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NOTE

Long-Term Shifts in the Lateral Distribution of Age-0 Striped Bass in the San Francisco Estuary

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Abstract

Like several other fishes in the pelagic community of the upper San Francisco Estuary, age-0 striped bass *Morone saxatilis* have shown a major decline based on a midwater trawl sampling program that has been conducted for over 40 years. We hypothesized that the apparent decline in age-0 striped bass might be partially attributable to a behavioral shift away from the channels sampled by the trawls. We found no evidence of an upstream–downstream shift in age-0 distribution. Instead, age-0 striped bass distribution remains closely associated with the low-salinity zone of the estuary. However, the survey data suggest a substantial long-term distribution shift away from channels and toward shoal areas. The hypothesis that young striped bass are undersampled by midwater trawls is supported by modeling of demographic patterns, which showed that the decline in numbers of age-0 fish was not consistent with increasing trends in age-1 fish. We hypothesize that reduced food availability in pelagic habitat is a major cause of apparent behavioral shifts by age-0 striped bass and some native fishes. Nonetheless, the magnitude of the shift toward shoal habitat does not appear to fully account for the extreme decline in age-0 striped bass abundance.

The global decline in coastal resources represents one of the most troubling trends for fisheries managers (Lotze et al. 2006), as inshore regions represent a substantial component of oceanic productivity. These changes are apparently accelerating, but the ultimate consequences are unknown (Worm et al. 2006). Long-term monitoring programs are essential for evaluating trends in these resources and for identifying the major factors that are responsible for variation in fish abundance, distribution, and health. In the United States, one of the longest-term estuarine monitoring programs occurs in the San Francisco Estuary (Figure 1), where sampling such as the fall midwater trawl (FMWT) survey conducted by the California Department of Fish and Game provides valuable data on the status of a suite of pelagic fishes. This survey has been conducted for over 40 years and was designed, in part, to measure trends in age-0 abundance of striped bass *Morone saxatilis*, the apex predator in the upper San Francisco Estuary. Analyses of striped bass population trends have yielded insight into the effects of freshwater outflow (Jassby et al. 1995; Kimmerer et al. 2009), habitat quality (Feyrer et al. 2007), and sources of mortality (Kimmerer et al. 2001). These data reveal a long-term decline in age-0 striped bass, including a step change (Figure 2) that occurred during the past decade (Sommer et al. 2007; Kimmerer et al. 2009; Thomson et al. 2010). The collapse of young striped bass and other members of the upper San Francisco Estuary's pelagic fish community is a major resource management issue of national significance (Service 2007; Sommer et al. 2007). The decline of the pelagic fish community has been a primary focus of high-profile disputes over the availability of freshwater for about 8% of the U.S. population and for a multibillion-dollar agricultural industry. Hence, the decline of striped bass and other fishes provides an instructive example of conflicts between fisheries and growing water demands.

