

Estuarine fish communities respond to climate variability over both river and ocean basins

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Abstract

Estuaries are dynamic environments at the land–sea interface that are strongly affected by interannual climate variability. Ocean–atmosphere processes propagate into estuaries from the sea, and atmospheric processes over land propagate into estuaries from watersheds. We examined the effects of these two separate climate-driven processes on pelagic and demersal fish community structure along the salinity gradient in the San Francisco Estuary, California, USA. A 33-year data set (1980–2012) on pelagic and demersal fishes spanning the freshwater to marine regions of the estuary suggested the existence of five estuarine salinity fish guilds: limnetic (salinity = 0–1), oligohaline (salinity = 1–12), mesohaline (salinity = 6–19), polyhaline (salinity = 19–28), and euhaline (salinity = 29–32). Climatic effects propagating from the adjacent Pacific Ocean, indexed by the North Pacific Gyre Oscillation (NPGO), affected demersal and pelagic fish community structure in the euhaline and polyhaline guilds. Climatic effects propagating over land, indexed as freshwater outflow from the watershed (OUT), affected demersal and pelagic fish community structure in the oligohaline, mesohaline, polyhaline, and euhaline guilds. The effects of OUT propagated further down the estuary salinity gradient than the effects of NPGO that propagated up the estuary salinity gradient, exemplifying the role of variable freshwater outflow as an important driver of biotic communities in river-dominated estuaries. These results illustrate how unique sources of climate variability interact to drive biotic communities and, therefore, that climate change is likely to be an important driver in shaping the future trajectory of biotic communities in estuaries and other transitional habitats.

Keywords: climate variability, demersal, estuary salinity zones, fish assemblage, freshwater outflow, North Pacific Gyre Oscillation, pelagic, San Francisco Estuary

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Introduction

Fish populations and communities fluctuate from year to year in response to interannual climate variability. Fish populations in the sea track ocean-basin scale processes that drive variability of ocean currents and temperature (Hsieh *et al.*, 2009), timing of the spring phytoplankton bloom (Platt *et al.*, 2003); or quantity and quality of planktonic food supply (Beaugrand & Kirby, 2010). Many of these processes are associated with multidecadal climate oscillations such as the North Atlantic Oscillation (Stige *et al.*, 2006) and Pacific Decadal Oscillation (Mantua *et al.*, 2002) that underlie striking changes in fish communities, such as synchronous alternations between anchovy and sardine regimes

across large regions of the Pacific Ocean (Alheit & Bakun, 2010). Freshwater fish populations and communities track different expressions of climate variability over river basins, such as annual fluctuations in precipitation and river discharge (Grossman *et al.*, 1998; Magalhães *et al.*, 2007), floodplain inundation (Sommer *et al.*, 2001), and water temperature (Nunn *et al.*, 2007). Less is known about climate-driven fluctuations of fish communities in estuaries, where rivers and oceans meet. Do communities in these transitional ecosystems respond primarily to processes of ocean–atmosphere coupling that propagate into estuaries from the sea (e.g. Attrill & Power, 2002), or primarily to atmospheric processes over land that propagate into estuaries through their tributary rivers (e.g. Kimmerer, 2002)?

Estuarine-dependent fishes have evolved a range of physiological adaptations and life histories to cope with and exploit estuarine habitats that vary along the salinity gradient between riverine freshwater and oceanic saltwater (Allen *et al.*, 2006). Estuarine fish communities

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include species that are permanent estuarine residents, marine species that migrate into estuaries to reproduce, rear, or mature, opportunists, and others that use estuaries as a migration corridor between rivers and oceans. Human populations are concentrated along coasts, so estuarine ecosystems have been transformed by habitat modifications, water diversions, introductions of non-native species, and pollution (Cloern & Jassby, 2012). These disturbances can be powerful enough to overwhelm natural processes driving biological variability. A compelling example is the Thames Estuary that had anoxic zones devoid of fish from 1920 to 1964 but was recolonized by 112 fish species after improved treatment of London's wastewater (Attrill, 1998). Therefore, the challenge of isolating effects of climate variability on estuarine communities is confounded by complexity arising from the salinity gradient, varied life histories and salinity tolerances among species, intense human disturbance, and connections of estuaries to both land and ocean (Cloern *et al.*, 2011). Given this complexity, can we detect fish community responses to interannual climate variability in estuaries? And, if we can, are they responses to processes operating over river basins, ocean basins, or both?

These are essential questions because sustainability of fish communities and the services they provide, such as food production, become increasingly uncertain as the effects of climate change unfold. Effective management and conservation of fisheries requires knowledge of how climate induces changes in community structure over short and long periods (Anderson & Piatt, 1999). In the freshwater domain, a global decline of fish and potential acceleration of species extinctions by climate change represents a major conservation challenge (Moyle *et al.*, 2013). For example, 82% of California's native freshwater species, but only 19% of non-native species, are classified as highly vulnerable to projected changes in river flow and water temperature likely to result from climate change. This suggests that climate change is going to cause dramatic change in California's fish fauna as native species are replaced by alien species (Moyle *et al.*, 2013). Fish assemblages in rivers of France are also projected to be substantially restructured by changes in precipitation and temperature (Buisson *et al.*, 2008). Comparable assessments anticipate deeply modified coastal fish assemblages and decreasing species richness as sea surface temperature continues to rise in regions such as the Mediterranean Sea (Albouy *et al.*, 2012). These projections, grounded in empirical relations of species distributions to their environment (Buisson *et al.*, 2008), are critical steps for identifying those species most vulnerable and for prioritizing actions to sustain them. Similar kinds of projections have not been targeted to the communities

of estuarine-dependent fish. A first step is to identify the important climatic drivers of community change and establish empirical relationships between them.

We identify linkages between estuarine fish community variability and climatic variability using a rich observational record from regular sampling along the salinity gradient of the San Francisco Estuary that began in 1980. San Francisco Estuary is the estuary of California's Sacramento and San Joaquin rivers that carry freshwater from runoff produced in a large (160 000-km²) watershed extending inland to the Sierra Nevada mountains (Fig. 1). The estuary is connected at the Golden Gate to coastal shelf waters of the northeastern Pacific Ocean influenced by the California Current system. Previous studies in San Francisco Estuary have established that abundances of a few fish species occupying low-salinity habitats are correlated with annual freshwater inflow (Jassby *et al.*, 1995; Kimmerer, 2002) and that abundances of a few other species occupying high-salinity habitats are correlated with the North Pacific Gyre Oscillation and Pacific Decadal Oscillation (Cloern *et al.*, 2010). These results suggest that the underlying processes of fish community dynamics might vary along estuarine salinity gradients: Species occupying seaward habitats have patterns of fluctuation tied to oceanic variability; and species occupying landward habitats have patterns of fluctuation tied to hydrologic variability.

