

Environmental Tolerances and Requirements of Splittail

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Abstract.—The range of splittail *Pogonichthys macrolepidotus* has decreased to less than a third of its original range due to loss or alteration of habitats. We measured the critical thermal minima (CT_{min}) and maxima (CT_{max}), critical dissolved oxygen minima (CDO_{min}), critical salinity maxima (CS_{max}), salinity endurance, and critical swimming velocity (U_{crit}) for age-0 (0.1–4.0 g), age-1 (10–48 g), and immature age-2 (72–201 g) splittails to assist in effective water and habitat management and restoration of this species. Neither thermal acclimation nor fish weight affected the CT_{min} (6.5–7.3°C), but CT_{max} (29–33°C) of fish acclimated at 17 and 20°C were higher than CT_{max} (21–22°C) of fish acclimated at 12°C. Mean CDO_{min} values were low (0.6–1.3 mg O₂/L) for all age-groups, although immature age-2 fish acclimated at 12°C had a lower CDO_{min} than any group acclimated at 17°C. Mean CS_{max} (20–29‰) did not vary with acclimation temperature, but increased with increasing weight for fish acclimated at 17°C. Mean time to loss of equilibrium in all age-groups generally decreased as salinity increased and was generally lower for age-0 fish than for those of other age-groups. Mean absolute U_{crit} (19.5–66.3 cm/s) increased with standard length (SL), but relative U_{crit} (3.4–6.8 body lengths/s) decreased with SL for fish acclimated at 17°C. Increases in acclimation temperature by 3°C for small age-0 fish and 5°C for age-2 fish increased absolute U_{crit} by 11 and 25 cm/s, respectively. We conclude that age-0, age-1, and especially age-2 fish are eurythermal, euryhaline, and tolerant of low DO levels and strong water currents. This general hardiness probably permits splittails to exist in harsh estuarine habitats such as dead-end sloughs. A lack of sufficient flooded vegetation for spawning and rearing, narrower environmental tolerances of other life stages (i.e., eggs, larvae, and adult spawners), or biotic factors (e.g., predation, competition) may be limiting splittail abundance and distribution.

The splittail *Pogonichthys macrolepidotus* (Ayres 1854) is the only surviving member of its genus and one of the most ancestral North American cyprinids endemic to the Sacramento–San Joaquin drainage of California (Moyle 1976). It once was one of the most abundant estuarine species in the Sacramento–San Joaquin estuary and supported a small hook-and-line fishery (Caywood 1974). It was once widely distributed in lakes and rivers throughout California's central valley (Rutter 1908) but disappeared from much of its native range because of loss or alteration of lowland habitats following dam construction, water diversion, and agricultural development. The species is now largely restricted to the Sacramento–San Joaquin estuary (Herbold et al. 1992; Moyle and Yoshiyama 1992) except during upstream spawning migrations (Moyle et al. 1995). Access to many spawning areas or upstream habitats is blocked by dams on the large rivers, and because splittails are seemingly incapable of negotiating existing fishways, they are restricted to water below the dams (Moyle et al. 1995). In 1994, the splittail had reportedly declined 62% over the previous 13-year period (Meng and Moyle 1995). Because of the

rapid population decline, the splittail was proposed for listing as a threatened species under the Endangered Species Act by the United States Fish and Wildlife Service (USFWS) in 1993, but listing was deferred in 1995 (Moyle et al. 1995). Although an unusual reproductive success occurred in 1995 that was associated with an exceptionally wet spring (P. Moyle, University of California, Davis, personal communication), the future of this species is far from secure. Continued decline in freshwater inflows into the estuary will eventually change both salinity and temperature levels, possibly decrease dissolved oxygen levels, and alter water flow velocities. In response to the decreased freshwater inflow, estuarine habitat will shift upstream into channelized areas that may not have the appropriate habitats for splittail. Such an upstream shift may make eggs, larvae, and young splittails vulnerable to export from the system via the large diversion pumps in the south delta (Meng and Moyle 1995). In addition, electrical power generating plants discharge warm water into the estuary. In spite of information on the splittail's age and growth, condition, reproductive biology, year-class strength, and distribution (Caywood 1974; Daniels and Moyle 1983; Meng and Moyle 1995), the species' environmental requirements

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and tolerances are relatively unknown. Therefore, the potential effects of these environmental changes on splittail abundance are unclear.