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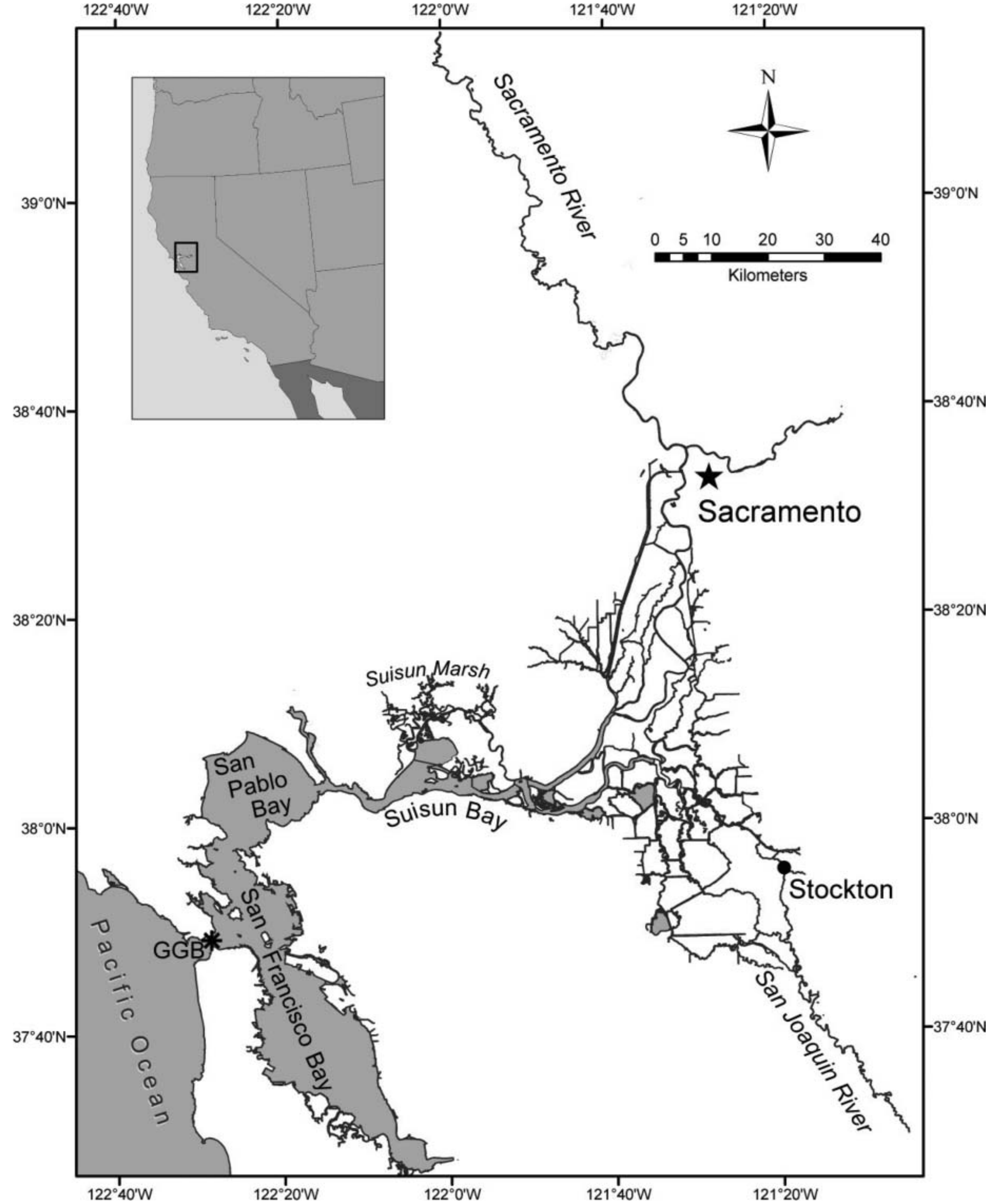

FIGURE 1. The San Francisco Estuary, California, and its watershed. The estuary includes the region from San Francisco Bay upstream to Sacramento and to a location 56 km upstream of Stockton. The Sacramento–San Joaquin Delta represents the portion of the estuary located upstream of the confluence of the Sacramento and San Joaquin rivers. Water flows from the rivers westward toward San Francisco Bay and past the Golden Gate Bridge (GGB) before reaching the Pacific Ocean. See Methods text for regions of sampling.

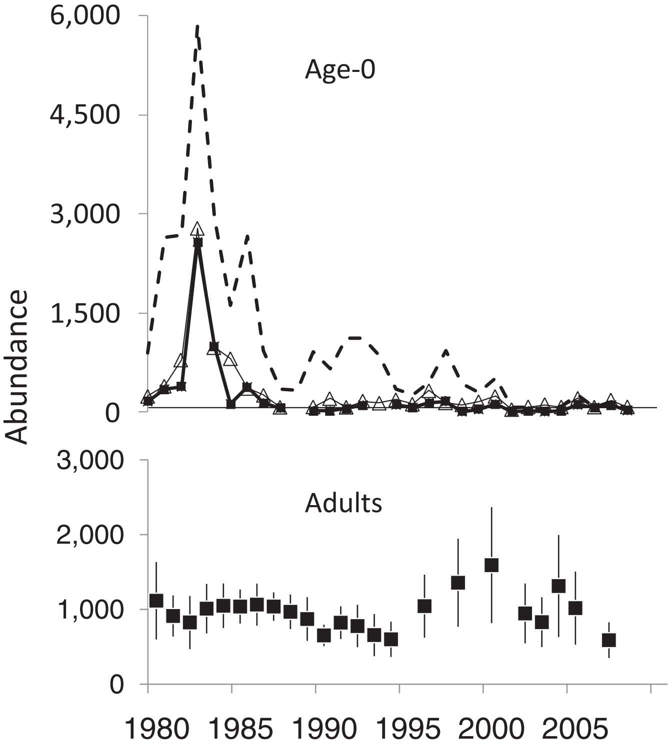

FIGURE 2. Trends in abundance of age-0 (upper panel) and adult (lower panel; units are × 1,000) striped bass in the San Francisco Estuary. Age-0 total catch is based on the fall midwater trawl survey (dotted line) conducted by the California Department of Fish and Game and the midwater trawl survey (squares) and otter trawl survey (triangles) conducted by the California Department of Fish and Game San Francisco Bay Study. The age-0 catch data represent relative abundance trends rather than population estimates (see Methods); hence, they do not have error bars. Adult abundance trends (±95% confidence interval) are based on Petersen estimates of the adult population (updated from Kimmerer et al. 2001).