Atmospheric processes that drive oceanographic variability (winds, currents, temperature, nutrient concentrations, productivity) can be distinct in some coastal regions from those driving variability over river basins (runoff, river discharge, and temperature). For example, we show time series of the upwelling index at 39°N derived from atmospheric pressure fields along the California coast, and a precipitation index as annual runoff to eight rivers in the San Francisco Estuary drainage basin (Fig. 2). Water project operations, including dams, have a stronger influence on the trend of estuarine outflow than on annual variability, indicating that climate, as represented by the 8 river index, is the primary driver of outflow variability at timescales between 1 month and ~20 years (Enright & Culbertson, 2009). Variability of coastal upwelling at this latitude is strongly associated with the North Pacific Gyre Oscillation (Di Lorenzo *et al.*, 2008) that oscillates over a period of several decades, and this low-frequency component is evident in Fig. 2a (autocorrelation of this series indicates a period of 3–4 decades). Precipitation varies over shorter periods, and cross-correlation of the upwelling with precipitation series of annual indices shows zero correlation at all lags. Therefore, these series depict independent expressions of climatic variability impinging on estuarine interfaces with oceans and

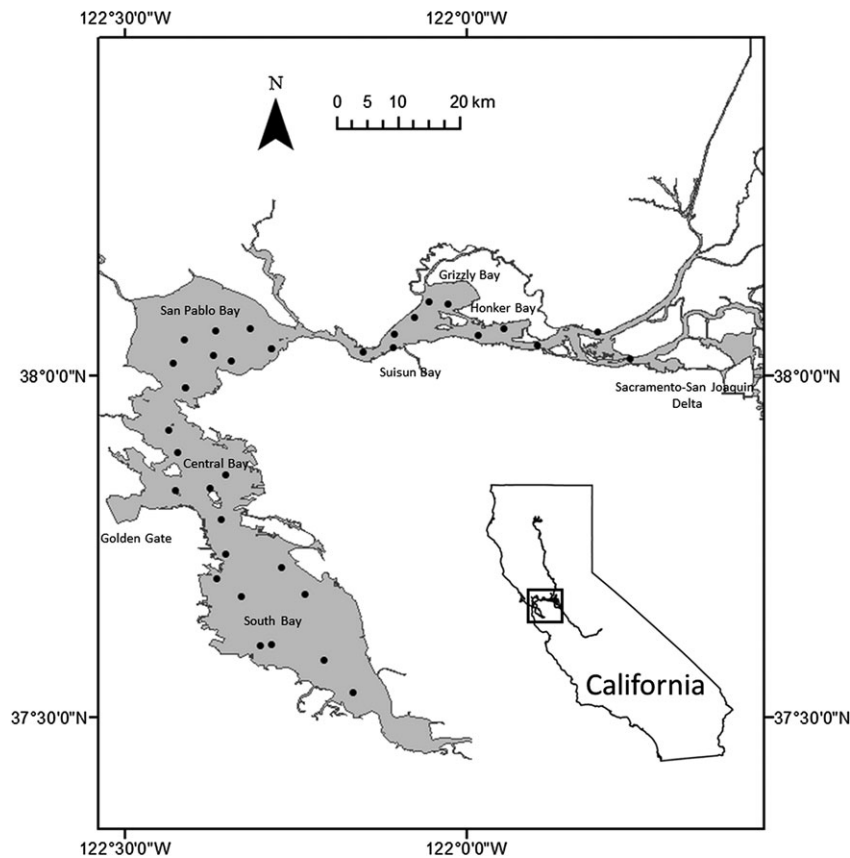


Fig. 1 San Francisco Estuary and fish sampling sites.

ivers. Thus, if fish communities are exposed to different climate-driven processes along estuarine salinity gradients, and if those processes are asynchronous, then we might expect different patterns of fish population fluctuations along the land–sea transition of estuaries. To explore this hypothesis, we analyzed multidecadal data from a well-studied estuary on the Pacific coast of North America to answer three basic questions: (i) Are pelagic and demersal fishes organized into species groups (guilds) that occupy different segments of the estuarine salinity gradient? (ii) Do the population abundances of the guilds identified in Question 1 exhibit similar long-term trends? and (iii) Do the population abundances of these guilds track indices of climate variability over the North Pacific or over the watershed of the estuary?

Materials and methods

San Francisco Estuary and long-term sampling of its fish populations

San Francisco Estuary is a large river-dominated estuary located on the Pacific coast of the United States in central California (Fig. 1). It has an open water surface area of approxi-

mately 1235 km² and a mean depth of 4.6 m (Kimmerer, 2004). From its connection to the Pacific Ocean at the Golden Gate, the estuary opens up into several relatively large embayments, including South Bay, Central Bay, and San Pablo Bay. South Bay, the region located primarily south of the Golden Gate, is a marine lagoon environment. Regions north and east of the Golden Gate are more affected by seasonal and annual variations in outflow from the watershed. Within San Pablo Bay and upstream into Suisun Bay, Grizzly Bay and Honker Bay, the system typically exhibits a range of conditions intermediate of marine and freshwater environments. The system ultimately becomes dominantly a freshwater environment in the Sacramento–San Joaquin Delta, an expansive maze of tidal channels at the confluence of California’s two longest rivers – Sacramento and San Joaquin. Broad shallow shoals (~1–3 m in depth) flank the sides of a relatively narrow and deep (~5–20 m) main channel within the large downstream embayments and the main rivers. Alternating semi-diurnal tides propagate from the Golden Gate through the Sacramento–San Joaquin Delta. Peak tidal velocity at the Golden Gate is about 175 cm s^{−1} (Cloern & Jassby, 2012), and tidal flows are stronger than net flows in most of the estuary except under conditions of extreme freshwater inflow (Kimmerer, 2004).