Our study was designed to define the splittail's environmental requirements and tolerances to assist in effective water and habitat management and restoration of this species. We addressed swimming performance (associated with effects of flow and fishway negotiations) along with limits of tolerance to environmental conditions (associated with habitat requirements). Specifically, the study aimed to determine the critical thermal minima (CT_{min}) and maxima (CT_{max}), critical dissolved oxygen minima (CDO_{min}), critical salinity maxima (CS_{max}), and critical swimming velocity (U_{crit}) of age-0, age-1, and immature age-2 splittails.

Methods

Fish collection and maintenance.—Classification of splittails by age-group was based on fish wet weight and standard length (SL) according to Daniels and Moyle (1983). Small (0.1–0.5 g; 2–3 cm SL) age-0 fish were collected at Georgiana Slough (in the northeastern part of the estuary); large age-0 (1–4 g; 4–7 cm), age-1 (10–42 g; 9–13 cm), and immature age-2 (80–200 g; 18–23 cm) fish were collected from Suisun Marsh (in the western part of the estuary) and at the state and federal pumping and fish salvage facilities in the southern part of the estuary. Fish were transported to laboratories at the University of California, Davis, in insulated coolers or fiberglass tanks with aerated water at ambient (collection) temperature; rock salt (NaCl) was added (4‰) to minimize osmotic stress on the fish. Age-0 fish were collected during spring and summer at 17–20°C and 0–1‰ salinity and were acclimated to 17 or 20°C; most age-1 and age-2 fish were collected during the fall, winter, and spring at 9–18°C and 0–5‰ salinity and were acclimated to 12 or 17°C. A few age-1 and age-2 fish, collected in late spring at 19–21°C and 1–4‰ salinity, were originally acclimated at 20°C but were later reacclimated to 17°C because the number of fish was smaller than the required sample size for the experiments. Fish were held in aerated flow-through aquaria (age-0 fish) or fiberglass tanks (age-1 and age-2 fish) with air-equilibrated well water. Thermal acclimation was conducted at 1°C/d from the collection temperature. Age-0 fish were fed *Artemia* sp. nauplii and fish crumbles; age-1 and age-2 fish were fed trout pellets. Fish were subjected to simulated natural photoperiod.

Tolerance Tests

Determinations of thermal, dissolved oxygen (DO), and salinity tolerance limits were conducted following modifications to the methods of Cox (1974) and Becker and Genoway (1979). Loss of equilibrium was used as the end point for the tolerance tests. Fish were maintained at acclimation temperature for at least 7 d and were not fed for 24 h before the start of an experiment. Fish were placed in test vessels or containers with flow-through water at acclimation temperature 15–18 h before the start of experiments to minimize transfer-related stress. Fish were weighed after each experiment and measured (SL) after swimming experiments. Some of the fish used for one test were also used for, at most, two different tests after at least 1 week of recovery after each test. None of the fish were used twice for the same experiment. In all tests, each fish was isolated. In the temperature and DO tolerance apparatus, fish were not visually isolated, but there was no indication that the behavior of one fish affected the behavior of others. Furthermore, there was a random placement of controls among the test fish.

Temperature.—Fish were held in individual Plexiglas vessels of a flow-through design (Cech et al. 1979) and were subjected to decreasing (0.08°C/min for CT_{min}) or increasing (0.1°C/min for CT_{max}) temperatures, starting from the acclimation temperature. Control fish were subjected to the same protocol but without the temperature changes. Inflow water was continuously aerated to ensure a high level of DO. Volumes of test vessels were 1.4 L (age-0 and age-1 fish) or 4.0 L (age-2 fish), and mean test water flow rates were 170 or 250 mL/min, respectively. Each vessel was equipped with a calibrated Yellow Springs Instruments thermister probe (YSI model 401), and temperature was monitored with a YSI telethermometer (model 44TD) every 10 min and at the end point. Immediately after recording an end point temperature, test water inflow to that vessel was stopped, and an acclimation temperature inflow was started.

Final thermal preferences and optimum temperatures for growth were estimated from CT_{max} data with regressions modified from Jobling (1981): final thermal preference = $(CT_{max} - 16.43)/0.66$; optimum temperature for growth = $(CT_{max} - 13.81)/0.76$. The Jobling (1981) equations were based on 49 fish species in 16 families. Estimates derived from these equations were only applied to fish acclimated to the higher temperature because

these equations were based on the upper incipient lethal temperatures (UILT) and CT_{max} for fish acclimated to the highest temperature.

