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Comparative environmental tolerances of threatened delta smelt (*Hypomesus transpacificus*) and introduced wakasagi (*H. nipponensis*) in an altered California estuary

Abstract In California's Sacramento-San Joaquin estuary, environmental protection and habitat restoration efforts directed at a threatened native osmerid, the delta smelt (*Hypomesus transpacificus*), are complicated by the presence of a morphologically similar non-native congener, the wakasagi (*H. nipponensis*), transported to the estuary from upstream reservoirs. In order to better define delta smelt critical habitat and to evaluate the potential for habitat overlap by these two species, we compared the tolerances of the two species to temperature, salinity, and water velocity, environmental factors that vary spatially and temporally within the estuary. For fishes acclimated to 17°C and fresh water (0 ppt), we measured critical thermal maxima and minima, chronic upper salinity tolerance limits, and critical swimming velocities. Wakasagi had higher critical thermal maxima (29.1°C vs. 25.4°C for delta smelt), lower critical thermal minima (2.3°C vs. 7.5°C for delta smelt), higher upper salinity tolerances (26.8 ppt vs. 19.1 ppt for delta smelt), and swam faster (for 6–6.9 cm SL fish, 43.3 cm s^{-1} vs. 28.2 cm s^{-1} for delta smelt) than delta smelt. This suggests that the wide seasonal and year-to-year fluctuations in temperature, salinity, and flow typical in the estuary would not exclude wakasagi, although their eggs and larvae may be less tolerant. With respect to these factors, the native delta smelt may be at a physiological disadvantage, particularly in habitats with suboptimal environmental conditions, and may be excluded from shallow-water habitat restoration sites, which are characterized by poor circulation, low flows, and more environmentally extreme conditions. The low abundance of wakasagi in the estuary recorded to date may indicate that factors other than temperature, salinity, and flow determine wakasagi distribution.

Introduction

California's Sacramento-San Joaquin drainage and estuary is a highly altered system that is intensively managed for water storage, use, conveyance, and export. Recent substantial population declines in most of the resident and transient fishes (Herbold and Moyle 1989; Herbold et al. 1992; Bennett and Moyle 1996) and multiple listings under the federal Endangered Species Act have refocused management efforts on fisheries protection and habitat restoration. Within the estuary and lower rivers, most recovery plans have concentrated on shallow-water habitat restoration and minimizing entrainment and screen losses of fishes at the thousands of water diversions located in these areas (CALFED 1999). However, the management emphasis on protection of native fishes has been hampered by the prevalence of non-native species (more than half of the fish species in the estuary are exotic; Herbold and Moyle 1989; Meng et al. 1994), the accelerating rate of invasion (Cohen and Carlton 1998), and inadequate understanding of the basic biology and habitat requirements of many of the endemic fishes as well as those of the recent introductions.

One of the most prominent and controversial species protection efforts has focused on the delta smelt (*Hypomesus transpacificus* McAllister), a small planktivorous osmerid found only in the Sacramento-San Joaquin estuary (Moyle et al. 1992). Following a drastic population decline in the early 1980s and continuing low abundances (Bennett and Moyle 1996), the species was listed as threatened under both federal and state endangered species acts in 1993. Protection and recovery have been complicated by the presence of a morphologically similar non-native congener, the wakasagi (*H. nipponensis* McAllister). Wakasagi were introduced in 1959 as a forage fish into a number of California reservoirs, including those on tributary rivers of the Sacramento-San

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Joaquin estuary (Wales 1962). During high flow events and reservoir water releases, wakasagi are transported downstream into the estuary where they commingle and, on occasion, interbreed with delta smelt (Stanley et al. 1995; Trenham et al. 1998). The first reported collection of wakasagi in the estuary was in 1974 although misidentified fish may have been collected earlier and incorrectly reported as delta smelt (Aasen et al. 1998). Both species mature within 1 year and spawn in the late winter/early spring, and age, life history stage, and size correlations are similar in the two species (Utoh 1988; Moyle et al. 1992; Katayama and Okata 1995; and personal observations). To date, sampling within the estuary and lower reaches of tributary rivers suggests that wakasagi occur within delta smelt habitat rarely and/or in low numbers (Aasen et al. 1998; Trenham et al. 1998) although the species seems to have become more common during the past decade (P.B. Moyle, University of California, Davis, personal communication). However, the wakasagi's presence exacerbates delta smelt protection problems, for example, difficulties distinguishing the two species in the field hamper delta smelt monitoring programs (G.A. Aasen, California Department of Fish and Game, personal communication). Wakasagi may also negatively affect delta smelt through competition for food and space, predation on larval delta smelt, and hybridization. Further, it is possible that planned habitat restorations specifically directed at enhancing delta smelt populations, such as creating shallow-water spawning and rearing habitat, may inadvertently favor non-native fishes, including wakasagi.

