The Collapse of Pelagic Fishes in the Upper San Francisco Estuary

El Colapso de los Peces Pelágicos en La Cabecera Del Estuario San Francisco

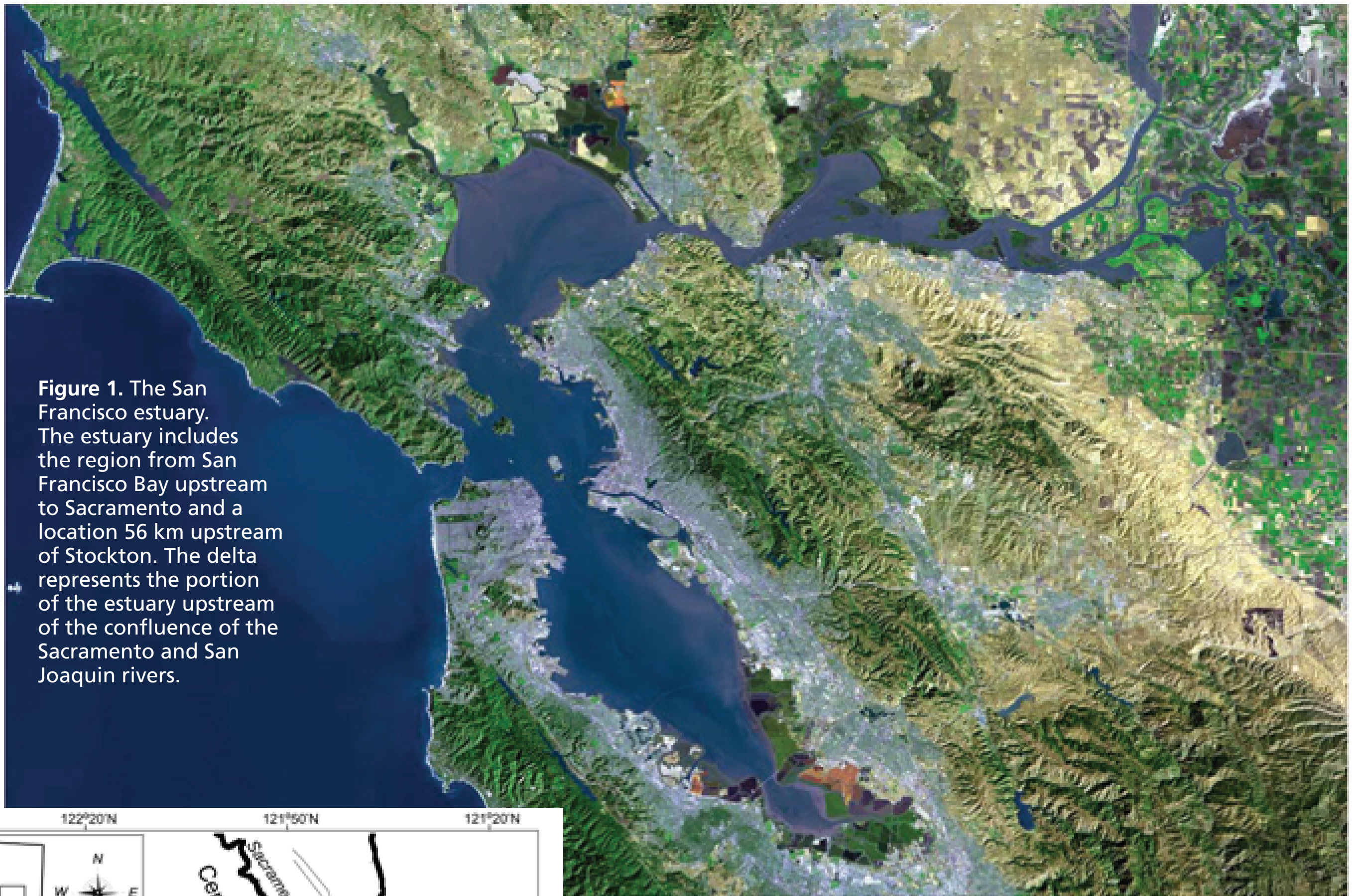
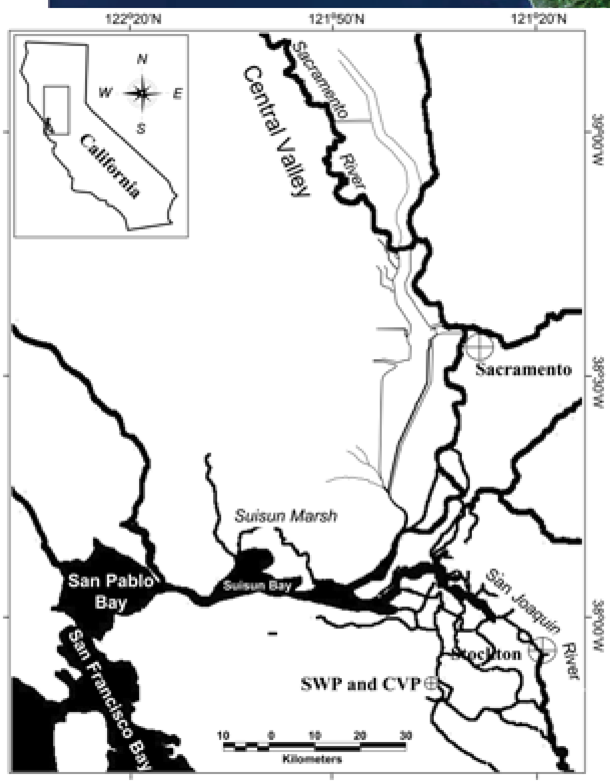


Figure 1. The San Francisco estuary. The estuary includes the region from San Francisco Bay upstream to Sacramento and a location 56 km upstream of Stockton. The delta represents the portion of the estuary upstream of the confluence of the Sacramento and San Joaquin rivers.