Dissolved oxygen.—Fish were held at ambient temperature in a temperature-controlled water bath in individual Plexiglas test vessels of a flow-through design similar (age 0) or identical (age 1 and age 2) to those used in the thermal tolerance tests. Volumes of test vessels were 0.8 L (age 0), 1.4 L (age 1) or 4.0 L (age 2), and the mean test water flow rates were 140, 170 or 250 mL/min, respectively. A 30-cm polyethylene tubing (1.67-mm internal diameter) was inserted into each of the test vessels for water sampling. Fish were subjected to decreasing levels of DO by passing inflowing water through a polyvinyl chloride stripping column (Cech et al. 1979) in which a counterflow of nitrogen gas (regulated through a gas flowmeter) altered DO content. Dissolved oxygen partial pressure (PO_2) in the inflow column was decreased at 1 torr/min (1 torr = 133.3 Pa; 14 torr $PO_2 \approx 1$ mg O_2/L) from approximately 150 torr PO_2 (approximating air saturation levels) to about 40 torr PO_2 . At this point, the rate of decrease was slowed to 0.5 torr/min until the end point was reached. The PO_2 was monitored (Cameron Instrument Co., model 100 DO meter) every 10 min and at the end point. Immediately after a fish's end point was recorded, test water inflow to that vessel was stopped, and an aerated water inflow was begun. Control fish were subjected to the same protocol but without changes in DO. No fish acclimated at 20°C and no fish less than 1 g were available for the DO tolerance tests.

Salinity.—Splittails were held in 10-L plastic buckets (age 0 and age 1) or 20-L glass aquaria (age 2) at the acclimation temperature with constant aeration in a shallow temperature-controlled water bath. Screened holes in the walls of each bucket and a standpipe in each aquarium maintained the 5-L (bucket) or 15-L (aquarium) volume. Each container was equipped with a plastic top to prevent fish from escaping. Experimental fish were subjected to increasing levels of salinity (3–4‰/h), starting at 0‰, by means of a rock salt (NaCl, the dominant solute in seawater) brine drip system. Salinity was monitored (YSI model 33 salinity-conductivity-temperature meter calibrated with a Radiometer CTM10 chloride titrator) every 20 min and at the end point. Control fish were subjected to the same protocol but with a freshwater drip system. Immediately after an end point, container salinity was recorded, the brine drip sys-

tem to that container was stopped, and a freshwater inflow was started.

Salinity Endurance Tests

Salinity endurance experiments were conducted in the same system as the salinity tolerance tests. Fish were not fed for 24 h before or during the experiments. After 15–18 h habituation, all freshwater inflows were stopped and a concentrated rock salt brine solution was slowly (5–6 min) introduced above the constantly bubbling airstone (for rapid mixing) until the desired salinity level (12 [age 0 only], 14 [age 0 only], 16, 20, 24, or 28‰) was reached. Behavior and status of fish were constantly monitored. For fish with end points greater than 24 h, at least two-thirds of the water volume was replaced by water of the same test salinity every 24 h. Immediately after the end point, the time to loss of equilibrium (TLE) was recorded and a freshwater flow was started. If TLE was not observed within 120 h, the experiment was ended. No fish acclimated at 20°C were available for salinity endurance experiments.

Swimming Performance

Splittail critical swimming velocities were determined at acclimation temperature with recirculating-water flumes (Brett 1964) incorporating a variable-speed motor. Flumes were 9 L (age 0 and age 1) and 102 L (age 2) in volume, partly immersed in a temperature-controlled water bath and calibrated with a digital Marsh-McBirney (model 201D) portable water current meter. Each fish was placed in the swimming chamber and after 1 h habituation with water flow at 3 cm/s (age 0 and age 1) or 5 cm/s (age 2), critical swimming velocity (U_{crit}) was measured by step increases of 10 cm/s in water velocity at 10-min intervals, starting at 10 cm/s, until the fish was fatigued (Beamish 1978). A fish was considered fatigued when it was impinged three times at the downstream end of the chamber. Absolute U_{crit} (cm/s) was calculated (Brett 1964) as follows: $U_{crit} = U_i + (10 \text{ cm/s})(T_i/10 \text{ min})$, where U_i = highest velocity (cm/s) maintained for 10 min and T_i = time (min) elapsed at fatigue velocity. Relative U_{crit} (body length/s) was calculated by dividing absolute U_{crit} by SL (cm). Tail beat frequencies (TBF) were measured for two age-2 fish by counting the number of tail beats over a 1-min period.