While the distribution, abundance, basic natural history, and genetics of the two species have been reasonably well documented (Utoh 1988; Moyle et al. 1992; Katayama and Okata 1995; Stanley et al. 1995; Aasen et al. 1998; Trenham et al. 1998) and, for delta smelt, swimming behavior and performance (Swanson et al. 1998), their environmental tolerances are poorly understood. In order to better define delta smelt critical habitat and environmental requirements, and to evaluate the potential of wakasagi for habitat overlap with the threatened native species, we compared the tolerances of delta smelt and wakasagi to three environmental factors, temperature, salinity and water velocity, that vary seasonally and geographically within the Sacramento-San Joaquin estuary and lower rivers.

Materials and methods

Fish collection and care

Delta smelt were collected from the Sacramento-San Joaquin estuary with a 3-mm-mesh purse seine using methods described in Swanson et al. (1996). Wakasagi were collected from Folsom Reservoir, a low elevation impoundment in the American River watershed, using similar methods. At collection, all fish were postmetamorphic (>2.5 cm SL). The two species were maintained in separate flow-through circular tanks (diameter: 1 m, volume: 200 l) supplied with non-chlorinated, air-equilibrated, temperature-controlled well water. The water had a pH of 7.9, total alkalinity

of 320 mg l^{-1}, hardness of 290 mg l^{-1}, and specific conductivity of 585 µmho cm^{-1}. For the first 2–8 days following collection, water temperature was maintained at 1–3°C below collection temperature and salinity at 2–8 ppt by the continuous addition of a concentrated NaCl solution (Leslie solar salt, 99.6% pure, Cargill Salt). During this period, the fish were treated on alternate days with an antibacterial solution (nitrofurazone, 2–10 mg l^{-1}) and an antifungal solution (formaldehyde, 0.1 ml l^{-1}) for 2–6 days. After the treatment was completed, salinity was decreased to 0 ppt and the temperature adjusted at 1°C day^{-1} to the experimental temperature, 17°C. All fish were maintained under a simulated natural photoperiod regime (38°N latitude) and fed a combination of live *Artemia* nauplii (Argent Chemical Laboratories) and a commercial diet (BioKyowa, Inc.). The fish were allowed to acclimate to these conditions for a minimum of 2 weeks before use in the experiments. Any single fish was used only once in each of the experiments. After the experiments, species identifications based on morphologic characters (chromatophore patterns, Sweetnam 1995) and collection location were confirmed by genetic analyses of subsamples using methods described in May (1996).

Temperature tolerance

Temperature tolerance limits were measured as critical thermal maxima (CT$_{max}$) and minima (CT$_{min}$) using the loss of equilibrium endpoint (Becker and Genoway 1979). The experimental apparatus consisted of six cylindrical plexiglass flow-through chambers (chamber volume: 1.5 l) equipped with flow-dispersing baffle plates and individual temperature probes (YSI 401, YSI Instruments, Inc.). Well water was supplied to the chambers from a temperature-controlled recirculating system (total volume: 120 l) before and during the experiment and from a separate flow-through system maintained at the acclimation temperature during the post-test recovery period. A single fish was placed in each chamber and allowed 5–13 h pre-experimental recovery from handling at the acclimation temperature. Temperature was then either increased 6°C h^{-1} or decreased 5–6°C h^{-1} and each chamber's temperature and each fish's behavior were monitored regularly. When an individual's tolerance limit was reached, the chamber temperature was recorded and then rapidly returned to 17°C by switching the water supply for that chamber to the flow-through water system. For delta smelt, chamber (post-experimental) salinity was also increased (4–10 ppt) to mitigate physiological stress responses such as osmotic imbalance (Wedemeyer 1972; Mazik et al. 1991). Controls (*n*=6 for delta smelt, *n*=16 for wakasagi) were handled identically but were not subjected to the temperature change. After all the fish had reached their endpoints and subsequently recovered, each was removed from its chamber, anesthetized with tricaine methanesulfonate (70 mg l^{-1}; MS222, Sigma Chemical Co.), weighed (wet weight, g) and measured (standard length, SL, cm, wakasagi only).