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ABSTRACT: Although the pelagic fish community of the upper San Francisco Estuary historically has shown substantial variability, a recent collapse has captured the attention of resource managers, scientists, legislators, and the general public. The ecological and management consequences of the decline are most serious for delta smelt (*Hypomesus transpacificus*), a threatened species whose narrow range overlaps with large water diversions that supply water to over 25 million people. The decline occurred despite recent moderate hydrology, which typically results in at least modest recruitment, and investments of hundreds of millions of dollars in habitat restoration and environmental water allocations to support native fishes. In response to the pelagic fish collapse, an ambitious multi-agency research team has been working since 2005 to evaluate the causes of the decline, which likely include a combination of factors: stock-recruitment effects, a decline in habitat quality, increased mortality rates, and reduced food availability due to invasive species.

RESUMEN: A pesar de que la comunidad de peces pelágicos de la cabecera del Estuario San Francisco históricamente ha mostrado una considerable variabilidad, su reciente colapso ha llamado la atención de manejadores, científicos, legisladores y público en general. Las consecuencias ecológicas y de manejo de dicha caída son particularmente graves para el "delta smelt" (*Hypomesus transpacificus*); una especie amenazada cuyo estrecho rango de distribución coincide con un gran reservorio hidrológico que suple de agua a más de 25 millones de personas. El colapso tuvo lugar a pesar de la modesta dinámica hidrológica del lugar, que al menos dio como resultado un reclutamiento igualmente moderado, y de una inversión de cientos de millones de dólares para la restauración del hábitat y el aseguramiento de cuerpos de agua que sirven de hábitat a los peces nativos. Como respuesta a la caída de los peces pelágicos, un ambicioso equipo de trabajo constituido por diversas agencias, ha venido trabajando desde 2005 para evaluar las causas del colapso, las cuales seguramente involucran diversos factores, tales como: efectos sobre la relación parentela-progenie, disminución de la calidad del hábitat, aumento en las tasas de mortalidad y una reducción en la disponibilidad de alimento debido a la presencia de especies introducidas.

Globally, the collapse of many of the world's fisheries remains the most important issue facing fisheries managers. The collapses are most pronounced in coastal regions, where declines have occurred on the scale of decades to millennia (Worm et al. 2006). With the 2007 American Fisheries Society Annual Meeting in San Francisco, the fisheries community will come together in close proximity to one of the more recent resource collapses in North America, the decline of pelagic fishes in the upper San Francisco Estuary (Figure 1). As in many other estuaries, the origin of this collapse dates back many decades, and coincides with increasing anthropogenic pressure (Lotze et al. 2006). However, an apparent recent change toward exceptionally low abundance indices for pelagic fishes caused great concern among California's resource managers, who had invested hundreds of millions of dollars in habitat restoration and environmental water for the upper San Francisco Estuary over the past decade. Our objectives in this paper are to describe the extent of the problem, its management consequences, and the evolving research effort to identify the causes.

THE SAN FRANCISCO ESTUARY

The San Francisco Estuary is the largest estuary on the U.S. Pacific Coast (Figure 1). It is formed by the confluence of two major sources of water: ocean water transported into the estuary by tides and freshwater runoff from small Coast Range streams and the Sacramento-San Joaquin watershed, which drains 40% of California's surface area including the western slope of the Sierra Nevada and the Central Valley. The estuary grades from marine dominance in central and southern San Francisco bays to freshwater dominance in the Sacramento-San Joaquin Delta. Suisun and San Pablo bays are the regions of greatest salinity variation, which occurs primarily through mixing of seawater with freshwater inflow from the delta. The northern part of Suisun Bay is fringed by Suisun Marsh, the largest contiguous wetland along the Pacific coast of the western United States.

The estuary has been heavily modified since California's Gold Rush in the mid-nineteenth century (Atwater et al. 1979; Nichols et al. 1986). A timeline of some of the major alterations is provided as Table 1, reflecting the long-term habitat modifications, frequent species introductions, and changes to hydrology. Over the past 150 years, large-scale reclamation of marshes fringing south San Francisco Bay, Suisun Marsh, and the delta for agriculture, mu-

Table 1. Timeline of some of the major anthropogenic changes to the San Francisco estuary.