The recent decline in the pelagic fish community is thought to be a result of multiple factors, including food web changes (i.e., from invasive species), sources of mortality, water quality, and reduced adult stock (Sommer et al. 2007; MacNally et al. 2010). With regard to the decline in young striped bass, at least two reasons led us to suspect that changes in catchability were a contributing factor. First, Kimmerer (2006) reported that the northern anchovy *Engraulis mordax*, another formerly common pelagic fish of the upper estuary, recently shifted downstream to a region that was largely outside of the core FMWT sampling area. Second, there seems to be a complete disconnect between declines in age-0 striped bass captured by the FMWT and separate estimates of the adult striped bass population, which show little trend (Figure 2). This observation was unexpected because Stevens et al. (1985) reported that adult abundance trends are affected by recruitment during the first year of life. Subsequent analyses by Kimmerer et al. (2000) found that juvenile striped bass production was historically a good predictor of adult population size at low age-0 population levels (e.g., FMWT total catch <1,000 fish in Figure 2). Kimmerer et al. (2000) reported that at higher levels of age-0 abundance, density dependence muted further improvements in the adult population. Such density-dependent relationships are fairly common in fisheries populations (Rose et al. 2001). However, recent age-0 striped bass abundance levels have declined far below the high-density thresholds identified by Kimmerer et al. (2000) but without the expected corresponding reduction in adults.

The divergent trends in age-0 and adult abundances could be partly explained by changes in mortality rates; however, an alternative explanation is that the catchability of young striped bass has changed such that the FMWT now underestimates production.

We hypothesized that the apparent decline in age-0 striped bass might be partially attributable to a behavioral shift away from the channels sampled by the FMWT. Our hypothesis was motivated, in part, by evidence from other regions that young striped bass can show geographic and ontogenetic shifts in distribution (Boynton et al. 1981; Secor 1999). Specifically, we address three primary study questions about young striped bass:

(1) Did they shift upstream or downstream relative to their historic distribution?
(2) Did they shift away from pelagic habitat (sampled by midwater trawls) and toward inshore areas?
(3) Do population data suggest that the FMWT survey has begun to undersample striped bass?

Our hope was that by answering these questions about the decline of age-0 striped bass, we would gain a better understanding of the collapse of the pelagic fish community in the upper San Francisco Estuary and perhaps in other regions. Our study also provides insight into the potential limitations of long-term monitoring programs and the susceptibility of estuarine populations to species invasions. Although the age-0 striped bass may not fully represent the range of other fishes or life stages present in the San Francisco Estuary, we reasoned that they would be a useful model for evaluation because (1) the striped bass is one of the best-studied fishes in the estuary; (2) the region's long-term fisheries monitoring program was created to help evaluate the age-0 life stage; and (3) trends in age-0 individuals of this apex predator have been used to identify some of the major environmental drivers of estuarine variability (e.g., Jassby et al. 1995; Kimmerer 2002) and to establish management goals for fishing effort (Field 1997).

STUDY AREA

The San Francisco Estuary is one of the largest estuaries on the Pacific coast (Figure 1). The estuary comprises a complex system of downstream bays (San Pablo and San Francisco bays), a brackish low-salinity zone (Suisun Bay), and the Sacramento–San Joaquin Delta, which is a broad, generally freshwater network of tidally influenced channels that receive inflow from the Sacramento and San Joaquin rivers. The San

Francisco Estuary grades from marine dominance in the central and southern portions of San Francisco Bay to freshwater dominance in the Sacramento–San Joaquin Delta. The estuary and its tributaries have been heavily altered by land reclamation, levees, dams, urbanization, introductions of nonnative species, and water diversions (Nichols et al. 1986; Sommer et al. 2007).

All ages of striped bass are found throughout the estuary, but adult striped bass also move into the ocean and along the California coastline (Turner and Chadwick 1972; Stevens et al. 1985). The species was originally introduced into the estuary in the late 1800s, supporting a commercial fishery that eventually closed in 1935; however, striped bass still support a popular recreational fishery. Spawning occurs during spring in the Sacramento–San Joaquin Delta and its tributaries, particularly the Sacramento River. Pelagic eggs and larvae are transported downstream into the delta and the low-salinity zone of the estuary, where they rear, later dispersing throughout the estuary. Early feeding focuses on invertebrates, followed by a gradual shift toward piscivory by the end of the first year of life (Feyrer et al. 2003; Bryant and Arnold 2007; Nobriga and Feyrer 2007). In general, age-0 production is strongly tied to spring outflow (Kimmerer 2002; Sommer et al. 2007) and year-class strength is set early in life (Kimmerer et al. 2000). Striped bass mature at 4–5 years of age and can live for several decades, but most of the current population in the estuary is younger than age 7. The species is perhaps the most important sport fish in the region, and there is a popular fishery for age-3 and older striped bass (Moyle 2002). Declines in the adult population during the 1980s led to efforts to augment the wild population with age-0 and age-1 fish produced from hatcheries (1981–1992) and with pen-reared juveniles collected from fish screens at water export facilities (1993–2000). However, these efforts were gradually eliminated by 2000. Augmentation appears to have had little effect on the numbers of age-0 fish, as abundance has continued to decline since the 1980s (Figure 2).