Statistical Analyses

Analyses of variance (ANOVA), Bonferroni's tests, and Dunn's nonparametric tests were con-

TABLE 1.—Mean critical thermal minima (CT_{min}) and maxima (CT_{max}), estimated upper limits of safe temperature (ULST), final temperature preferences, and thermal growth optima for age-0, age-1, and age-2 splittails acclimated to different temperatures. There were no significant differences in CT_{min} values; within an age-group, an asterisk denotes a significantly higher CT_{max} value ($P < 0.05$).

Age-group	Acclimation temperature (°C)	N	CT_{min} (°C)		CT_{max} (°C)		Temperature (°C) of:			
			Mean	(SE)	N	Mean	(SE)	ULST	Final preference	Growth optimum
Small age 0	20	8	7.0	(0.15)	10	32.0	(0.33)*	27	24	24
	17	9	6.5	(0.10)	8	30.8	(0.37)	26	22	22
Large age 0	20	5	7.3	(0.14)	6	33.0	(0.21)*	28	25	25
	17	4	6.8	(0.10)	4	30.0	(0.41)	25	21	21
Age 1	17	6	7.0	(0.29)	5	28.9	(0.34)*	24	19	20
	12				4	20.5	(0.88)	16		
Age 2	17	6	7.3	(0.12)	5	29.0	(0.21)*	24	19	20
	12	7	7.0	(0.18)	7	21.9	(1.20)	17		

ducted to quantitatively compare values among different tests (e.g., thermal tolerance tests at different acclimation temperatures for different age-groups). Student's *t*-tests or Mann-Whitney non-parametric tests were used to compare data for fish acclimated at two different temperatures. Regression analyses were applied to show relationships between fish weight and CT_{max} , CS_{max} , and U_{crit} , and between TLE and salinity. Aptness for the linear or the polynomial regression model was based on the least mean squared residual and probability values. All of the above statistical analyses were conducted with SIGMASTAT software. Analyses of covariance were conducted with SYSTAT software to determine significant interaction effects of acclimation temperature and fish weight on CT_{min} , CT_{max} , CS_{max} , TLE, and U_{crit} . Statistical differences were considered significant at $P < 0.05$.

Results

Tolerance Tests

Temperature.—As the temperature approached the critical minimum or maximum, most of the splittails were observed darting or turning around (presumably an escape behavior), increasing ventilatory frequency, and gasping (mostly in CT_{max} measurements). Posttest recovery (restoration of equilibrium) took 1–10 min. Four small and one large age-0 fish did not recover from the test; data from these fish were not included in the statistical analyses. None of the control fish died.

Whereas fish weight and acclimation history had no effect on CT_{min} (6.5–7.3°C), they had important influences on CT_{max} (Table 1). Mean CT_{max} increased with acclimation temperature, decreased with \log_{10} (weight), and had a combined effect ex-

pressed as follows: $CT_{max} = 12.017 + 1.036(\text{acclimation temperature}) - 4.405 \cdot \log_{10}(\text{wet weight}) + 0.241(\text{acclimation temperature} \times \log_{10}[\text{wet weight}])$; $r^2 = 0.924$; $P < 0.001$; $N = 49$. For the small and large age-0 fish, an increase of 3°C in acclimation temperature resulted in significant 1.2 and 3.0°C increases in CT_{max} , respectively. For age-1 and age-2 fish, a 5°C increase in acclimation temperature resulted in significant 8 and 7°C increases, respectively. Table 1 also provides the estimated temperatures for final thermal preferences and growth optima of different age-groups of splittail (data derived from equations in Jobling 1981). Based on the safety factor of 5°C (Bridges 1971), upper safe thermal limits were estimated from CT_{max} (rounded to the nearest °C) for different age-groups acclimated at different temperatures (Table 1).

Dissolved oxygen.—As DO level decreased to the end point, splittails increased activity (turning, swimming, or darting around), then decreased activity but increased ventilatory frequency and gasping. Posttest recovery generally took 3 min or less; none of the fish died.