Event	Year(s) of Occurrence
Hydraulic gold mining	1849-1884 [a]
Channelization and wetland reclamation	1860-1930[a]
Early fish introductions	1871-1908[b]
Contra Costa Canal Diversion	1940
Shasta Dam closure	1942
Friant Dam closure	1948
Central Valley Project Tracy Pumping Plant	1951
Threadfin shad introduction	1954-1963[c]
Oroville Dam construction and closure	1957-1968
State Water Project Banks Pumping Plant	1963-1969[d]
Clifton Court Forebay	1974
Overbite clam introduction	1986
Period of rapid nonnative copepod invasions	1963-1994[e]
Bay-Delta Accord signed	1994[f]

[a] Mount (1995)
[b] This was the period of most intentional sport fish introductions including striped bass (*Morone saxatilis*), American shad (*Alosa sapidissima*), carp (*Cyprinus carpio*), and several species of centrarchidae and ictaluridae.
[c] Threadfin shad (*Dorosoma petenense*) was introduced into southern California in 1954. It was detected in upper San Francisco Estuary fishery surveys by 1963 (Turner 1966).
[d] Increasing numbers of pumps came online during this period.
[e] Increasing shipping traffic and associated ballast water releases during this period led to the establishment of seven zooplankton species in the upper San Francisco Estuary: *Oithona davisae, Limnoithona sinensis, Sinocalanus doerri, Pseudodiaptomus forbesi, Tortanus dextrilobatus, Acartiella sinensis,* and *Limnoithona tetraspina* (Kimmerer and Orsi 1996; Kimmerer 2004)
[f] The Bay Delta Accord resulted in substantial changes delta outflow and export requirements (Koehler 1995)

nicipal, and industrial uses removed 95% of historical wetlands from the estuary. Other principal changes included channelization and dredging of rivers, removal of large woody debris, substantial alteration of the flow regime, and introduction of numerous exotic organisms. As an indication of the degree of alteration by introduced species, the estuary has been called the most invaded on the planet (Cohen and Carlton 1998). Additional changes are likely in the near future: for example, the quagga mussel (*Dreissena bugensis*) was discovered in southern California in late 2006. In the likely event that the quagga mussel invades the upper San Francisco estuary, it could have effects similar to zebra mussels (*Dreissena polymorpha*), a close relative that has severely degraded other regions of the United States (Strayer et al. 1999).

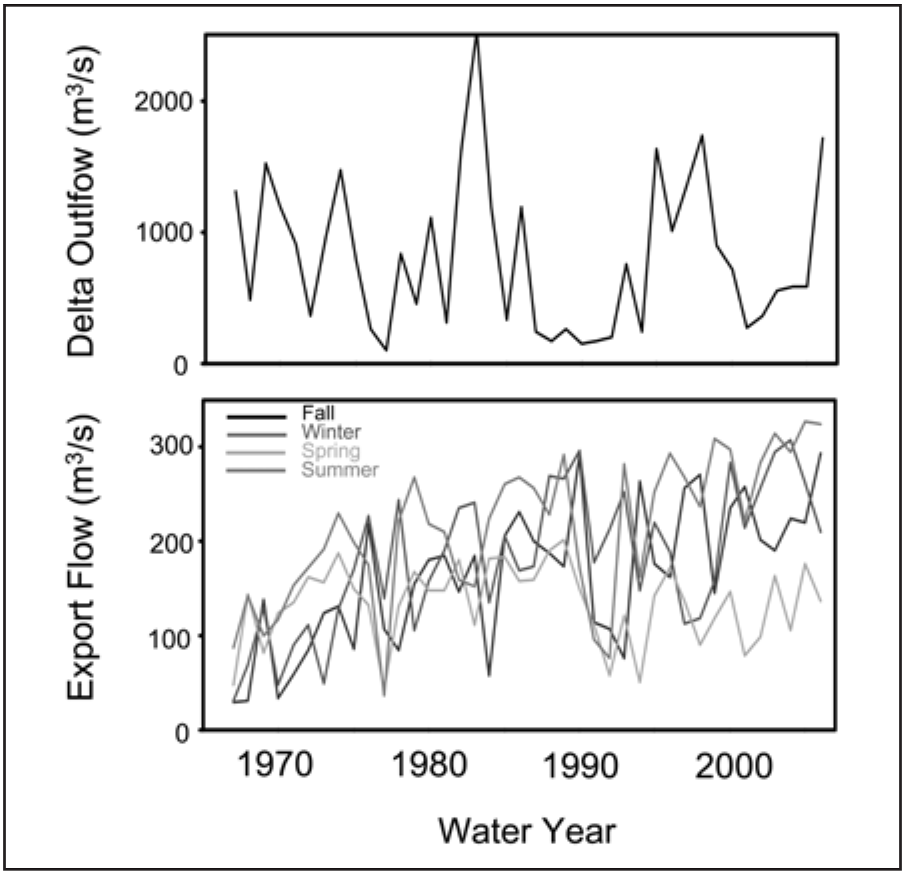
During the past 60 years, the delta has been increasingly maintained as a permanent freshwater environment through large-scale regulation and manipulation of river flows in order to maintain high quality water for agriculture, municipal, and industrial uses. Two large water diversions and two smaller diversions in the delta (Figure 1), components of the State Water Project (SWP) and federal Central Valley Project (CVP), are allowed to export up to 35%-65% of river inflows depending on the time of year (Table 2; Figure 2). More than 2,500 smaller, privately-owned water diversions are also scattered throughout the Suisun Bay/Marsh and delta to supply water for municipalities, waterfowl management, and agriculture (Herren and Kawasaki 2001). The combined net annual diversion rate from these smaller facilities is 2 km^3, comprising a substantial fraction of water use in the delta (Kimmerer 2002a).