METHODS

Field data.—The FMWT sampled pelagic habitat monthly from September to December at 116 fixed stations throughout the northern region of the estuary (Figure 1). At each station, a 12-min stepped-oblique tow was conducted with a midwater trawl of variable mesh sizes (from 20.3-cm mesh at the 3.7-m^2 mouth to 1.3-cm mesh at the cod end; Feyrer at al. 2007; Rosenfield and Baxter 2007). As noted previously, the survey represents one of the best long-term fishery data sets for the estuary and was established specifically to cover the geographic range of age-0 striped bass. The survey includes relatively good coverage of each of the estuary's major embayments and channels where young striped bass are located. The survey has been conducted each fall since 1967 except during 1974 and 1979. As will be discussed below, the catch data can also be employed to model population trends estimated by using a series of assumptions.

The California Department of Fish and Game San Francisco Bay Study has sampled 35 fixed stations monthly since 1980 (with some exceptions) by using a midwater trawl (Bay MWT) and an otter trawl (Bay otter trawl; Hatfield 1985; Rosenfield and Baxter 2007). Sampling locations ranged from San Francisco Bay through San Pablo and Suisun bays and into the Sacramento–San Joaquin Delta (Figure 1). However, we limited the analysis to the latter three regions because the catch of young striped bass is rare in San Francisco Bay, which represents the marine portion of the estuary. Similarly, although the survey sampled during multiple months, we only used September–December data to provide some comparability with the FMWT data. The Bay MWT used the same net and towing method as the FMWT. Bay MWT data were available for the period 1980–2009 (except for all months in 1989 and 1994 and November and December in 1990–1993 and 1999). The Bay otter trawl had a 0.6-cm knotless-mesh cod end and was towed for 5 min on the bottom. Bay otter trawl data were also available for 1980–2009 (except for all months in 1989 and November and December in 1990–1993 and 1999).

The adult striped bass survey deploys drift gill nets and large fyke traps during the spring spawning migration (April and May) to capture adults for tagging as part of an ongoing mark–recapture study to estimate adult (age-3 and older) population size (Kimmerer et al. 2001). Abundance estimates were calculated by using a Bailey-modified version of the Petersen equation stratified by sex and age (Stevens et al. 1985). Fish were tagged with disk dangler tags. The ratio of tagged to untagged fish in the population was estimated during annual summer–fall creel censuses in the San Francisco Bay area and during subsequent spring tagging. Tagging has occurred annually since 1969 except for a brief period in the mid- to late 1990s, during which it occurred every other year. Research vessels equipped with net reels deployed 183-m drift gill nets (10–14-cm stretch mesh) near the confluence of the Sacramento and San Joaquin rivers; up to 12 fyke traps were also fished daily on the Sacramento River upstream of the delta. The fyke traps were 3 m in diameter × 6 m long and were covered in 5-cm square mesh.

Analyses.—To address the question of whether fish distribution shifted upstream or downstream from the survey area, we calculated the mean centers of distribution (MCDs) for age-0 striped bass in the FMWT by using an approach similar to that of Dege and Brown (2004). Data from the two Bay surveys were excluded from MCD calculations because the upstream range of young striped bass was not consistently covered. The annual MCD was calculated by multiplying the distance in river kilometers (RKM) from the mouth of the San Francisco Estuary (i.e., Golden Gate Bridge) to each station by the striped bass catch at that station (catch), summing across all stations, and then dividing by the total catch of striped bass (total catch):

$$\text{MCD} = \Sigma(\text{RKM} \times \text{catch})/\Sigma(\text{total catch}).$$