Physical and biological properties of San Francisco Estuary are controlled by complex interactions of processes that operate at varying frequencies and spatial scales. The prevailing Mediterranean climate is characterized by a warm and dry

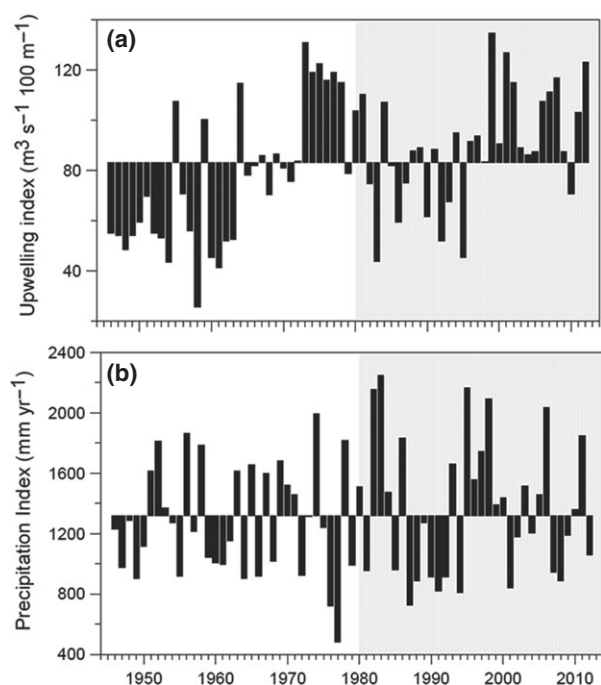


Fig. 2 Indices of interannual climate variability expressed: (a) over the coastal NE Pacific Ocean (upwelling index at 39°N, NOAA Pacific Fisheries Environmental Laboratory; <http://www.pfeg.noaa.gov/products/pfel/modeled/indices/upwelling/upwelling.html>), and (b) over the San Francisco Bay watershed (unimpaired runoff from 8 northern Sierra Nevada rivers, California Department of Water Resources; <http://cdec.water.ca.gov/cgi-progs/precip1/8STATIONHIST>).

summer–fall period and a cool and wet winter–spring period, which controls the amount of freshwater flow entering the estuary from the watershed. Flows in the system are also highly managed because the estuary supplies water for over 25 million people and a multibillion dollar agricultural industry. Annual freshwater flow is highly variable, averaging $736 \text{ m}^3 \text{ s}^{-1}$ (standard deviation = $618 \text{ m}^3 \text{ s}^{-1}$) across the years 1980–2012, which encompass our study period. San Francisco Estuary is also intimately linked to conditions in the northeastern Pacific Ocean through the connection at the Golden Gate. Seasonal and interannual conditions in the northeastern Pacific Ocean are driven by global climate patterns, which have been characterized by indices such as the North Pacific Gyre Oscillation (NPGO) and the PDO (Mantua *et al.*, 2002; Di Lorenzo *et al.*, 2008). Negative values of the PDO and positive values of the NPGO generally correspond to cool water conditions with positive upwelling anomalies and higher productivity along the Pacific Coast. Climate-induced regime shifts have been linked to key physical–biological processes in the northeastern Pacific Ocean and adjacent estuaries (e.g. Mantua *et al.*, 2002; Peterson & Schwing, 2003; Cloern *et al.*, 2007, 2010; Sydeman *et al.*, 2013).

San Francisco Estuary fish populations have been monitored at 35 core sites spanning the freshwater to marine environments of the estuary on a monthly basis since 1980 by the

California Department of Fish and Wildlife (Armor & Herrgessell, 1985; Fig. 1). The monthly effort is conducted with an otter trawl to sample demersal species and a midwater trawl to sample pelagic species.

Climate indices

We compiled annual (calendar year) time series of climate indices that are known ecosystem drivers in the northeastern Pacific Ocean (Mantua *et al.*, 2002; Peterson & Schwing, 2003; Di Lorenzo *et al.*, 2008; Sydeman *et al.*, 2013) and the San Francisco Estuary (Jassby *et al.*, 1995; Kimmerer, 2002; Cloern *et al.*, 2007, 2010). Data were obtained as follows: sea surface temperature (SST) measured at the Farallon Islands from the Scripps Institution of Oceanography Shore Stations Program (shorestation.ucsd.edu/index.html), monthly upwelling index anomalies at 39°N from the National Oceanic and Atmospheric Administration's Pacific Fisheries Environmental Laboratory (www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/data_download.html), PDO from the University of Washington (jisao.washington.edu/pdo/), NPGO from the Georgia Institute of Technology (www.o3-d.org/npgo/npgo.php), and the volume of freshwater flow entering the estuary (OUT) from the State of California's DAYFLOW Database (www.water.ca.gov/dayflow/).

When aggregated to annual means, there was notable multicollinearity in the climate indices. NPGO was significantly ($P < 0.05$) correlated with PDO ($r = -0.55$), SST ($r = -0.51$) and the upwelling index ($r = 0.54$) but not ($P > 0.05$) with OUT ($r = -0.28$). Several studies have addressed the interrelationships between these climate indices (e.g. Di Lorenzo *et al.*, 2008; Chenillat *et al.*, 2012). Among the correlated indices, we retained NPGO for analyses of association with fish data because it is a broad climatic integrator (Di Lorenzo *et al.*, 2008) and has established associations with regional biota (Cloern *et al.*, 2007, 2010; Sydeman *et al.*, 2013).

Study question (1): Are pelagic and demersal fishes organized into species groups (guilds) that occupy different segments of the estuarine salinity gradient?

The San Francisco Estuary fish monitoring data set is extremely complex. It encompasses over three decades of monthly data on 137 species with diverse life histories across a broad freshwater to marine transition (see the Table S1 for a list of species and their salinity ranges). We used principal component analysis (PCA) to reduce the dimensionality of the data set to its primary modes of variability based on the empirical salinity ranges observed for individual species. Salinity ranges for individual species were defined as the interquartile range of observations when salinity was measured for samples in which a species was present. Surface salinity and bottom salinity have been measured coincident with each sample since 1981, while only surface salinity was measured in 1980; demersal samples from 1980 were therefore excluded from this analysis because of the lack of corresponding salinity measurements at the appropriate depth. There were insufficient observations to calculate interquartile

ranges for 34 species. There were sufficient observations to define 50 species into distinct age groups based upon known life history differences (*sensu* Bulger *et al.*, 1993). Ultimately, a total of 135 cases (species and species age groups) were available for this analysis. The data were summarized into a presence-absence matrix where variables (columns) consisted of 33 salinity incremental integer values ranging from 0 to 32, and the rows were the 135 individual cases. The analysis was implemented using the correlation matrix and varimax rotation. Similar to previous analyses (Bulger *et al.*, 1993), we used principal component (PC) loading values of ≥ 0.5 to delineate modes.