The fish community of the San Francisco Estuary is especially rich (e.g., Matern et al. 2002; Feyrer and Healey 2003; Nobriga et al. 2005), with 87 species collected since 1993 from just two of the sampling programs—the fall midwater trawl conducted by the California Department of Fish and Game (DFG) and salvage of fishes at the screens of the SWP pumping plant (http://baydelta.water.ca.gov/). Species richness is inflated by the presence of introduced species, which comprised over 40% of the total number reported in the two surveys. As in other estuaries (e.g., Bulger et al. 1993), salinity plays a major role in the distributions of individual species and life stages; anadromous, marine-resident, estuarine, and freshwater-resident assemblages are all represented. In general, introduced species are most abundant in the freshwater-resident assemblage (Feyrer and Healey 2003; Nobriga et al. 2005)

Table 2. Summary of annual export volumes (km^3) from the four state and federal water diversions in the Sacramento-San Joaquin Delta for water years following the Bay-Delta Accord (1995-2005). The Contra Costa and Tracy diversion facilities are part of the federal Central Valley Project (CVP). The Harvey O. Banks and North Bay Aqueduct diversion facilities are part of the State Water Project (SWP).

Water diversion	1st year of operation	Average volume (range)
Contra Costa	1940	0.15 (0.12–0.23)
Tracy (CVP)	1951	3.10 (2.60–3.50)
Banks (SWP)	1968	3.60 (2.10–4.90)
North Bay Aqueduct	1988	0.05 (0.03–0.07)

Figure 2. Delta outflow (m^3/s) averaged over water years (top) and export flow (m^3/s) averaged over seasons (bottom). Water years begin on 1 October of the previous calendar year. Seasons are in 3-month increments starting in October. Export flows are the sum of diversions to the federal Central Valley Project and State Water Project pumping plants. The outflow and export data are from California Department of Water Resources (http://iep.water.ca.gov/dayflow).



THE PELAGIC ORGANISM DECLINE ("POD")

The Interagency Ecological Program (IEP), a consortium of nine state and federal agencies, has been monitoring fish populations in the San Francisco Estuary for decades, and has developed one of the longest and most comprehensive data records on estuarine fishes in the world. One of the most widely-used IEP databases is fish catch from the fall midwater trawl survey, which has been regularly conducted by DFG since 1967 (Stevens and Miller 1983; Sommer et al. 1997). This survey samples the pelagic fish assemblage in the upper estuary, the tidal freshwater and brackish portion of the system from the delta to San Pablo Bay. The most abundant resident pelagic fishes captured are two native species, delta smelt (*Hypomesus transpacificus*; Figure 3) and longfin smelt (*Spirinchus thaleichthys*), and two introduced species, striped bass (*Morone saxatilis*) and threadfin shad (*Dorosoma petenense*).

The San Francisco Estuary is physically very dynamic, so it is not surprising that annual abundance of all of these populations is extremely variable (Figure 4), and that much of this variability is associated with hydrology (Figure 2). Historically, the lowest abundance levels for the pelagic fishes typically have occurred in dry years, such as a six-year drought during 1987–1992. Consistent with this observation, several of these species show strong statistical associations with flow during their early life stages (Stevens and Miller 1983; Jassby et al. 1995; Kimmerer 2002a).

As some of the leading scientists in the IEP, we became concerned when fall midwater trawl abundance indices for these four pelagic fishes began to decline around 2000 (Figure 4). The situation deteriorated over the next several years. Abundance indices for 2002-2005 included record lows for delta smelt and young-of-the-year striped bass, and near-record lows for longfin smelt and threadfin shad. By 2004, these declines became widely recognized and discussed as a serious issue, and collectively became known as the Pelagic Organism Decline (POD).

The extreme variability in the data makes it difficult to say whether these indices are truly at unprecedented low levels. Mean catch per trawl with 95%

Figure 3. Adult delta smelt, a federally-listed species whose range overlaps with diversions that supply water for over 25 million people.

