Long-term shifts in the lateral distribution of age-0 striped bass *Morone saxatilis* in the San Francisco Estuary

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Abstract

Like several other fishes in the pelagic community of the upper San Francisco Estuary, a 40+ year midwater trawl sampling program shows a major decline in age-0 striped bass *Morone saxatilis*. We hypothesized that the apparent decline in age-0 striped bass might partially have been due to a behavioral shift away from the channels sampled by the trawls. We found no evidence that there had been 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 towards shoal areas. The hypothesis that young striped bass are under-sampled by midwater trawls is supported by modeling of demographic patterns, which showed that the decline in age-0 numbers 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 in age-0 striped bass and some native fishes. Nonetheless, the magnitude of the shift towards 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 (Lohtze et al. 2005), 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 to evaluate trends in these resources, and to identify the major factors responsible for variation in abundance, distribution, and health. In the United States, one of the longest-term estuarine monitoring programs is the San Francisco Estuary (Figure 1), where sampling such as the California Department of Fish and Game Fall Midwater Trawl ("FMWT") provide valuable data on the status of a suite of pelagic fishes. This four decade-long survey was designed, in part, to measure trends in age-0 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 revealed a long-term decline in age-0 striped bass, including a step change (Figure 2) during the past decade (Sommer et al. 2007; Kimmerer 2009; Thompson et al. 2010). The collapse of young striped bass and the rest of the pelagic fish community of the upper San Francisco Estuary 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 fresh water for about 8 percent of the population of the United States and a multi-billion dollar agricultural industry. Hence, the decline of striped bass and other fishes provide an instructive example of conflicts between fisheries and growing water demands.

The recent decline in the pelagic fish community is thought to be a result of multiple factors including changes in the food web from invasive species, sources of mortality, water quality, and reduced adult stock (Sommer et al. 2007; MacNally et al. 2010). For young striped bass, at least two reasons led us to suspect that changes in catchability may have been a contributing factor. First, Kimmerer (2006) reported that another formerly common pelagic fish of the upper Estuary, northern anchovy *Engraulis mordax*, recently shifted downstream to a region largely outside of the core FMWT sampling area. Second, there seems to be a complete disconnect between declines in age-0 fish captured by the FMWT and separate estimates of the adult striped bass population, which show little trend (Figure 2). This was unexpected as Stevens et al. (1985) reported that adult abundance trends are affected by recruitment during their 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 <1000 in Figure 2). At higher levels of age-0 abundance, Kimmerer et al. (2000) found that 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 abundance levels have declined far below the high-density thresholds identified by Kimmerer et al. (2000) without the corresponding expected reduction in adults.

Part of the reason for the divergent age-0 and adult trends could be 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 partially have been due 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 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) towards inshore areas? 3) Do population data suggest that the survey has begun to under-sample striped bass?

By answering these questions about the decline of age-0 striped bass, our hope was that we would gain a better understanding of the collapse of the pelagic fish community in the upper San Francisco Estuary and perhaps other regions. The studies also provide 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 in the San Francisco Estuary, we reasoned that they would be a useful model for evaluation because: 1) It is one of the best-studied fishes in the Estuary; 2) the region's long-term fisheries monitoring program was created to help evaluate this life stage; and 3) age-0 fish trends 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), comprised of a complex system of downstream bays (San Pablo, San Francisco), a brackish low salinity zone (Suisun Bay), and the Sacramento-San Joaquin Delta, a broad, generally freshwater network of tidally-influenced channels that receive inflow from the Sacramento and San Joaquin rivers. The Estuary grades from marine dominance in Central and South San Francisco bays to freshwater dominance in the Delta. The Estuary and its tributaries have been heavily altered by land reclamation, levees, dams, urbanization, invasive species, and water diversions (Nichols et al. 1986; Sommer et al. 2007).