Study question (2): do the population abundances of the guilds identified in question 1 exhibit similar long-term trends?

This question was addressed by determining whether any of the guilds exhibited long-term trends in interannual abundance over the time series. The fish catch data were aggregated into separate interannual abundance indices for pelagic and demersal fishes for each salinity guild identified in the PCA described above. The abundance indices were calculated as total catch standardized by total effort for the months of February–October for the demersal fishes and April–October for the pelagic fishes to cover periods of peak abundance with a continuous record. Effort for the pelagic fish sampling was calculated as the total volume of water filtered by the mid-water trawl, and for the demersal fish sampling, it was the total area swept by the otter trawl. The nonparametric Mann–Kendall test was used to determine whether there was a monotonic upward or downward trend over time in the interannual abundance indices. Northern anchovy *Engraulis mordax* was separated from the rest of the pelagic community for this analysis because its overall dominance overwhelmed the variability patterns of other species.

Study question (3): do the population abundances of these guilds track indices of climate variability over the North Pacific or over the estuary watershed?

Single-factor permutational analysis of variance (PERMANOVA; Anderson, 2001; Anderson *et al.*, 2008) was used to test for differences in community structure (species relative composition) within each of the salinity guilds for pelagic and demersal fishes between first-order regimes of NPGO and OUT. In this application, PERMANOVA is a distance-based multivariate analysis of variance procedure that generates *P*-values through permutation, thereby avoiding the assumptions associated with normal distributions. Here, we used the Bray–Curtis similarity measure, type III (partial) sums of squares, and 999 unrestricted permutations of the raw data. First-order regimes were defined as binary variables corresponding to the sign (– or +) of the standardized climate variability indices, that is, cool (+) vs. warm (–) regimes of NPGO and wet (+) vs. dry (–) regimes of OUT (Fig. 3). NPGO regimes were defined as the sign of 12-month calendar year mean values. OUT regimes for each

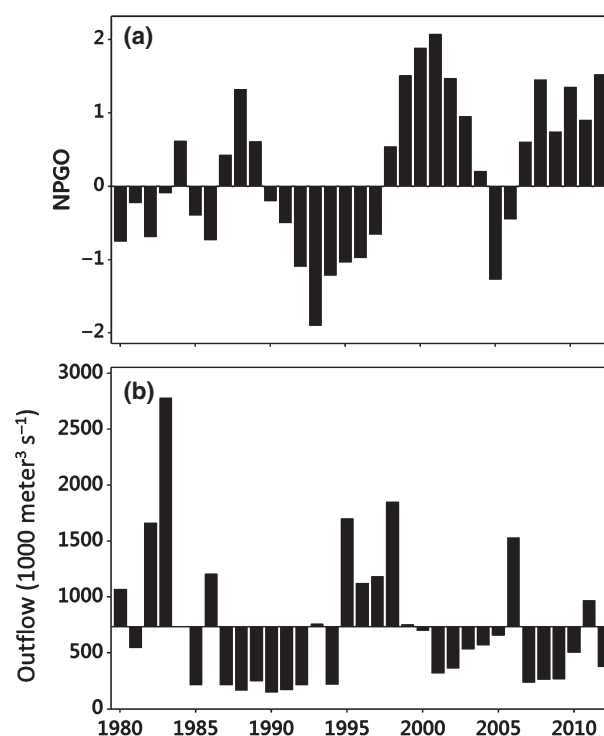


Fig. 3 Time series of (a) North Pacific Gyre Oscillation (NPGO) and (b) total freshwater outflow in San Francisco Estuary. Values are 12-month calendar year means. Base position for outflow is 736 (1000 m³ s^{–1}), which is the 1980–2012 average value. In both (a) and (b), values above the base position represent positive (+) regimes and values below the base value represent negative (–) regimes, as applied in analyses described in the text.

12-month calendar year from 1980 to 2012 were generated by standardizing to the mean of all calendar years between 1980 and 2012; that is, individual years with values above the 1980–2012 mean were considered wet (+) and those below the mean were considered dry (–). PERMANOVAS were conducted on community similarity matrices constructed using the Bray–Curtis coefficient in the PRIMER software package (Anderson *et al.*, 2008). Species known to have invaded the estuary partway through the time series, for example, shimofuri goby *Tridentiger bifasciatus* and shokihaze goby *Tridentiger barbatus*, were removed from this analysis.

When a significant difference in community structure was identified between primary regimes of a climate variability index (PERMANOVA $P \leq 0.05$), we used the similarity percentages (SIMPER) routine in PRIMER to identify the individual species responsible for the community structure difference, thereby determining the individual species within each community in each guild most associated with a climate variability index. SIMPER decomposes the average Bray–Curtis dissimilarities between all pairs of intergroup samples (i.e. all instances of one regime against all instances of the opposite regime for the covariate of interest) into the percentage contributions by individual species.

Results

Study question (1): are pelagic and demersal fishes organized into species groups (guilds) that occupy different segments of the estuarine salinity gradient?

The PCA reduced the dimensionality of the San Francisco Estuary fish monitoring data set to five primary modes (PCs) of variability, together explaining 86% of the variability in the data set (Fig. 4). We interpreted these five primary modes of variability as overlapping estuarine salinity guilds, which we termed limnetic (salinity = 0–1), oligohaline (salinity = 1–12), mesohaline (salinity = 6–19), polyhaline (salinity = 19–28), and euhaline (salinity = 29–32). The estuarine salinity guilds were aggregated by the individual salinity increments having

a PC loading ≥ 0.5 on each of the five modes (PCs). The only exception was that the upper limit of the polyhaline zone and the lower limit of the euhaline zone were extended to include all positive values, as this appeared to be the natural breakpoint or transition between these modes. It is important to note that this analysis was focused on identifying the presence of salinity guilds and their component species. Thus, an individual species may be a member of one or more salinity guilds.

Study question (2): do the population abundances of the guilds identified in question 1 exhibit similar long-term trends?