Salinity tolerance

Salinity tolerance was measured as the maximum salinity the fish could survive for ≥12 h following a gradual salinity increase. Individual fish were placed in 10-l, circular polyethylene containers filled with 5 l of fresh well water (0 ppt salinity). Each container was equipped with an air diffuser stone for mixing and aeration, and was partially submerged in a temperature-controlled water bath. Salinity was increased by 2 ppt every 12 h for delta smelt and every 24 h for wakasagi by the addition of a salt solution made from fresh water and a concentrated NaCl solution. During each salinity change 75–95% of the water in the containers was replaced and excess water overflowed through screened holes located 10 cm below the top of the container. In control containers (4 or 5 of 10 containers in the first sets of experiments with each species), 75–95% of the water was replaced with fresh water at the same times. Salinity was measured using a YSI Model 33 S-C-T meter (Yellow Springs Instruments, Inc.) or a salinity refractometer (American Optical). Fish were fed live *Artemia* nauplii, and

uneaten food and fecal material were removed daily. Fish behavior and status were monitored throughout the experiment and, when a fish died, it was removed, weighed and measured, and the container salinity was recorded. The upper salinity tolerance limit was defined as the salinity from the experimental interval immediately preceding death.

Maximum swimming velocities

Tolerance to water velocity was measured in terms of critical swimming velocity, U_{crit}, the maximum velocity a fish can sustain for some prescribed period of time (Brett 1964). Maximum swimming velocities were measured in a variable speed, recirculating water flume (total volume: 9 l). A single fish was placed in the swimming chamber (diameter: 9.1 cm, length: 24 cm) and allowed a minimum of 50 min to recover from handling at a water velocity of 2–6 cm s^{-1} (Swanson et al. 1998). Velocity in the flume was then increased by 3–4 cm s^{-1} every 10 min until the fish fatigued. Fatigue was indicated by failure of the fish to hold its position in the chamber, repeated impingements on the downstream screen, and inability to reorient to the current and swim following impingement. U_{crit} (cm s^{-1}) was calculated from Brett (1964):

$$U_{crit}=U_i+[U_{ii}\times(T_i/T_{ii})]$$

where U_i=highest velocity maintained for the prescribed time (cm s^{-1}), U_{ii}_velocity increment (=3–4 cm s^{-1}), T_i=time elapsed at fatigue velocity, T_{ii}_prescribed swimming period (=10 min). After the experiment, the fish was removed from the chamber, anesthetized with MS222, weighed, and measured.

Statistical methods

All data are expressed as mean±SD. Comparisons among species and size classes (size class increment, 1.0 cm SL, U_{crit} results only) were made using analyses of variance (ANOVA) and two-tailed t-tests. Effects of fish size on U_{crit} were also examined using regression analysis. Statistical procedures were conducted using Sigmastat software.

Results

Temperature and salinity tolerance

Wakasagi CT_{max} was significantly higher ($P<0.01$, $F=28.998$, $df=1,22$) and CT_{min} was significantly lower ($P<0.001$, $F=110.465$, $df=1,28$) than similarly measured values for delta smelt (Table 1). Wakasagi also tolerated significantly higher salinities than delta smelt ($P<0.001$, $F=38.048$, $df=1,17$; Table 1).
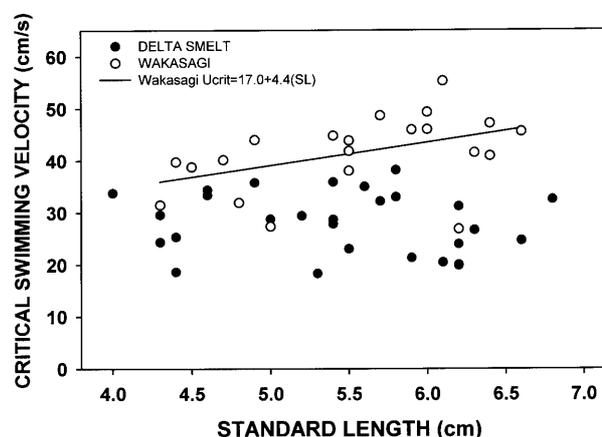
Maximum swimming velocities