The annual MCDs were plotted in two different ways to examine different aspects of the distribution. First, we plotted the annual results to evaluate whether there was evidence of a geographical change in distribution along the axis of the estuary. Our second analytical method was to examine distribution relative to salinity. This approach is particularly useful in estuaries, where the salinity field can shift substantially based on seasonal and annual changes in inflow. Age-0 striped bass have historically been associated with the low-salinity zone (Dege and Brown 2004; Feyrer et al. 2007). The salinity metric X_2 is defined as the distance (km) of the 2-practical salinity unit isohaline from the Golden Gate Bridge and is a well-recognized regional indicator of the low-salinity zone (Jassby et al. 1995; Kimmerer 2002; Feyrer et al. 2007). Low values of X_2 reflect a downstream movement of the salinity field under higher flow conditions, whereas high values of X_2 reflect an upstream movement of the salinity field under low-flow conditions. We plotted the MCDs relative to the mean September–December X_2 to determine whether fish distribution followed that of the salinity field during autumn. A linear regression was used to test for a statistically significant relationship between the FMWT MCDs and X_2. A plot of the relationship was visually inspected to determine whether recent years (2000–2009; when there was a step change in abundance) deviated substantially from the historical association between distribution and X_2.

We examined whether age-0 striped bass shifted their distribution away from channel habitat by comparing trends in catch for channel (depth > 7 m) and shoal (depth < 7 m) areas for each of the surveys. The 7-m depth threshold is a standard station criterion that has been used by the California Department of Fish and Game for each of the surveys. The evaluation was performed for all years since 1980, when data were available for all three trawl surveys. The total number of shoal stations (FMWT = 17; Bay MWT = 14; Bay otter trawl = 11) and channel stations (FMWT = 60; Bay MWT = 10; Bay otter trawl = 7) varied among the surveys. For each survey and year, we calculated the catch at shoal stations expressed as a percentage of the total catch. Spearman's rank correlation tests (coefficient: r_S) were used to evaluate whether there were statistically significant increases in the shoal catch percentage for each survey over time. We reasoned that an increase in age-0 striped bass catch at the shoal stations would provide evidence of a shift in distribution toward inshore areas. Statistical computations were conducted with Minitab version 15 (Minitab, Inc., State College, Pennsylvania). In general, results of statistical tests were deemed significant when *P*-values were 0.05 or less.

Finally, we evaluated whether population data suggested that the FMWT has begun to undersample young striped bass. As noted above, there was already evidence that adult and young-of-the-year trends no longer track one another (Figure 2). Because the age-0 and adult age-classes are ontogenetically distant, we reasoned that it would be instructive to examine trends for consecutive age-classes. Specifically, FMWT-based model estimates of the age-0 population were compared with model estimates for age-1 fish in the subsequent year as calculated from adult Petersen estimates. The synthesized data series for each age-class were intended to represent modeled abundance trends rather than absolute population sizes with error estimates. For example, development of error estimates for the age-1 class was well beyond the scope of this study as the model relied on the use of hatchery fish survival with an unknown error distribution (see below). Key data for striped bass (e.g., capture efficiency of the FMWT) are also not known, so model estimates of age-0 abundance must be interpreted with caution. We therefore used the model output to examine relative trends, particularly whether the patterns were reasonable (e.g., numbers of age-1 fish should be generally lower than the numbers of age-0 fish) and showed congruence.

We used the approach of Newman (2008) to model age-0 striped bass population size from the FMWT data. Capture probability data were not available for striped bass, so we relied on a function based on fish length for another pelagic fish (delta smelt *Hypomesus transpacificus*); this function was developed from the FMWT data collected during August 1991 (Newman 2008). Based upon this functional capture probability model, the number of each fish of length *L* captured by the FMWT at each station (in a given sampling month) was first expanded to the total number of fish of length *L*. Next, the total number of age-0 fish of length *L* at each station was summed for each sample area *A* (for a given sampling month) and divided by the total volume of water swept by the net for each *A*. The resulting ratio was then multiplied by the total water volume in each *A* to obtain an estimate of the total number of fish in each *A* (for a given sampling month). Finally, the sum of the total number of fish in each *A* across all areas of the estuary yielded a monthly model estimate of the systemwide total number of age-0 fish. The estuarywide model abundance estimates for each of the four FMWT survey months were averaged to generate a single abundance value for each year.

Modeling the age-1 striped bass population was more problematic because this life stage is not targeted by any survey in the estuary. Therefore, it was necessary to back-calculate the age-1 estimates from the number of age-3 fish in adult Petersen estimates (Figure 2). The back-calculation was performed by using annual survival estimates of age-1 to age-3 hatchery striped bass that were stocked into and recovered from the estuary each year between 1981 and 1990 (Harris and Kohlhorst 2002). We assumed that survival rates for the hatchery fish would be a reasonable estimate of survival rates for wild fish, as the latter data were not available. Note that the data used for this analysis represent a time period (1981–1990) that did not explicitly cover the step decline in age-0 abundance over the past decade (Thomson et al. 2010). Nonetheless, these years provide insight into the long-term decline in striped bass (Stevens et al. 1985; Feyrer et al. 2007) and also bracket a major ecosystem change—the disruption of the estuarine food web after the 1986 invasion by the bivalve *Corbula amurensis* (Kimmerer 2002).

