock-recruit relationships are generally poor for opportunistic-type fishes such as threadfin shad (Winemiller 2005). It is therefore not surprising that we found little evidence for consistent stock-recruit or stage-recruit effects on the population. However, there did appear to be a complete “disconnect” between summer salvage density and FMT CPT, suggesting that factors occurring during the summer-to-fall transition might be one possible critical period. There are two factors in particular that are of concern for threadfin shad during this time period, dissolved oxygen and the toxic algae *Microcystis aeruginosa*, both of which occur in the center of threadfin shad distribution. Episodes of low dissolved oxygen concentration commonly occur in the San Joaquin River and have been known to cause die-offs of threadfin shad. Such events are difficult to characterize and quantify but might be responsible in part for the sudden declines in abundance sometimes observed from one year to the next. In recent years there have been dense blooms of *M. aeruginosa* geographically centered where threadfin shad are most abundant (Lehman and others 2008). The blooms also occur during the critical late summer/early fall when newly spawned fish are recruiting to the population (Lehman and others 2007). The effects of *M. aeruginosa* on threadfin shad could be direct by inhibiting feeding or indirect by affecting food availability. For a variety of herbivorous crustacean zooplankton, *M. aeruginosa* can be toxic, non-nutritious, or inhibit feeding on co-occurring nutritious food (Fulton and Paerl 1987). Further, several *M. aeruginosa* strains have been shown to increase toxin production when exposed to fish (Jang and others 2004). Other factors such as predation and low water temperatures are also known to affect threadfin shad populations in other systems (Parsons and Kimsey 1954; Griffith 1978; Blommer and Gustaveson 2002; McLean and others 2006). In the delta winter temperatures occasionally approach minimum tolerances of threadfin shad and predators such as striped bass and largemouth bass can be highly abundant (Feyrer and Healey 2003; Nobriga and Feyrer 2007).

One general limitation of our study is the dependence on correlations with limited data. We acknowledge that infrequent regionally-focused events, such as those suggested above, can be difficult to detect with such methods and therefore may incorrectly be assumed to be unimportant (Rose 2000). Further, non-linear effects and interactions between factors are likely to be important, but are rarely detected with such methods. Improved field observations and controlled laboratory studies designed specifically for threadfin shad, which can then inform modeling studies, are desperately needed to better understand the factors that affect threadfin shad population dynamics in the delta.

In summary, threadfin shad has had exceptional success in the Sacramento-San Joaquin Delta. In particular, channels of the south delta with deep, clear, fresh water and high zooplankton densities support high fish abundance and growth rates. Like other regions where this species occurs, population trends have been highly variable without clear stock-recruitment relationships. While there have been similar periods of low abundance in the past, the persistently low fraction of samples with shad present is unprecedented and coincides with declines in several other pelagic fishes. Hence, there is reason to believe that threadfin shad currently may not be thriving in the delta. However, the future of the delta likely includes warmer temperatures and increases in the amount of open water habitat from the flooding of islands, which may work to the advantage of this introduced species (Lund and others 2007).

ACKNOWLEDGEMENTS

This study was conducted under the auspices of the Interagency Ecological Program for the San Francisco Estuary. In particular, we thank members of the pelagic organism decline management team for facilitating support: C. Armor, R. Breuer, R. Baxter, M. Chotkowski, S. Culberson, M. Gingras, B. Herbold, A. Mueller-Solger, and M. Nobriga. We also thank R. Gartz, K. Fleming, K. Souza, E. Gleason, and P. Cadrett for database support, and J. Pierce for drawing Figure 1.

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