All ages of striped bass are found throughout the Estuary, but adult fish 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, where it supported a commercial fishery that eventually closed in 1935, but still supports a popular recreational fishery. Spawning occurs during spring in the delta and its tributaries, particularly the Sacramento River. Pelagic eggs and larvae are transported downstream into the delta and low salinity zone of the Estuary, where they rear and disperse throughout the Estuary. Early feeding focuses on invertebrates, followed by a gradual shift towards piscivory by the end of their first year (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 is less than 7 years. The species is perhaps the most important sport fish in the region, with 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 pen-rearing of juveniles collected from fish screens (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 stepped oblique 12-minute tow was conducted with a midwater trawl of variable meshes starting with 20.3 cm mesh at the 3.7 m^2 mouth of the net and 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 was conducted each fall since 1967 except for 1974 and 1979. As will be discussed below, the catch data can also be used to model population trends estimate using a series of assumptions.

The San Francisco Bay Study sampled 35 fixed stations monthly since 1980, with some exceptions, using a midwater trawl (Bay MWT) and an otter trawl (Bay Otter) (Hatfield 1985; Rosenfield and Baxter 2007). Sampling locations range from San Francisco Bay, through San Pablo and Suisun Bays, and into the Delta (Figure 1). However, we limited the analysis to the latter three regions because catch of young striped bass is rare in San Francisco Bay, which represents the marine portion of the Estuary. Similarly, while the survey samples multiple months, we used September-December to provide some comparability with the FMWT. The Bay MWT used the same net and towing method as the FMWT. Bay MWT data were available for all years during 1980-2009 except for 1989 and 1994, and November and December of 1990-1993 and 1999. The Bay Otter trawl had a 5.5-cm knotless mesh cod end and was towed for 5 minutes on the bottom. Bay Otter data were available for all years during 1980-2009 except for 1989, and November and December of 1990-1993 and 1999.

The adult striped bass survey set drift gill nets and large fyke traps during the spring (April to May) spawning migration to capture adult striped bass for tagging as part of an ongoing mark recapture study to estimate adult (age 3+) population size (Kimmerer et al. 2001). Abundance estimates were calculated using a Bailey-modified version of the Petersen equation, stratified by sex and age (Stevens et al. 1985). Fish were tagged with disc 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 subsequent spring tagging. Tagging occurred annually since 1969 except for a brief period in the mid to late 1990s when it occurred every other year. Research vessels equipped with net reels deployed 183 meter drift gill nets (10–14 cm stretch mesh) near the confluence of the Sacramento and San Joaquin Rivers; also, up to 12 fyke traps were fished daily upstream of the delta on the Sacramento River. The 3 meter diameter by 6 meter-long fyke traps were covered in 5 cm square mesh.

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

$$\text{MCD} = \Sigma\ (\text{RKM}^*\text{Fish catch})/\Sigma\ (\text{Total catch})$$

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 was the distance of the 2 psu isohaline (X2) from the Golden Gate Bridge, a well-recognized regional indicator of the low salinity zone (Jassby et al. 1995; Kimmerer 2002; Feyrer et al. 2007). Low values of X2 reflect a downstream movement of the salinity field under higher flow conditions, while high values of X2 reflect an upstream movement of the salinity field under low flow conditions. We plotted the MCDs relative to the mean September-December X2 to see if fish distribution followed that of the salt field during autumn. A linear regression was used to test whether there was a statistically significant relationship between FMWT MCDs and X2. A plot of the relationship was visually inspected to determine if recent years (2000-2008; when there was a step change in abundance) deviated substantially from the historical association between distribution and X2.

We examined whether age-0 striped bass shifted their distribution away from channel habitat by comparing trends in catch for channel (>7 m depth) and shoal (<7 m depth) areas for each of the surveys. The 7 m depth threshold is a standard station criterion that has been used by California Department of Fish and Game for each of the surveys. The evaluation was done 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 = 11) and channel stations (FMWT = 60; Bay MWT = 10; Bay Otter = 7) varied for each survey. For each survey and year, we calculated the percentage of the total catch from shoal stations. Spearman's correlation tests were used to evaluate whether there were statistically significant increases in the percentage of shoal catch for each survey over time. We reasoned that an increase in catch at the shoal stations would provide evidence of a shift in distribution towards inshore areas. Statistical computations were conducted using Minitab 15 Statistical Software (Minitab, Inc. State College, Pennsylvania). In general, results of statistical tests were deemed significant when $p \leq 0.05$.