Interannual indices of total fish abundance (minus northern anchovy) of both pelagic and demersal fishes

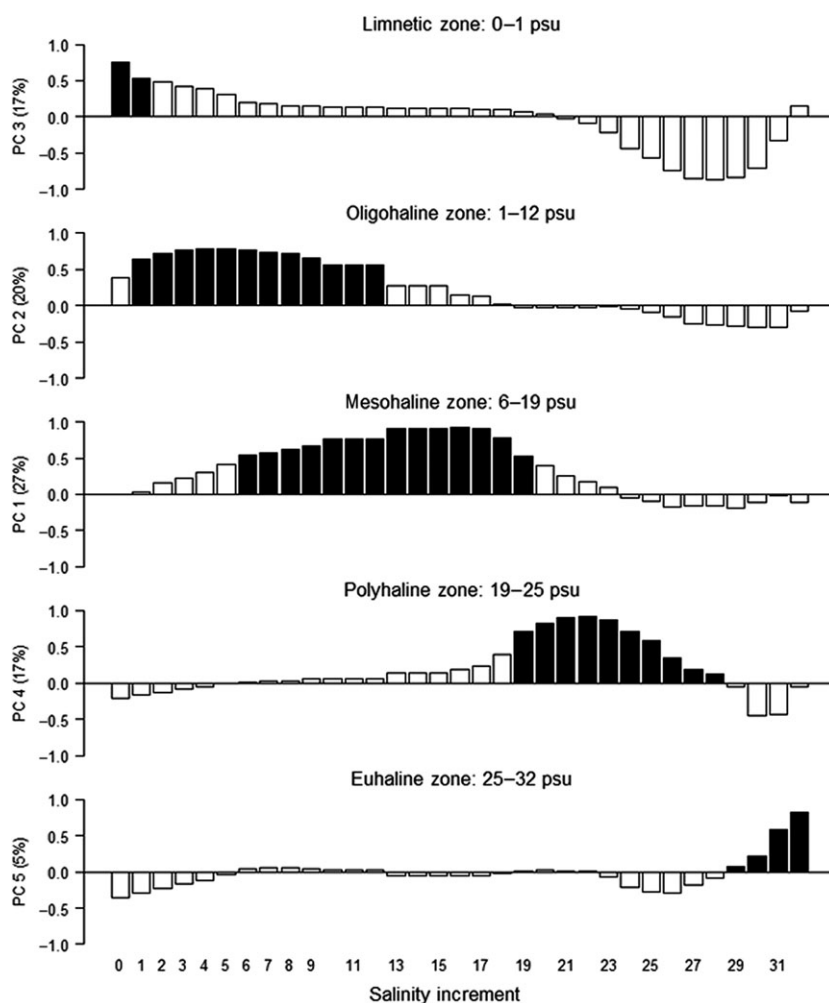


Fig. 4 Barplot depiction of values for the loadings of salinity increment values on five principal components. The principal component analysis was based on interquartile ranges of salinity habitation for 135 individual cases of species and life stages summarized into a presence-absence matrix across 33 incremental integer values of salinity. Principal components and the amount of variability explained are identified in the vertical axis labels. Filled bars indicate loadings ≥ 0.5 and were used to delineate salinity guilds that are labeled in the panel headings. Note that the polyhaline and euhaline guilds each include two filled bars with loadings < 0.5 .

(Fig. 5) in the upper estuary (limnetic, and oligohaline guilds) and the pelagic mesohaline guild exhibited statistically significant ($P \leq 0.01$) negative long-term trends, while demersal fishes in the polyhaline and euhaline guilds exhibited statistically significant ($P \leq 0.03$) positive long-term trends. All interannual abundance indices of age-0 and age-1+ northern anchovy (Fig. 6) exhibited long-term negative trends, with six of 10 cases being statistically significant ($P \leq 0.02$). Thus, there were not consistent trends

between guilds or between the demersal and pelagic communities.

Study question (3): do the population abundances of these guilds track indices of climate variability over the North Pacific or over the estuary watershed?

Statistically significant ($P < 0.05$) differences in demersal fish community structure were apparent between NPGO regimes in the polyhaline and euhaline guilds

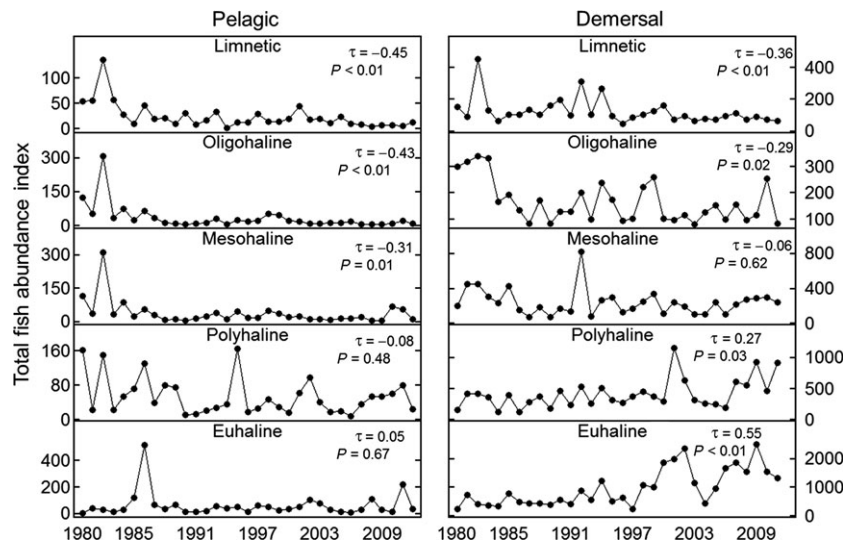


Fig. 5 Time series of total fish abundance indices (total catch corrected for total effort *10 000) in each estuarine salinity guild. Trends as Mann-Kendall's tau and 2-sided P -values are shown for each time series. Note that y-axes are on different scales and that abundance data for northern anchovy *Engraulis mordax* are shown separately in Fig. 6.