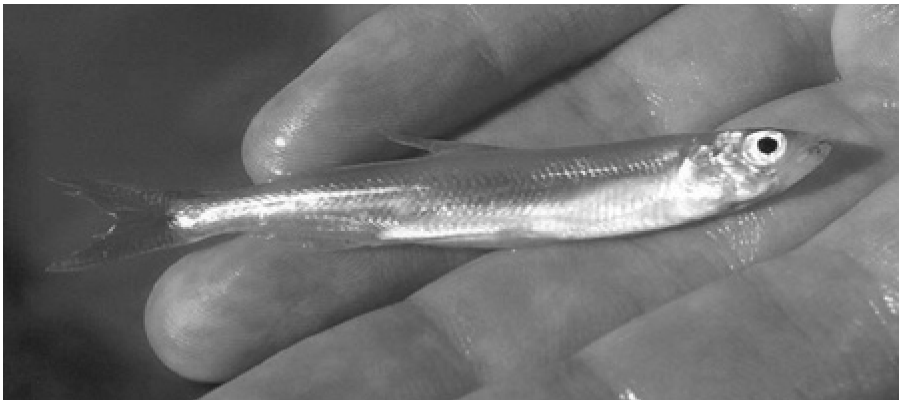
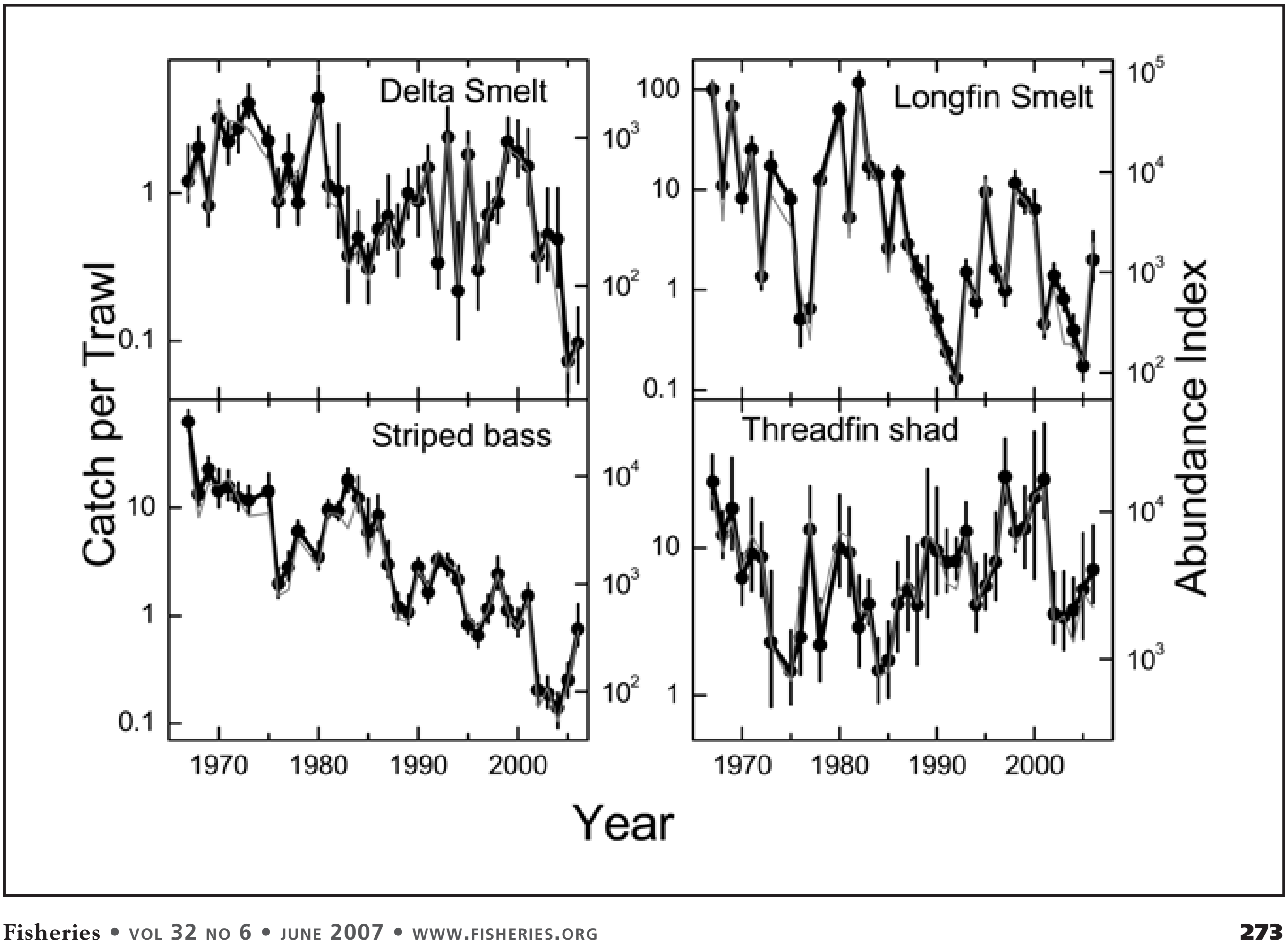
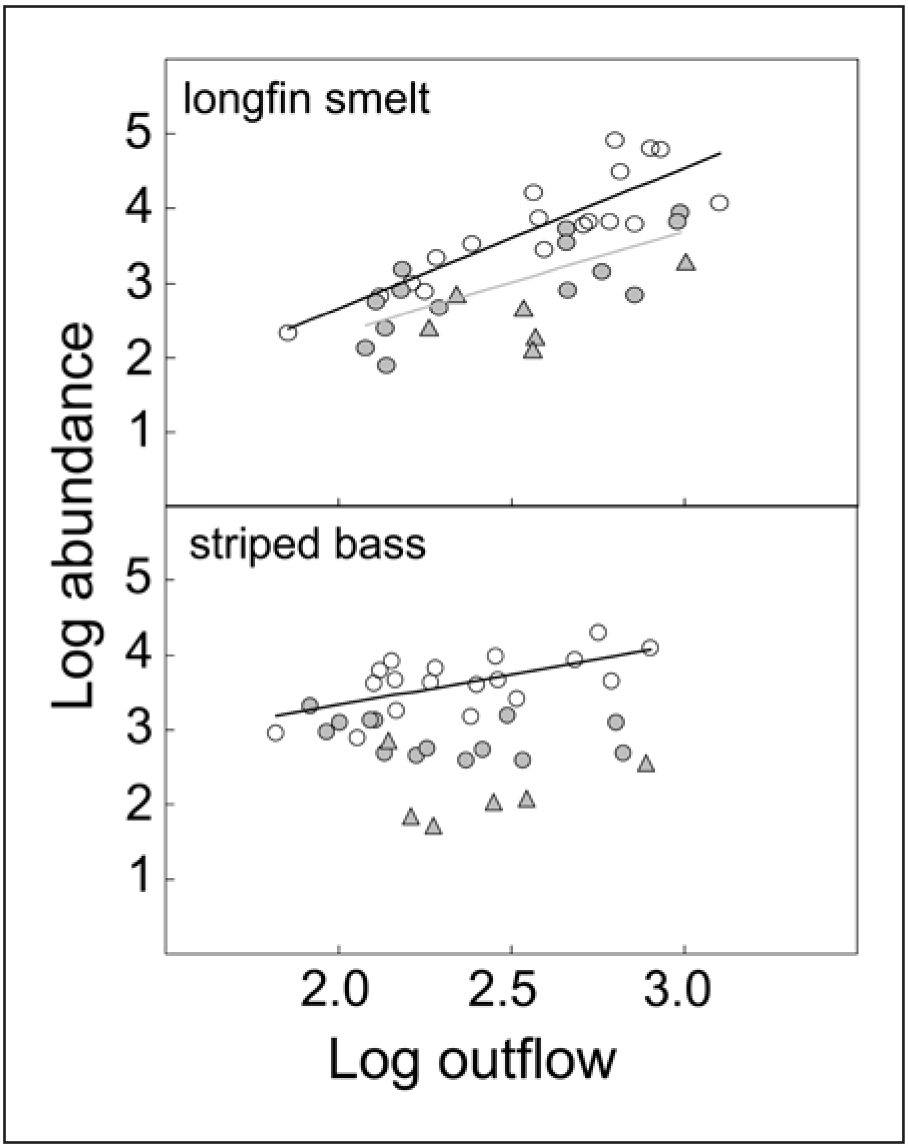