Finally, we evaluated whether population data suggested that the FWMT has begun to under-sample 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, we compared FMWT-based model estimates of the age-0 population to model estimates for age-1 fish the following year calculated from adult Peterson estimates. The synthesized data series for each age class were intended to represent modeled abundance trends not absolute population size 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 such as the capture efficiency of the FMWT are also not known for striped bass, 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 should be generally lower than age-0) 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) that was developed using the FMWT 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 sample area. The resulting ratio was then multiplied by the total water volume in each area A to obtain an estimate of the total number of fish in each area (for a given sampling month). Finally, the sum of the total number of fish in each area *A* across all areas of the estuary yielded a monthly model estimate of the total number of age-0 system-wide. The estuary-wide 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 population was more problematic because this life stage is not targeted by any survey in the Estuary. Therefore, we had to rely on back-calculating age-1 estimates from the number of age-3 fish in adult Peterson estimates (Figure 2). The back-calculation was done using annual survival estimates of age-1 to age-3 hatchery striped bass stocked and recovered in 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, which were not available. Note the time period for which we had data for this analysis (1981-1990) did not explicitly cover the step-decline in abundance over the past decade (Thompson 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 bracket a major ecosystem change, the disruption of the estuarine food web following the 1986 invasion of the bivalve *Corbula amurensis* (Kimmerer 2002).

Results

The striped bass MCDs showed substantial variability over the study period for the FMWT, but no long-term trend (Figure 3). Most of the variability in the distribution was associated with the salinity field as indicated by the statistically significant relationships between X2 and the MCD (Figure 4; F=25.88, df=39, P=0.002; MCD = 26.0 + 0.627 X2). There was no evidence that recent years (when there was a step-change in abundance) deviated from the historical relationship between distribution and X2 (Figure 4). If there had been a substantial change in distribution away from the salt field, the data points for recent years should have been outside of the range of variability of the historical data, or shown a systematic shift above or below the historical relationship.

Each of the three surveys showed a trend towards higher relative 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 (Spearman's R = 0.477, p = 0.008) and Bay Otter (Spearman's R = 0.504, p = 0.005), but not the Bay MWT. Catch in shoals averaged 21% of the FMWT total during the 1980s and 36% in the 2000s. Similarly, the Bay MWT shoal catch increased from 35% in the 1980s to 42% of the total catch in the 2000s. The Bay Otter shoal stations also showed an increase from 77% to 93% of the total catch. However, none of the changes were of the same magnitude as total catch, which dropped from the 1980s to the 2000s by about 90% (Figure 2).

Modeled age-0 population estimates ranged from 280,000 to 3.6 million while age-1 population estimates for the following year were 2.1 to 14 million during 1981-1990, the period when data were available to compare the two time series (Figure 6). During the first several years, the modeled age-1 population followed the expected pattern with generally lower estimated abundance than age-0 and similar annual increases and decreases; however, the time series diverged by the mid-1980s with 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 X2. Instead, the data indicate that young bass show an apparent shift from offshore towards inshore areas. Our results are consistent with studies by Schroeter (2008), who documented a movement of age-0 bass away from large, deep sloughs to small shallow sloughs of Suisun Marsh (Figure 1), the largest marsh in the Estuary. Similarly, recent sampling by Nobriga and Feyrer (2007) reported 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 than offshore habitat (Boynton et al. 1981; Robichaud-LeBlanc et al. 1998). As a consequence, young striped bass are likely under-sampled by the pelagic-oriented FMWT. Under sampling 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. year 1, 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, age-1) showed divergent trends.

The long-term lateral shift in distribution may have been caused by movement towards inshore areas (i.e. active behavior) or by differences in mortality for fish that colonize pelagic 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 in part a result of behavioral and ecological plasticity in this species. Active distributional shifts seem fairly reasonable result 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. 2007). 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 is correct, our study documents a new pattern of variability—long-term lateral shifts in age-0 distribution. Previous studies on 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 showing multi-decadal shifts in lateral distribution.