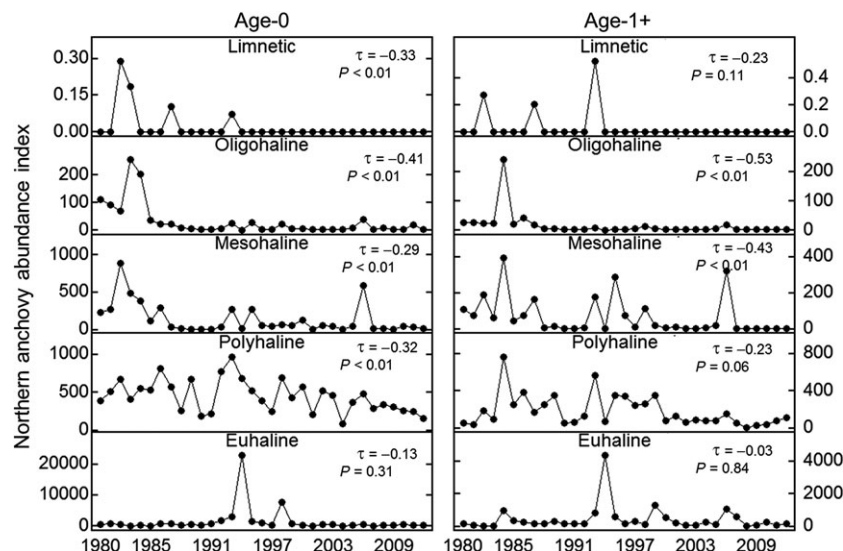


Fig. 6 Time series of northern anchovy *Engraulis mordax* abundance indices (total catch corrected for total effort *10 000) in each estuarine salinity guild. Mann-Kendall's tau and 2-sided P -values are shown for each time series. Note that y-axes are on different scales.

and between OUT regimes in the oligohaline, mesohaline, and polyhaline guilds. Statistically significant ($P < 0.05$) differences in pelagic fish community structure were apparent between NPGO regimes in the polyhaline and euhaline guilds and between OUT regimes in the oligohaline, mesohaline, polyhaline, and euhaline guilds. Notably, both the pelagic and the demersal communities in the limnetic guild did not exhibit statistically significant differences between OUT or NPGO regimes ($P > 0.05$).

As indicated by the SIMPER routine, a diverse group of individual species contributed to the statistically significant differences in community structure between climate regimes. We focus here on individual species which contributed $\geq 10\%$ of the difference between climate regimes with statistically significant differences in community structure (Table 1). Species contributing $\geq 10\%$ of the difference between NPGO regimes in the

pelagic communities included age-0 Pacific herring *Clupea pallasii* (cool and warm regimes; see discussion), age-0 longfin smelt (warm regimes), and age-0 jacksmelt *Atherinopsis californiensis* (cool regimes).

Species contributing $\geq 10\%$ of the difference between NPGO regimes in the demersal communities included age-0 English sole *Parophrys vetulus*, age-0 and age-1 + bay goby *Lepidogobius lepidus*, and age-0 plainfin midshipman *Porichthys notatus*, which were associated with cool regimes.

Species contributing $\geq 10\%$ of the difference between OUT regimes in the pelagic communities included age-0 and age-1 + northern anchovy, age-0 longfin smelt, age-0 and age-1 jacksmelt, which were associated with wet regimes, and age-0 Pacific sardine and northern anchovy, which were associated with dry regimes.

Species contributing $\geq 10\%$ of the difference between OUT regimes in the demersal community included

Table 1 Species contributions to statistically significant ($P \leq 0.05$ in pairwise PERMANOVA tests) differences in pelagic or demersal fish community composition in estuarine salinity guilds between warm (–) or cool (+) regimes of the North Pacific Gyre Oscillation (NPGO) and high (+) or low (–) regimes of freshwater estuarine outflow (OUT). Species contributing $\geq 10\%$ of a difference are shown. Abundance is the interannual total catch corrected for total effort *10 000

Climate index	Guild	Community	Species	Average abundance		Average dissimilarity	Contribution (%)
				(–)	(+)		
OUT	Oligohaline	Demersal	Striped bass <i>Morone saxatilis</i> age-0	63	35	11	19
OUT	Oligohaline	Demersal	Yellowfin goby <i>Acanthogobius flavimanus</i> age-0	20	30	9	15
OUT	Oligohaline	Pelagic	Northern anchovy <i>Engraulis mordax</i> age-0	19	49	25	35
OUT	Oligohaline	Pelagic	Longfin smelt <i>Spirinchus thaleichthys</i> age-0	1	37	17	23
OUT	Mesohaline	Demersal	Striped bass <i>Morone saxatilis</i> age-0	41	13	7	10
OUT	Mesohaline	Demersal	Bay goby <i>Lepidogobius lepidus</i> age-0	19	36	7	10
OUT	Mesohaline	Demersal	White croaker <i>Genyonemus lineatus</i> age-0	1	57	7	10
OUT	Mesohaline	Pelagic	Northern anchovy <i>Engraulis mordax</i> age-0	60	275	37	52
OUT	Mesohaline	Pelagic	Northern anchovy <i>Engraulis mordax</i> age-1+	37	121	21	29
OUT	Polyhaline	Demersal	English sole <i>Parophrys vetulus</i> age-0	75	41	7	12
OUT	Polyhaline	Demersal	Longfin smelt <i>Spirinchus thaleichthys</i> age-0	3	59	7	13
OUT	Polyhaline	Demersal	Bay goby <i>Lepidogobius lepidus</i> age-1+	75	51	7	12
OUT	Polyhaline	Demersal	English sole <i>Parophrys vetulus</i> age-1+	72	43	6	10
OUT	Polyhaline	Pelagic	Northern anchovy <i>Engraulis mordax</i> age-0	307	435	18	45
OUT	Polyhaline	Pelagic	Northern anchovy <i>Engraulis mordax</i> age-1+	70	245	16	40
OUT	Euhaline	Pelagic	Pacific herring <i>Clupea pallasii</i> age-0	65	23	30	40
OUT	Euhaline	Pelagic	Jacksmelt <i>Atherinopsis californiensis</i> age-0	2	8	9	12
OUT	Euhaline	Pelagic	Pacific sardine <i>Sardinops sagax caerulea</i> age-0	5	2	8	10
NPGO	Polyhaline	Demersal	Bay goby <i>Lepidogobius lepidus</i> age-1+	40	91	8	13
NPGO	Polyhaline	Demersal	English sole <i>Parophrys vetulus</i> age-0	35	86	7	13
NPGO	Polyhaline	Demersal	Bay goby <i>Lepidogobius lepidus</i> age-1+	26	49	5	10
NPGO	Polyhaline	Pelagic	Pacific herring <i>Clupea pallasii</i> age-0	34	39	37	59
NPGO	Polyhaline	Pelagic	Longfin smelt <i>Spirinchus thaleichthys</i> age-0	10	1	6	10
NPGO	Euhaline	Pelagic	Pacific herring <i>Clupea pallasii</i> age-0	40	36	29	40
NPGO	Euhaline	Pelagic	Jacksmelt <i>Atherinopsis californiensis</i> age-0	4	8	9	12
NPGO	Euhaline	Demersal	Bay goby <i>Lepidogobius lepidus</i> age-1+	115	385	14	22
NPGO	Euhaline	Demersal	English sole <i>Parophrys vetulus</i> age-0	34	201	8	13
NPGO	Euhaline	Demersal	Plainfin midshipman <i>Porichthys notatus</i> age-0	73	161	8	12

age-0 yellowfin goby *Acanthogobius flavimanus*, age-0 longfin smelt, age-0 and age-1 + bay goby, and age-0 white croaker associated with wet regimes, and age-0 striped bass and age-0 and age-1 + English sole associated with dry regimes.