Figure 4. Trends in four pelagic fishes during 1967–2006 based on the fall midwater trawl, a DFG survey that samples the upper San Francisco estuary. Symbols with heavy lines and error bars (left y axis) show mean catch per trawl (all stations) with approximate 95% confidence intervals determined by bootstrap analysis (Kimmerer and Nobriga 2005), and the thin lines (right y-axis) show abundance indices. No sampling occurred in 1974 or 1979. Development of abundance indices from catch data is described by Stevens and Miller (1983). Note that the y-axes are on logarithmic scales.



confidence intervals developed using resampling methods indicate that the recent indices are indeed quite low, and for some species the lowest on record (Figure 4). Abundance improved somewhat for each species during 2006, but the levels remain relatively poor as compared to long-term trends. Moreover, these low abundance levels are remarkable in that winter and spring river flows into the estuary were moderate or very wet (2006) during the recent years (Figure 2), conditions that typically result in at least modest recruitment of most of the pelagic fishes. Longfin smelt is perhaps the best example of this point as the species shows a very strong relationship with delta outflow (Figure 5). The introduction of the overbite clam (*Corbula amurensis*) in 1986 and associated changes in the food web reduced the magnitude of the response of longfin smelt without altering its slope (Kimmerer 2002b). Specifically, the grazing effects from *Corbula* are thought to have resulted in a substantial decline in phytoplankton and calanoid copepods, the primary prey of early life stages of pelagic fishes. As a consequence, comparable levels of flow did not generate the expected levels of fish biomass (as indexed by abundance) after 1986. During the POD years, the abundance indices for longfin smelt deviated substantially downward from both the pre- and post-*Corbula* relationships with outflow. The situation is similar for young-of-the-year striped bass, whose historical association with outflow was also altered by *Corbula*, and apparently again during the POD years, when abundance indices were well below the original relationship with outflow. Hence, it appears that the response of these pelagic fishes to environmental conditions has fundamentally changed.

Figure 5. Log-log relationships between fall midwater trawl abundance indices and delta outflow for longfin smelt and young-of-the-year striped bass. Delta outflow values represent the mean levels (m^3/s) during January–June for longfin smelt, and during April–July for striped bass. The data are compared for pre-*Corbula* invasion years (1967–1987; white circles), post-*Corbula* invasion (1988–2000; dark circles), and during the POD years (2001–2006; triangles). Fitted lines indicate linear regression relationships that are statistically significant at the $P < 0.05$ level.