The mechanisms responsible for the distribution shift may vary, but evidence from other aquatic systems suggests that they are frequently mediated by invasions, which result in competition or predation problems (Brown and Moyle 1991). We do not think that it is a coincidence that several of the apparent changes in young striped bass occurred in 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 following the introduction of *Corbula amurensis*, which grazed plankton (Kimmerer et al. 1994; Kimmerer 2002), while littoral fishes increased in abundance coincident with the proliferation of aquatic weeds (Brown and Michniuk 2007; Nobriga 2009). Our study suggested that much of the distribution shift towards shoal habitat occurred in the mid-1980s (Figure 5). Likewise, the modeled abundance trends of age-0 and age-0 diverged during the same period (Figure 6). Following the invasion of Corbula 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 following the *Corbula* 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 suggest that another pelagic species, longfin smelt *Spirinchus thaleichthys*, responded with a similar downstream shift in distribution (Baxter et al. 2008).

We propose that young striped bass moved into shallower habitat because of better foraging opportunities in inshore areas or conversely deteriorating food supply in channels. The direction of the shift contrasts with northern anchovy and perhaps longfin smelt, which moved downstream following a collapse of the food web in Suisun Bay. While additional field studies are needed to test the hypothesis that foraging success is greater in inshore than offshore habitat, it is notable that the diet of young striped bass changed in response to a bivalve invasion during the late 1980s (Feyrer et al. 2003; Bryant and Arnold 2007). Perhaps the best evidence is work by Schroeter (2008), who reported that the movement of young striped bass from deeper channels towards 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 our results do not show that the apparent shift in distribution is the only mechanism responsible for the long-term decline of young striped bass. The data suggest that a greater portion of juvenile bass use shoals, 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 suggest that much of the distribution shift occurred in

1980s well before declines accelerated sharply in the 2000s (Thomson et al. 2010). There is good evidence that several other factors 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) both found evidence of serious contaminant effects on young striped bass. Losses to water diversions may also sporadically affect 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 a couple of ways: through reductions in habitat area during key seasons (Feyrer et al. 2007; Kimmerer et al. 2009); and long-term increases in water clarity (Feyrer et al. 2007) that resulted in reduced catchability of striped bass in the FMWT. In any case, our paper shows that management of striped bass requires a comprehensive understanding of not only 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 fisheries declines in coastal and estuarine habitat cannot be reduced to single environmental factors such as alien species, contaminants or water diversions.

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Figures

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

Figure 2: Trends in age-0 (upper panel) and adult (lower panel; units are x 1000) striped bass abundance in the San Francisco Estuary. Age-0 total catch is based on the FMWT (dotted line), Bay MWT (squares), and Bay Otter (triangles). As noted in the Methods, the age-0 catch data represent relative abundance trends rather than population estimates; hence, they do not have error bars. Adult results with 95% confidence intervals are based on Peterson estimates of adult population (updated from Kimmerer et al. 2001).

Figure 3: Mean centers of distribution (MCD) for age-0 striped bass as sampled by the FMWT. The distributions are based on the distance (km) from the Golden Gate Bridge.

Figure 4: Relationship between salinity (as indexed by X2) and the mean centers of distribution (MCD) for age-0 striped bass as sampled by the FMWT. Both data series are based on the average distance (km) from the Golden Gate Bridge during the September-December period. Each data point is labeled by year. To aid in the evaluation of whether

there has been a change in the historical relationship between fish distribution and salinity, recent years and marked with dark circles and earlier years are indicated by clear squares.

Figure 5. Percent of catch from shoal stations in the FMWT (dotted line), Bay MWT (squares), and Bay Otter (triangles).

Figure 6: Modeled abundance of striped bass for age-0 (diamonds) and age-1 (circles). The age-0 data were shifted by one year to allow direct comparison of the year classes.