RESULTS

The striped bass MCDs showed substantial variability over the study period for the FMWT but exhibited no long-term trend

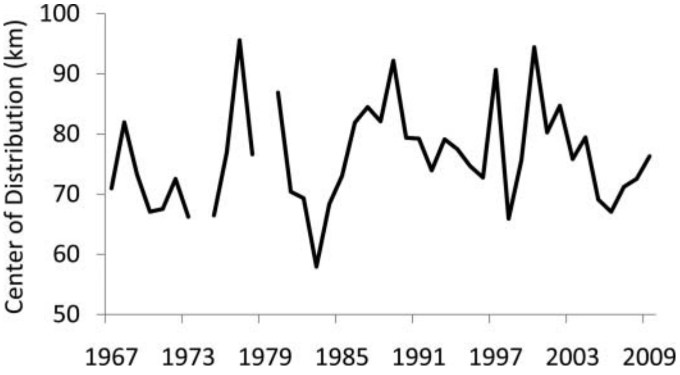

FIGURE 3. Mean centers of distribution (distance [km] from the Golden Gate Bridge) for age-0 striped bass as sampled by the fall midwater trawl survey (California Department of Fish and Game).

(Figure 3). Most of the variability in the age-0 distribution was associated with the salinity field, as indicated by the statistically significant relationship between X_2 and the MCD (Figure 4; $F = 25.88$, df $= 39$, $P = 0.002$; MCD $= 26.0 + 0.627 \cdot X_2$). There was no evidence that recent years (characterized by a step change in abundance) deviated from the historical relationship between striped bass distribution and X_2 (Figure 4). If there had been a substantial change in distribution away from the salinity field, the data points for recent years should have been outside the range of variability of the historical data or should have shown a systematic shift above or below the historical relationship.

Each of the three surveys (FMWT, Bay MWT, and Bay otter trawl) showed a trend toward higher relative age-0 catch in the shoals (Figure 5). In general, much of the change seems to have occurred in the mid-1980s. The increases were statistically significant for the FMWT survey ($r_S = 0.477$, $P = 0.008$) and the Bay otter trawl survey ($r_S = 0.504$, $P = 0.005$) but not for the Bay MWT survey. Shoal catch averaged 21% of the FMWT total catch during the 1980s and 36% of the FMWT total catch in the 2000s. Similarly, the Bay MWT shoal catch increased from 35% of total catch in the 1980s to 42% of total catch in the 2000s. Catches at the Bay otter trawl shoal stations also showed an increase from 77% to 93% of the total catch. However, none of the changes in shoal catch were of the same magnitude as changes in total catch, which dropped by about 90% from the 1980s to the 2000s (Figure 2).

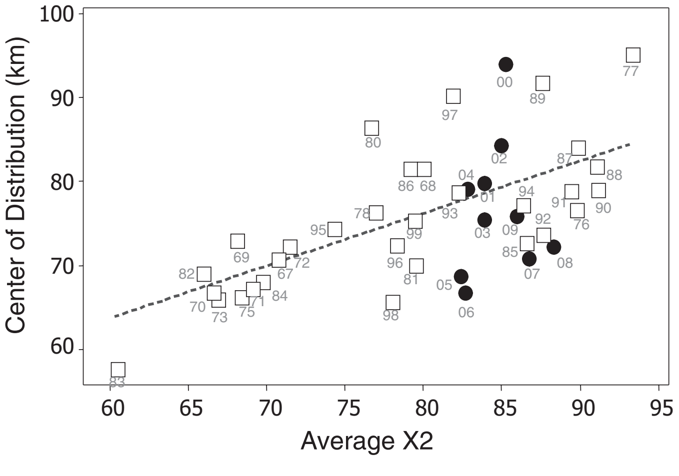

FIGURE 4. Relationship between salinity (as indexed by X_2, the distance [km] of the 2-practical salinity unit isohaline from the Golden Gate Bridge) and the mean centers of distribution (distance [km] from the Golden Gate Bridge) for age-0 striped bass as sampled by the fall midwater trawl survey (California Department of Fish and Game). Both data series are based on averages for the September–December period. Each data point is labeled with the last two digits of the sampling year (i.e., 1967–2009). To aid in the evaluation of whether the relationship has changed, data from recent years are denoted by black-shaded circles and data from earlier years are indicated by open squares.