Mean CDO_{min} values were low (9–18 torr PO_2 or 0.6–1.3 mg O_2/L) for all age-groups (Figure 1). They were not affected by weight (1–187 g) or by the interaction of weight with acclimation temperature (12 and 17°C), but age-2 fish acclimated at 12°C had a significantly lower mean CDO_{min} (9 torr PO_2 or 0.6 mg O_2/L) than any age-group acclimated at 17°C (15–18 torr PO_2 or 1.1–1.3 mg O_2/L).

Salinity.—As salinity level increased to end points, splittails increased activity (turning, swimming, darting around, or trying to jump out of the container), then decreased activity before losing

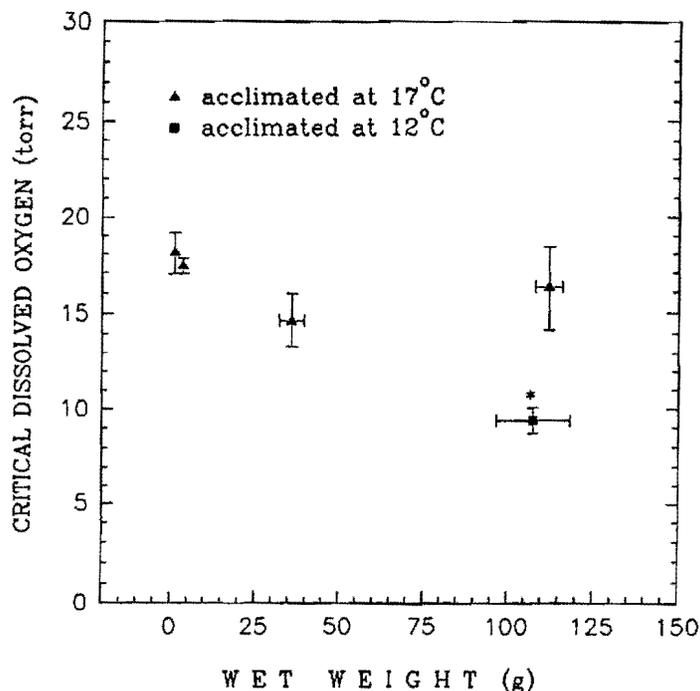


FIGURE 1.—Mean (\pm SE) critical dissolved oxygen minima (torr) of age-2 splittails acclimated at 12 and 17°C, in relation to mean (\pm SE) weight. Sample sizes range from 4 to 10. Asterisk indicates a critical oxygen pressure significantly lower than all others ($P < 0.05$).

equilibrium. Posttest recovery generally took 6 min or less. Six small and three large age-0 fish died during the experiment, and data from these fish were not included in the statistical analyses. None of the control fish died.

Although fish were acclimated to freshwater, mean CS_{max} values were high (20–29‰; Figure 2). Mean CS_{max} (22–27‰) for fish acclimated to 17°C increased with an increase in fish weight (0.2–192 g; $r^2 = 0.40$, $P < 0.001$; $N = 27$) and was described by the following: $CS_{max} = 21.89 + 0.05(\text{wet weight})$. Increase in acclimation temperature did not significantly affect the CS_{max} for age-0 and age-2 fish. This could not be tested for age-1 fish, which were acclimated to only one temperature. There was no interaction effect of acclimation temperature and weight on the CS_{max} .

Salinity Endurance Test

Splittails at high salinity levels (24 and 28‰) behaved similarly to those in salinity tolerance tests, whereas those at lower salinity levels increased their activity less before the end point. Most fish acclimated to 17°C recovered from the experiment in 1 min or less, whereas fish acclimated to 12°C generally took 5 min to recover.

Control, age-0 fish at 12 and 14‰, and age-1 and age-2 fish at 16‰ maintained their equilibria and survived for the duration of the experiment.

Mean time to loss of equilibrium (TLE) in all age-groups generally decreased as salinity increased (Figure 3, regression equations in Table 2). Mean TLE at 16 and 20‰ were significantly lower for age-0 fish than for those of other age-groups. From the regressions (Table 2), salinity tolerance levels were estimated for different TLE periods for different splittail age-groups (Table 3). The age-0 fish had the lowest CS_{max} and also the lowest estimated salinity tolerance levels for different TLE periods. Interaction of weight (0.9–121 g) and acclimation temperature (12 and 17°C) had no significant effect on the TLE.