Discussion

Estuarine fish salinity guilds

The 33-year data set on pelagic and demersal fishes spanning the freshwater to marine regions of the estuary suggested the existence of five overlapping estuarine salinity fish guilds. Considering the PCA explained 86% of the variation in a data set spanning three decades and consisting of over 17 000 samples (trawls) and 3 000 000 fish observations, we posit it meaningfully reduced the dimensionality of this highly complex data set. Overlapping salinity guilds reflect the fact that fish are motile organisms that are not constrained to discrete salinity units as distribution boundaries. The derived salinity zonation scheme for San Francisco Estuary was generally similar to that developed for the mid-Atlantic region of the United States (Bulger *et al.*, 1993) in that each has five overlapping salinity guilds. The primary difference between the two is that the San Francisco Estuary scheme exhibits guilds with broader salinity ranges and a higher degree of overlap between guilds of lower salinity. This difference might reflect true functional differences or it might be caused by the inclusion of multiple estuaries and invertebrate species in the mid-Atlantic scheme (Bulger *et al.*, 1993). The relatively broad, overlapping guilds of the San Francisco Estuary salinity zonation scheme generally resemble the gradual change in fish community composition observed along the salinity gradients in estuaries in southwest Florida, USA (Tampa Bay and Charlotte Harbor; Greenwood, 2007). Where available data exist for other systems, the application of salinity zonation schemes could potentially be a useful classification tool for evaluating major forces driving community structure within and among estuaries across the world.

Interannual fish abundance trends

There were similarities and differences in the patterns of interannual abundance indices of pelagic and demersal fishes across the estuarine salinity gradient. Long-term pelagic fish abundance declines in limnetic, oligohaline, and mesohaline guilds clearly reflected well-documented patterns in the San Francisco Estuary (Sommer *et al.*, 2007; MacNally *et al.*, 2010; Thomson *et al.*, 2010). Interestingly, we show for the first time that demersal fish abundance in the limnetic and

oligohaline guilds has also declined (or has remained relatively stable if the recently introduced gobies are considered). This suggests it is unlikely that the apparent loss of fish production in the pelagic zone (as inferred from counts of fish) in the estuary has been transferred to fish production in the demersal zone. Future research would benefit by extending similar analyses to estimates of fish biomass and, because of documented lateral shifts in age-0 striped bass distribution (Sommer *et al.*, 2011), littoral habitats, plus demersal invertebrates such as bivalves and shrimp to more thoroughly address this issue. Long-term increases of demersal fish abundance in the lower estuary (polyhaline and euhaline guilds) have also been reported previously (Cloern *et al.*, 2007, 2010).

Northern anchovy abundance indices declined throughout the estuary, with six of ten cases being statistically significant. In the limnetic and oligohaline guilds, northern anchovy was essentially absent after 1986, consistent with previous hypotheses that a collapse of food resources after introduction of the bivalve *Potamocorbula amurensis* has shifted northern anchovy distribution downstream (Kimmerer, 2006). The overall decline is consistent with a regional decline in northern Anchovy where the prevailing hypothesis is that the stock has moved off of the coast and to the south with cold summer upwelling (Bjorkstedt *et al.*, 2012).

Intriguingly, pelagic and demersal fish populations had opposite patterns of change over time. Specifically, pelagic fish abundance decreased in the limnetic, oligohaline, and mesohaline guilds, while total demersal fish abundance increased in the polyhaline and euhaline guilds (Fig. 5). This pattern emerged at least partly because pelagic and demersal species respond differently to climate variability. This is exemplified in the diversity of adaptations and life histories exhibited by species to cope with and exploit estuarine habitats that vary along the salinity gradient between riverine freshwater and oceanic seawater.

Climate variability as a driver of fish community structure

Our results demonstrate that fish guilds along an estuarine salinity gradient respond to features of climate variability, specifically processes of ocean-atmosphere coupling that propagate into estuaries from the sea, and atmospheric processes over land that propagate into estuaries through their tributary rivers. For the SFE, these results provide a unified framework for understanding seminal studies that demonstrated connections between single climate features and component parts of estuarine biota (Jassby *et al.*, 1995; Attrill & Power, 2002; Cloern *et al.*, 2010).

Our results show there is no single canonical response of estuarine-dependent fishes to climate variability, reflecting the complex patterns of biological variability in estuaries subjected to multiple global- and local-scale forcings. They also demonstrate that these forcings include apposing upstream and downstream responses to the climate system, that is, outflow and ocean conditions in our study, that extend into estuaries to influence species composition and abundance beyond immediately adjacent regions. For example, statistically significant effects of OUT were observed in the oligohaline, mesohaline, polyhaline, and euhaline zones, while the statistically significant effects of ocean conditions as indexed by the NPGO were observed in the euhaline and polyhaline zones. Thus, the effects of OUT propagated further down the estuary salinity gradient than the effects of NPGO that propagated up the estuary salinity gradient, exemplifying the role of variable freshwater outflow as an important driver of biotic communities in river-dominated estuaries. Finally, our results highlight the critical importance of sustained long-term observations for capturing multiple components of climate variability that can be exploited as experiments.

Numerous fishes have evolved a diversity of adaptations and life histories to cope with and exploit estuarine habitats that vary with salinity between riverine freshwater and oceanic seawater. These communities include species that are permanent estuarine residents, marine species that migrate into estuaries to reproduce or mature, low-salinity-tolerant freshwater fishes, and others that use estuaries as a migration corridor between rivers and oceans. Thus, there is a predisposition for certain species within estuaries to respond more strongly to changes in ocean conditions, or conditions upstream or within estuaries.