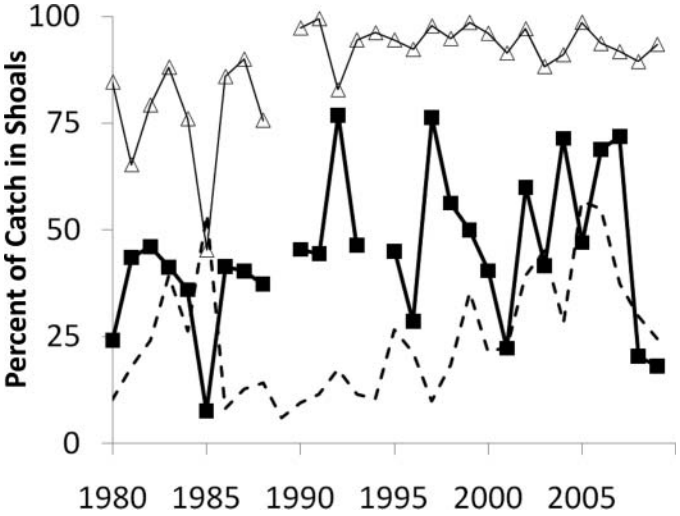

FIGURE 5. Age-0 striped bass catch from shoal stations expressed as a percentage of total age-0 catch in the fall midwater trawl survey (dotted line) conducted by the California Department of Fish and Game and the midwater trawl survey (squares) and otter trawl survey (triangles) conducted by the California Department of Fish and Game San Francisco Bay Study.

Modeled age-0 population estimates ranged from 280,000 to 3.6 million, whereas age-1 population estimates for the subsequent year ranged from 2.1 million to 14 million during 1981–1990, the period represented in both time series (Figure 6). During the first several years, the modeled age-1 population followed the expected pattern, exhibiting generally lower estimated

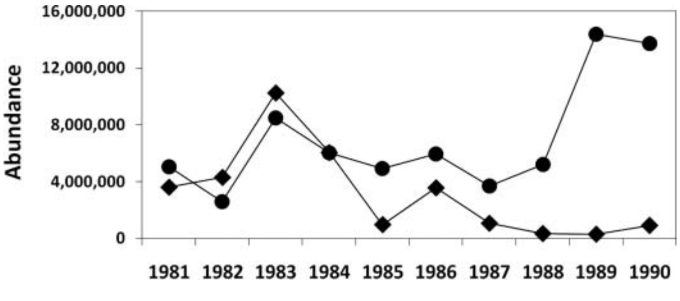

FIGURE 6. Modeled abundance of age-0 (diamonds) and age-1 (circles) striped bass in the San Francisco Estuary. Data for age-0 fish were shifted by 1 year to permit direct comparison of the year-classes.

abundance than age-0 fish and similar annual increases and decreases; however, by the mid-1980s, the two time series had diverged due to a much higher age-1 modeled population and declining age-0 numbers.

DISCUSSION

Our results support the hypothesis that an apparent shift in the distribution of young striped bass led to a reduction in their use of channel habitat. The distribution shift was not upstream or downstream, since the FMWT showed no change in the MCD of age-0 striped bass in relation to the axis of the estuary or X_2. Instead, the data indicate that young striped bass apparently shifted from offshore toward inshore areas. Our results are consistent with studies by Schroeter (2008), who documented movement of age-0 striped bass away from large, deep sloughs and into small, shallow sloughs of Suisun Marsh (Figure 1), the largest marsh in the estuary. Similarly, recent sampling by Nobriga and Feyrer (2007) suggested high densities of age-1 striped bass in shallow-water areas of the upper San Francisco Estuary. This pattern is not surprising, as studies from other regions show higher densities of age-0 striped bass in inshore habitat than in offshore habitat (Boynton et al. 1981; Robichaud-LeBlanc et al. 1998). As a consequence, young striped bass are probably undersampled by the pelagic-oriented FMWT. Undersampling of age-0 striped bass is consistent with our modeling of the abundance of older age-classes. Specifically, the abundance of older fish (e.g., age 1 and adults) was higher than expected based on the modest numbers of young fish captured in the FMWT, and the two ontogenetically close life stages (age 0 and age 1) showed divergent trends.