Wakasagi achieved and sustained significantly higher swimming velocities than delta smelt (4–4.9 cm SL, $P<0.05$, $F=7.399$, $df=1,12$; 5–5.9 cm SL, $P<0.001$, $F=19.792$, $df=1,18$; 6–6.9 cm SL, $P<0.001$, $F=26.46$, $df=1,13$) (Fig. 1). For delta smelt, size did not affect swimming performance; mean U_{crit} was 28.1±5.9 cm s^{-1} (data for 4–6.8 cm SL fish in 17°C from Swanson et al. 1998). In contrast, U_{crit} increased significantly with increases in size for wakasagi ($P<0.05$, $F=4.586$, $df=1,20$). Large wakasagi (6–6.9 cm SL, $n=8$) swam almost twice

Table 1 Mean (±SD) critical thermal maxima (CT_{max}, °C) and minima (CT_{min}, °C) and upper salinity tolerance limits (SAL_{max}, ppt) of delta smelt and wakasagi. Fish sizes (range, cm SL) are below and sample sizes are in parentheses

	Delta smelt	Wakasagi
CT_{max}	25.4±1.7	29.1±1.3
	3.8–4.7[a]	3.8–4.5
	(16)	(8)
CT_{min}	7.5±1.2	2.3±0.9
	3.9–4.8[a]	4.0–4.7
	(23)	(7)
SAL_{max}	19.1±2.1	26.8±3.0
	5.5–6.4	5.4–6.5
	(14)	(5)

[a] Delta smelt SL calculated from the regression: SL (cm)= 3.214+[1.455×weight (g)], $n=56$, $r^2=0.902$, data from Swanson et al. (1998)

Fig. 1 Critical swimming velocities (cm s^{-1}) of delta smelt and wakasagi. Least squares *regression line* (wakasagi data only) shows significant relationship with fish standard length. Delta smelt critical swimming velocities showed no significant relationship with length. Delta smelt data are from Swanson et al. (1998)

as fast (43.3±8.7 cm s^{-1}) as large delta smelt (24.9±5.0 cm s^{-1}, $n=8$).

Discussion

Results of these experiments indicate that delta smelt and wakasagi are eurythermal, euryhaline, and generally competent swimmers, all characteristics that would be expected for estuarine planktivores. However, the non-native wakasagi tolerated greater extremes in temperature, higher salinities, and could swim faster than delta smelt. Therefore, the wide year-to-year and seasonal fluctuations in temperature, salinity, and flow typical of the Sacramento-San Joaquin estuary should not exclude post-metamorphic wakasagi (although their eggs and larvae may be more sensitive to these conditions, and other abiotic or biotic factors may preclude successful invasion and establishment). With respect to these variables, wakasagi are physiologically capable of occupying all

Table 2 Comparison of critical thermal maxima (°C) of fishes from the Sacramento San Joaquin estuary that are sympatric with the delta smelt

Species (life history stage)	Acclimation temperature	CT$_{max}$[a]	Source
Delta smelt	17	25	This study
Wakasagi	17	29	This study
Splittail (young-of-the-year)	17	31	Young and Cech (1996)
Chinook salmon (smolt)	16.5	26–27	C. Swanson, K. Marine, and J.J. Cech Jr, unpublished work
Inland silverside (subadult/adult)	17	31	C. Swanson and J.J. Cech Jr, unpublished work

[a] All CT$_{max}$ were measured using the apparatus, methods, and heating rate (6°C h^{-1}) described in Methods

habitats that are environmentally accessible to delta smelt (i.e., complete habitat overlap). Further, in sub-optimal temperature, salinity, or flow conditions near its tolerance limits, the native delta smelt may be at an physiological disadvantage relative to the more tolerant exotic.

Temperature

While fishes rarely encounter temperature fluctuations as rapid as those employed in these experiments, temperature tolerance limits measured using the critical thermal method are useful for comparing the relative thermal resistance of different species (Becker and Genoway 1979; Currie et al. 1998). Additionally, most researchers consider critical thermal limits ecologically defensible indices that are correlated with thermal preferences (Jobling 1981; Tsuchida 1995) and distributions and abundances of fishes in thermally variable environments (Matthews 1987; Cech et al. 1990; Castleberry and Cech 1992).