MANAGEMENT IMPLICATIONS OF THE POD

Delta smelt has been listed as a threatened species since 1993 under the federal Endangered Species Act (ESA; Bennett 2005). The geographic range of delta smelt is relatively narrow, and overlaps with the SWP and the CVP diversions (Figure 1) which supply water to over 25 million people in the state and to over 500,000 ha of farmland in the San Joaquin Valley alone, supporting a multi-billion dollar agriculture industry. Moreover, the delta smelt is primarily an annual species, so multiple age classes are not available to buffer the population against environmental catastrophes. As a consequence, for many years the species has been the focus of a wide range of protective management actions. Each year, decisions about water use costing millions of dollars are affected by the status and distribution of delta smelt. Much of the effort to improve the delta smelt population has been led by CALFED, an interagency group formed largely because of long-term declines in delta smelt and other native fishes (Koehler 1995). To help improve the status of delta smelt and other native fishes, the CALFED effort invested $335 million in over 300 habitat restoration projects through 2002, and developed a large allocation of water for use by fisheries agencies, the Environmental Water Account (CALFED 2003). Note, however, that only a portion of these actions have been focused directly towards pelagic fishes.

Among the numerous consequences of the recent low abundance indices was a March 2006 petition by environmental groups to change the federal and state listing status of delta smelt from "threatened" to "endangered" based on the argument that its extinction risk has increased. The collapse of the delta smelt population and the other pelagic fishes also resulted in a U.S. Fish and Wildlife Service ESA reconsultation (Section 7) for the operation of the SWP and CVP diversions, several lawsuits filed against the water projects, numerous front-page newspaper articles, and hearings by the U.S. Congress and the California legislature. As of the writing of this article, the SWP is under court order to cease water diversions within 60 days unless a California Endangered Species Act permit is obtained to cover incidental take of delta smelt and other listed species. The principal outcome of all this activity is substantial uncertainty about the reliability of the state's water supply.

THE POD INVESTIGATION

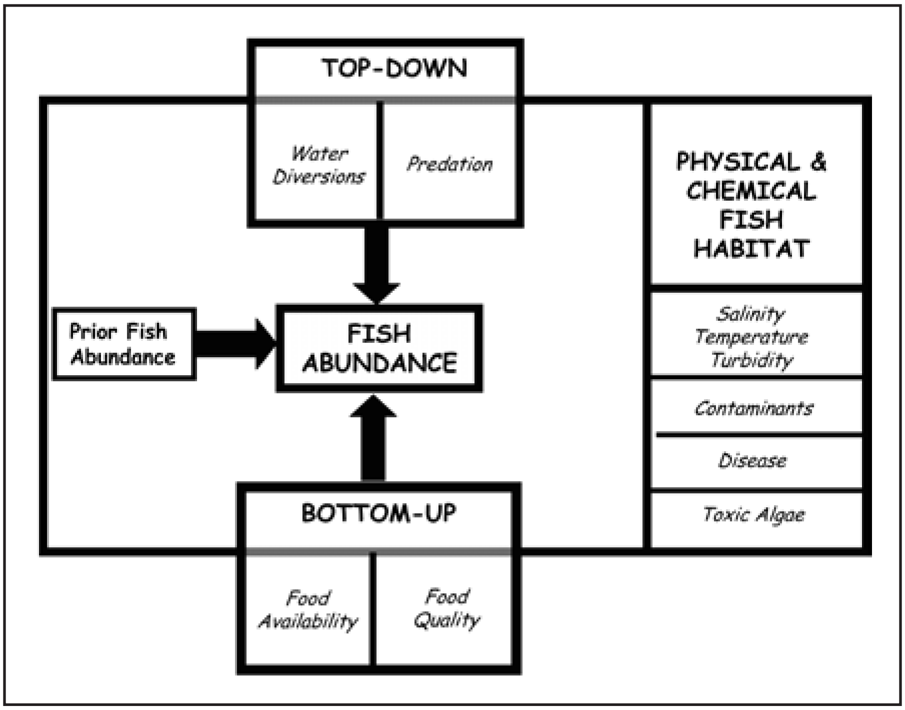
In response to the POD, the IEP formed a work team in 2005 to evaluate the potential causes of the decline (IEP 2005, 2006). The team organized an interdisciplinary, multi-agency effort including staff from DFG, California Department of Water Resources, Central Valley Regional Water Quality Control Board, U.S. Bureau of Reclamation, U.S. Environmental Protection Agency, U.S. Geological Survey, CALFED, San Francisco State University, and the University of California at Davis. A suite of 47 studies was selected based on the ability of each project to evaluate the likely mechanisms for the POD, and the feasibility of each project in terms of methods, staffing, costs, timing, and data availability. In addition to funding for regular IEP monitoring, the program's budget was augmented by $2.4 million in 2005, and $3.7 million each for 2006 and 2007 to fund the recommended research. Because of the high profile of the POD study, the team has committed to an unusually high level of outreach to agencies, the public, and the scientific community.