The long-term lateral shift in distribution may have been caused by movement toward inshore areas (i.e., active behavior) or by differences in mortality for fish that colonize pelagic habitat versus shoal habitat (i.e., an apparent shift). Our study was not designed to differentiate the two potential mechanisms. However, it is highly likely that the shift in striped bass distribution is at least partly a result of behavioral and ecological plasticity in this species. Active distributional shifts seem fairly reasonable given that young striped bass are highly mobile and have the ability to colonize multiple regions outside of their native range and a wide range of habitat types, including rivers, estuaries, coastal ocean, and reservoirs (e.g., Johnson et al. 1992; Secor 1999; Moyle 2002; Vatland et al. 2008). Similarly, early life stages of striped bass are known to exhibit complex behaviors, such as vertical migrations in relation to tides (Bennett et al. 2002). Behavioral flexibility may be relatively common in estuarine fishes that must deal with high levels of daily, seasonal, and annual variability. Whether or not our hypothesis of behavioral shifts by striped bass is correct, our study documents a new pattern of variability—long-term lateral shifts in age-0 distribution. Previous studies of juvenile striped bass have documented seasonal and ontogenetic changes in lateral distribution (Robichaud-LeBlanc et al. 1998) as well as interannual changes in the use of upstream versus downstream habitat (e.g., Secor 1999). However, we are not aware of any other studies that show multidecadal shifts in the lateral distribution of young striped bass.

The mechanisms responsible for the distribution shift may vary, but evidence from other aquatic systems suggests that such shifts are frequently mediated by invasions, which result in competition or predation problems (Brown and Moyle 1991). It is probably not a coincidence that several of the apparent changes in young striped bass occurred after the mid-1980s, when a bivalve invasion radically altered the food web in the low-salinity zone of the San Francisco Estuary (Kimmerer et al. 1994; Kimmerer 2002). In particular, the pelagic food web suffered after the introduction of *C. amurensis*, which grazes on plankton (Kimmerer et al. 1994; Kimmerer 2002), while an increase in littoral fish abundance coincided with the proliferation of aquatic weeds (Brown and Michniuk 2007; Nobriga 2009). Our study suggests that much of the striped bass distribution shift toward shoal habitat occurred sometime after the mid-1980s (Figure 5). Likewise, the modeled abundance trends of age-0 and age-1 striped bass diverged during the same period (Figure 6). After the invasion by *C. amurensis*, there was also a step change in the historical relationship between young striped bass abundance and estuarine outflow (Kimmerer 2002; Sommer et al. 2007).

Several fish species showed decreased abundance after the *C. amurensis* invasion, perhaps because they had limited behavioral plasticity. However, northern anchovy moved into higher-salinity water, where food web changes may have been less severe (Kimmerer 2006). Initial results indicate that another pelagic species, the longfin smelt *Spirinchus thaleichthys*, responded with a similar downstream shift in distribution after the invasion (Baxter et al. 2008).

We propose that young striped bass moved into shallower habitat to attain better foraging opportunities in inshore areas or conversely to avoid the deteriorating food supply in channels. The direction of the shift contrasts with that of northern anchovy and perhaps longfin smelt, which moved downstream after the food web collapse in Suisun Bay. Although additional field studies are needed to test the hypothesis that foraging success is greater in inshore habitat than in offshore habitat, it is notable that the diets of young striped bass changed in response to the *C. amurensis* invasion during the late 1980s (Feyrer et al. 2003; Bryant and Arnold 2007). Perhaps the best evidence is provided by Schroeter (2008), who reported that the movement of young striped bass from deeper channels toward shallower habitats in Suisun Marsh was associated with changes in food availability. Similarly, studies from other regions suggest that foraging success can be much greater in inshore habitat (Boynton et al. 1981).

We wish to emphasize that our results do not show that the apparent distribution shift is the only mechanism responsible for the long-term decline of young striped bass. The data suggest that a greater proportion of juvenile striped bass use shoal areas, but the changes are not sufficient to account for the steep decline in abundance, which fell by 90% or more (Figure 2). Moreover, the data indicate that much of the distribution shift occurred in the 1980s, well before the sharply accelerated declines that were observed during the 2000s (Thomson et al. 2010). There is good evidence that several other factors have contributed to the decline of striped bass (MacNally et al. 2010). Demographic changes have had a strong effect on the striped bass population—particularly the loss of older, more-fecund age-classes (Kimmerer et al. 2000). Similarly, Bennett et al. (1995) and Ostrach et al. (2008) found evidence of serious contaminant effects on young striped bass. Losses to water diversions may also sporadically affect the survival of early juveniles (Stevens et al. 1985; Kimmerer et al. 2001). Finally, changes in habitat quality may have contributed to the decline in at least two ways: (1) through reductions in habitat area during key seasons (Feyrer et al. 2007; Kimmerer et al. 2009) and (2) through long-term increases in water clarity (Feyrer et al. 2007), which resulted in reduced catchability of striped bass in the FMWT. In any case, the present study shows that management of striped bass requires a comprehensive understanding not only of the limiting factors based on long-term monitoring but also of fish distribution and behavior. Indeed, these results suggest that large-scale management problems, such as fisheries declines in coastal and estuarine habitat, cannot be reduced to single environmental factors like alien species, contaminants, or water diversions.

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