Water temperatures within the Sacramento-San Joaquin estuary are largely dependent on season, inflowing river temperatures (which may be influenced by habitat alteration and water management operations upstream), weather, topography (e.g., shallow dead-end sloughs vs. deep channels), and thermal inputs from heated effluents (e.g., electric power plant discharges). While estuary temperatures below 6°C are rare, in some areas, including those thought to be important delta smelt habitat, temperatures frequently can reach 24–26°C (Moyle et al. 1986; Pacific Gas and Electric 1992). Results of these experiments suggest that the non-native wakasagi would be capable of exploiting thermally extreme habitats within the system, for example restored shallow-water habitat that is characterized by low flows and poor circulation, that delta smelt could not. In addition, effluent temperatures of the two power plants located in the estuary are frequently 5–10°C warmer than intake water temperatures and can exceed 27°C (Finlayson and Stevens 1977; Pacific Gas and Electric 1992), temperature increases and levels that would likely be lethal for delta smelt but not wakasagi.

Compared to a number of other ecologically similar and sympatric native and non-native species, delta smelt are relatively sensitive to acute temperature increases (Table 2). In addition to the wakasagi, the native splittail

(*Pogonichthys macrolepidotus*) and recently introduced (mid-1970s) inland silverside (*Menidia beryllina*) both tolerated substantially higher mean temperatures. Even chinook salmon (*Oncorhynchus tshawytscha*) smolts acclimated to a slightly lower temperature had a slightly higher mean CT$_{max}$ than delta smelt. These comparisons suggest that delta smelt may be at disproportionate risk from further temperature increases within their habitat that might result from extreme climate conditions, anthropogenic activities, and/or global warming.

Salinity

Upper salinity tolerances measured in this study represent the maximum osmoregulatory capacity for salinity increase of the fish. Unlike the critical thermal limits experiments, the gradual salinity increase allowed the fish to physiologically adapt to the changing osmoregulatory demands (Evans 1993). At salinities above the tolerance limit, death probably resulted from osmotic imbalance. Assuming that delta smelt and wakasagi internal osmotic concentrations resemble those of other freshwater and estuarine teleosts (equivalent to 9–12 ppt salinity; Moyle and Cech 1996), the results indicate that wakasagi and, to a lesser extent, delta smelt can tolerate somewhat hyperosmotic environments. The salinity tolerance of the delta smelt was comparable to that of similarly sized young-of-the-year splittail (Young and Cech 1996).

In our laboratory, delta smelt and wakasagi both tolerated higher salinities than those that either species has been recorded to inhabit within the Sacramento-San Joaquin estuary and San Francisco Bay system (delta smelt: 0–14 ppt, Moyle et al. 1992; wakasagi: 0–10 ppt, Aasen et al. 1998). This suggests that, in California, neither species appears to exploit environments in which the salinity approaches their tolerance limits. Therefore, the greater euryhalinity of the non-native wakasagi may not necessarily impart any particular habitat-breadth advantage within this estuarine system. However, the lower salinity tolerance of the delta smelt should normally prevent it from traversing oceanic (marine) waters to reach nearby estuaries. In fact, the delta smelt is the only species that is completely dependent on the Sacramento-San Joaquin estuary (Herbold and Moyle 1989; Moyle et al. 1992). In contrast, wakasagi seem capable of invading the more saline San Francisco Bay and even coastal Pa-

Table 3 Comparison of critical swimming velocities (cm s^{-1}) of fishes from the Sacramento San Joaquin estuary that are sympatric with the delta smelt

Species	Temperature (°C)	SL (cm)	U_{crit} (cm s^{-1})	Source
Delta smelt	17	4–4.9	29	This study
		5–5.9	29	
		6–6.9	25	
Wakasagi	17	4–4.9	38	This study
		5–5.9	42	
		6–6.9	43	
Inland silverside	17	4–5	32	P.S. Young, C. Swanson, and J.J. Cech Jr, unpublished work
Splittail	17	3–5	20–30	Young and Cech (1996)
Chinook salmon	17	4–5	36	P.S. Young, C. Swanson, and J.J. Cech Jr, unpublished work

cific ocean waters under some conditions. In Japan, some wakasagi populations are reported to be anadromous, with juvenile and subadult fish spending at least part of their lives in coastal waters before migrating upstream to spawn (Utoh 1988).

Salinity is probably the most important abiotic environmental factor determining delta smelt distribution within the estuary, particularly during the summer and fall rearing season. Juvenile and subadult delta smelt apparently move with tidal flows and are most abundant in waters with salinities of 1–2 ppt regardless of tidal cycle or geographic location (Moyle et al. 1992; Swanson et al. 1996). Wakasagi are too rare within the estuary to determine distributional tendencies precisely, although Aasen et al. (1998) reported their distribution to be similar to that of delta smelt. Additional study of wakasagi salinity preferences would be useful to evaluate the degree to which this fish may tend to occupy similar areas in the estuary as the native delta smelt.