The diverse response patterns of fish communities in San Francisco Estuary to climate variability are complex but can be exemplified by a few key species. English sole is an example of a species that responds to climate variability expressed primarily through ocean conditions. It occurs throughout the Pacific coast of North America. Spawning occurs in coastal habitats from approximately September through April (Kruse & Tyler, 1983; Krygier & Percy, 1986). Pelagic larvae settle as demersal juveniles along the coast and in estuaries, with evidence of active transport or migration into estuaries (Gunderson *et al.*, 1990). Estuaries function as juvenile nursery habitats during the first year of life (Olson & Pratt, 1973; Gunderson *et al.*, 1990). The abundance of young English sole in the estuary peaked during cool phases of the NPGO, in part because of enhanced physical and biological conditions for spawning, survival, and recruitment into estuaries. Specifically, cooling ocean conditions may allow a southward

shift of adult English sole, thereby positioning more spawners to take advantage of prevailing winter currents to transport progeny into San Francisco Estuary. Longfin smelt is an example of a species that responds to climate variability expressed primarily through freshwater outflow. It is an anadromous species that spawns in the upper San Francisco Estuary from December to April (Moyle, 2002; Rosenfield & Baxter, 2007). The abundance of age-0 longfin smelt peaks during years of high freshwater outflow, likely because of enhanced physical and biological conditions for spawning, survival, and recruitment within the estuary (Jassby *et al.*, 1995; Kimmerer, 2002; Kimmerer *et al.*, 2009). Striped bass is an example of a species that exhibits habitat-associated responses to climate variability expressed primarily as freshwater outflow. Striped bass is a large and long-lived anadromous species. Spawning occurs primarily upstream of San Francisco Estuary in the Sacramento River from approximately April through June. Eggs drift with river currents as they develop and hatch. Juvenile striped bass initially occur in low-salinity habitats where they grow, later dispersing throughout the estuary. Pelagic-oriented age-0 striped bass have been associated with high flow conditions (Stevens, 1977), while demersal-oriented age-0 striped bass in this study were associated with dry regimes. The former is likely because of enhanced physical and biological conditions for survival, transport, and recruitment into the estuary for eggs and larvae (Stevens, 1977), while the latter is likely because reduced pelagic carrying capacity in dry years drives striped bass to alternative habitats (Sommer *et al.*, 2011). Pacific herring is an abundant and ecologically relevant forage fish that, within SFE, is generally associated with cool regimes. The results of our analysis were somewhat equivocal regarding the role of NPGO on Pacific herring in that there was an association with warm and cool regimes. This is likely because upwelling or water temperature may be the more meaningful variable for this species, as has been shown in other systems (Reum *et al.*, 2011).

Effects of climatic drivers on the San Francisco Estuary fish community were apparent despite strong local internal drivers and perturbations that could confound such responses. Estuaries are among the most complex ecosystems, and San Francisco Estuary is an especially complex system that has undergone dramatic human-caused morphological, hydrological, chemical, and biological alterations that have changed ecological functions and habitats (Nichols *et al.*, 1986; Arthur *et al.*, 1996; Brooks *et al.*, 2012; Cloern & Jassby, 2012; Whipple *et al.*, 2012). Although these internal drivers are known to have affected the response of some individual species to climatic drivers (Kimmerer, 2002, 2006),

climatic drivers remain a dominant underlying force structuring the estuary and its biological communities (Cloern *et al.*, 2007). Notably, this is largely in contrast to the freshwater Sacramento–San Joaquin Delta positioned at the landward edge of the estuary, where physical and biological alterations have largely overridden natural processes leading to a fish community dominated by non-native species (Feyrer & Healey, 2003; Nobriga *et al.*, 2005).

Conservation and management implications

Management of the numerous ecosystem services provided by estuaries in the face of global climate change represents a major conservation challenge. Estuaries are especially vulnerable to effects of global climate change because of the diversity of processes through which climate affects estuaries. Estuaries around the world, including San Francisco Estuary, are likely to be affected by alterations in the timing and magnitude of freshwater outflow, water temperature, ocean conditions, sea-level rise, and many other factors (Knowles & Cayan, 2002; Scavia *et al.*, 2002; Cloern *et al.*, 2011; Gilanders *et al.*, 2011). Assessments of climate change impacts must therefore be based on empirical relationships between climate variability and appropriately scaled biological response variables. Climate variability affects fish populations on all levels of organization from individuals to assemblages (Rijnsdorp *et al.*, 2009). Understanding how communities and species respond to climate variability is challenging and requires long-term data spanning a range of conditions to elucidate functional relationships (Attrill & Power, 2002; Cloern *et al.*, 2007; Cloern *et al.*, 2010; Cloern & Jassby, 2012).

Our results examining three decades of data demonstrating connections between fish species and climatic drivers along the salinity gradient of San Francisco Estuary (Table 1) can be used to infer the potential effects of future climate change on fishes in San Francisco Estuary. Projections with downscaled global climate models indicate that San Francisco Estuary biota is likely to be subjected to increased water temperature, elevated salinity and sea level, and decreased precipitation and outflow (Cloern *et al.*, 2011; Feyrer *et al.*, 2011; Brown *et al.*, 2013). Future conditions exhibiting decreased outflow are most likely to affect fishes in the oligohaline, mesohaline, polyhaline, and euhaline salinity guilds (Table 1). Decreased outflow could potentially negatively affect populations of longfin smelt, bay goby, yellowfin goby, northern anchovy, jacksmelt, and white croaker. Populations of species that are likely to be positively affected include Pacific herring and Pacific sardine. Expected changes to the North Pacific Ocean are much less certain and may include increased temperature (Furtado *et al.*,

2011). Future conditions exhibiting changes to NPGO are most likely to affect fishes in the polyhaline and euhaline zones (Table 1). Generally, cooler conditions with positive NPGO values could negatively affect populations of longfin smelt, while populations of bay goby, English sole, jacksmelt, and plainfin midshipman would likely benefit. While these projections could be improved through a better understanding of the mechanisms underlying the relationships and their interactions with internal drivers, they provide managers an empirically grounded perspective for anticipating long-term challenges to managing fish populations.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Fishes observed in San Francisco Estuary during monthly otter trawl and midwater trawl sampling from 1980 to 2012.