The POD study is organized around a relatively simple conceptual model to describe possible mechanisms by which a combination of long-term and recent changes in the ecosystem could produce the observed pelagic fish declines (Figure 6). This conceptual model is rooted in classical food web and fisheries ecology and contains four major components: (1) prior fish abundance, which posits that continued low abundance of adults leads to reduced juvenile production (i.e., stock-recruitment effects); (2) habitat, which posits that estuarine water quality variables, disease, and toxic algal blooms affect estuarine species; (3) top-down effects, which posits that predation and water project entrainment affect mortality rates; and (4) bottom-up effects, which posits that food web interactions in Suisun Bay and the west delta have limited fish abundance. For each model component, our working hypotheses are that the component was responsible for an adverse change at the time of the POD and that this change resulted in a population-level effect.

The first model component, prior adult abundance, is based on the expected influences of stock-recruitment effects. At least weak stock-recruitment effects have been reported for delta smelt (Bennett 2005), although environmental factors are thought to dominate at most abundance levels. Recent habitat changes (Model Component 2) include shifts in flow patterns, largely a consequence of upstream dam operations that have resulted in lower winter and spring inflow and higher summer inflow to the delta (Kimmerer 2002b), and fall salinity encroachment (Feyrer et al. 2007). Changes in habitat include basic water quality variables such as salinity, turbidity, and temperature. In addition, a broad suite of herbicides and insecticides are applied throughout the watershed, which can result in toxicity to fish and their prey (Werner et al. 2000; Kuivila and Moon 2004). Recent changes in pesticide applications include the increasing use of pyrethroids, which are highly toxic to aquatic organisms (Weston et al. 2004). Moreover, blooms of the toxic blue-green alga *Microcystis aeruginosa* have been observed in the delta since 1999 (Lehman et al. 2005).

Because large volumes of water are drawn from the estuary (Table 2; Figure 2), water diversions and inadvertent fish entrainment are among the best-studied top-down effects (Model Component 3) in the San Francisco Estuary. The diversions are known to entrain most species of fish in the upper estuary (Brown et al. 1996), and are of particular concern in dry years, when the distributions of young striped bass, delta smelt, and longfin smelt shift closer to the SWP and CVP water diversion facilities (Stevens et al. 1985; Sommer et al. 1997). As an indication of the magnitude of the effects, approximately 110 million fish were salvaged at the SWP screens and returned to the delta over a 15-year period (Brown et al. 1996). However, this estimate does not include other substantial effects including mortality of fish in the waterways leading to the diversion facilities, losses of larvae <20 mm FL that are not collected on fish screens, and losses at the CVP. The effects of predation are less well-understood in the estuary. A recent proliferation of aquatic weeds has provided habitat resulting in a substantial increase in

Figure 6. The basic conceptual model for the pelagic organism decline (POD).



inshore predators such as centrarchid fishes (Nobriga et al. 2005; Brown and Michniuk 2007). However, it is unclear whether the littoral communities have a major effect on the dynamics of pelagic fishes.

The last model component, bottom-up effects, also has received substantial attention in the estuary as a consequence of the extreme level of species introductions, resulting in major changes in the pelagic food web (Cohen and Carlton 1998). Phytoplankton biomass (as indexed by chlorophyll *a*) has declined over the last 4 decades, and species composition has shifted, with a sharp decline in diatom abundance and production in Suisun Bay and the western delta (Lehman 2002; Jassby et al 2002; Kimmerer 2005). Key groups of zooplankton have likewise declined in abundance and biomass, with sharpest changes among calanoid copepods, a primary prey for early life stages of pelagic fishes (Kimmerer and Orsi 1996; Kimmerer 2006).

CONCLUSIONS

Unlike the collapses of commercial fisheries for Pacific salmon (*Onchorhynchus* spp.) or Atlantic cod (*Gadus morhua*), the POD involves an entire fish assemblage, including rare native species as well as some of the most abundant introduced species in the estuary. As such, it has focused attention not only on traditional fishery management concerns such as harvest and water management, but has led to new ecological studies of water quality and several synergistic processes.

Fortunately, the San Francisco Estuary has an exceptionally long and detailed history of environmental monitoring. The collapse required an integrated research program to analyze the problem. Analysis of the historical data, coupled with an intensive program of sharply focused studies, has permitted the rapid development of a better understanding of factors that have affected fish abundance in both the short and long term. This multi-faceted approach should greatly assist in planning for aquatic resource protection from increasing human demands and other stressors such as global warming and the imminent invasion by quagga mussels.

The scope of the POD investigations has also generated high expectations for "real-time" reporting and interpretation of the results. The pressing need to reverse the decline has also led to demands for specific practical actions to remediate problems that we only understand broadly. Management actions based on incompletely integrated results run the risk of ineffectiveness (Hutchings et al. 1997). Although the available data have allowed us to generate a conceptual model of the major factors, the individual and cumulative importance of the stressors remains unclear. Hence, effective management actions to reverse the POD will require quantitative models that can integrate the effects of multiple stressors and more detailed investigations into the causes and mechanisms of the declines. Moreover, management actions will be most useful if they can be implemented using an adaptive approach that allows fisheries scientists and resource managers to learn from designed manipulations of the upper San Francisco estuary. Such actions are currently being considered as part of the approach to deal with the POD ♋.

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