Swimming ability

Use of critical swimming velocities to assess tolerance to water flows must be interpreted cautiously. U_{crit} evaluates the physiological capacity of the fish for sustained, high-intensity activity. It is useful for comparisons among species and different environmental conditions (Videler and Wardle 1991), and to predict the ability of the fish to escape localized, high velocity flows such as those associated with water diversions. For example, Rohlwing et al. (1998) reported that European smelt (*Osmerus eperlanus*) infected with a muscle parasite (*Pseudoterranova decipiens*, Nematoda) that reduced their swimming performance (Sprengel and Luechtenberg 1991) experienced more frequent contact with a power plant intake screen than uninfected conspecifics. However, U_{crit} provides little information on preferred or optimum swimming velocities, or on other potential behavioral responses to flowing water such as avoidance. For small pelagic planktivores like delta smelt and wakasagi, behavior rather than ability may be more im-

portant in defining their responses and tolerances to high water velocities (Swanson et al. 1998).

Delta smelt and wakasagi achieved and sustained swimming velocities that were generally comparable to or, for the delta smelt, somewhat lower than U_{crit} values measured for other small, sympatric fishes acclimated to similar temperatures (Table 3). Between the two congeners, wakasagi consistently swam faster and the discrepancy in swimming performance increased with fish size. Swimming performance of delta smelt was size-independent, unlike the pattern of higher U_{crit} with increases in size found in wakasagi and most other fishes (Webb 1977; Videler and Wardle 1991). Thus, large wakasagi had substantially greater swimming capacity than large delta smelt. While delta smelt spend most of their lives in slightly brackish waters, maturing adults (>5 cm SL; Mager 1996) migrate upstream into freshwater areas of the estuary to spawn (Moyle et al. 1992). Most of the more than 2000 water diversions that are located within the Sacramento-San Joaquin estuary (Nichols et al. 1986; Jassby et al. 1995) are concentrated in these upstream areas where salinities are lower. Therefore, by virtue of proximity, spawning adults (and larvae, delta smelt eggs are adhesive, Mager 1996) are particularly vulnerable to lethal entrainment, a human activity thought to be a significant contributor to the species' decline (US Fish and Wildlife Service 1994; Bennett and Moyle 1996). The relatively poor swimming ability of these delta smelt suggests that, compared to wakasagi, this species would be at greater risk from entrainment.

Implications for wakasagi invasion and delta smelt protection

Why are wakasagi still rare in the Sacramento-San Joaquin estuary? The system is highly invasible and the rate at which exotic species are becoming established is increasing (Cohen and Carlton 1998). It is geologically young with a depauperate fish assemblage, it is heavily modified and already highly invaded, and many of the native fishes, like delta smelt, are severely depleted

(Bennett and Moyle 1996; Moyle and Light 1996a, 1996b). Yet, despite their broad environmental tolerances and ability to spawn sympatrically with delta smelt (as evidenced by reports of delta smelt-wakasagi hybrids; Trenham et al. 1998), wakasagi apparently have not established large breeding populations in the estuary. One possible explanation is that wakasagi eggs and larvae are less tolerant of environmental conditions typical of the estuary; for many fishes, the early life stages are the most sensitive of the life cycle (von Westernhagen 1988). Alternatively, appropriate spawning habitat may not be available in the estuary. Japanese wakasagi spawn in coastal and tributary streams of lakes and reservoirs (Utoh 1988; Katayama and Okata 1995). In California, wakasagi transported through the estuary and subsequently exported more than 160 km south in water project canals have become established in the San Luis reservoir, rather than in the estuary. Exported delta smelt are not found in the reservoir (Hess et al. 1995).

For the native delta smelt, deleterious effects of previous habitat alteration on delta smelt populations (e.g., freshwater diversion from the system, Moyle et al. 1992; Bennett and Moyle 1996), combined with increasing rates of invasion (Cohen and Carlton 1998), may have pushed this vulnerable species to its limits. Unlike wakasagi that can re-invade the estuary from source populations upstream, catastrophic population declines of the already depleted delta smelt in this heavily modified and stressed system could be irreversible (Moyle and Light 1996a). Further habitat modifications, particularly those that exacerbate extreme environmental conditions, such as seasonal high temperatures in poorly circulated shallow waters, could inadvertently favor non-native species like the wakasagi and trigger an ecological time bomb that results in abiotic and/or biotic conditions that exceed the capacity of the delta smelt to persist within this system.

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