Swimming Performance

Splittails in all age-groups swam well in the water flume, although most age-1 and age-2 fish (especially at 12°C) were generally inactive in the holding tanks. We observed that tail beat frequency (TBF) increased as water current increased, although it was quantified for only a few individuals. For example, at 17°C, two age-2 fish (99 and 100 g wet weight, 19.1 and 18.7 cm SL, respectively)

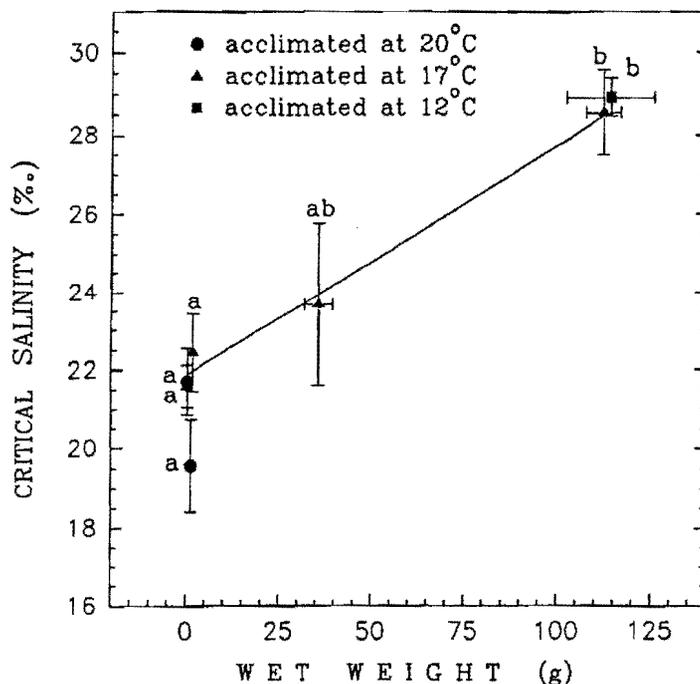


FIGURE 2.—Mean (\pm SE) critical salinity maxima of splittails in relation to mean (\pm SE) weight at different acclimation temperatures. Regression line is plotted for fish acclimated at 17°C only; $N = 4-8$; symbols lacking a common letter are significantly different ($P < 0.05$).

increased TBF from 1.18 Hz at 10 cm/s to 3.22 Hz at 70 cm/s. Interestingly, 9 of 28 small age-0 fish, and 2 of 21 large age-0 fish held onto the upstream screen with their mouths when the water current was greater than 30 cm/s. Some of the age-1 and age-2 fish also attempted this behavior when the current was greater than 40 cm/s, but they were unsuccessful because of the fine screen mesh. None of the fish died during the experiments.

Mean U_{crit} was significantly affected by both standard length and water temperature (small age-0 and age-2 fish only). Mean absolute U_{crit} (19.5–66.3 cm/s) increased ($r^2 = 0.74$, $P < 0.001$; $N = 43$) with standard length (SL, 2.3–20.7 cm) for fish acclimated at 17°C (Figure 4) and was described by the following: $U_{crit} = 14.441 + 2.604(\text{SL})$. However, mean relative U_{crit} (3.4–6.8 body lengths/s) decreased ($r^2 = 0.41$, $P < 0.001$; $N = 43$) with standard length (SL, 2.3–20.7 cm) (Figure 5) and was described by the following: $U_{crit} = 7.296 - 0.223(\text{SL})$. A 3°C increase in acclimation temperature in small age-0 fish significantly increased the absolute U_{crit} by 11 cm/s, but not the relative U_{crit} . A 5°C increase in acclimation temperature in age-2 fish significantly increased

the absolute U_{crit} by 25 cm/s and the relative U_{crit} by 1.26 body lengths/s.

Discussion

Overall, our studies show that splittails are highly tolerant of thermal changes, salinity increases, dissolved oxygen decreases, and strong water currents. All of these measures compare well with those reported for other native and introduced California cyprinids; the splittail salinity tolerances were noteworthy.

Temperature

The thermal tolerance of fish is generally estimated either as the incipient lethal temperature (ILT) or as critical thermal maxima or minima (CTM). For the splittail, thermal tolerance was determined by measuring CTM, which involves a rapid increase or decrease in temperature, with loss of equilibrium as the end point. The CTM is considered the ecological lethal index because animals in nature may encounter such temperatures as acute fluctuations above their tolerance limits (Hutchison 1976). This method is particularly useful in assessing temperature tolerances of fishes subjected to periodic thermal discharge (Bridges

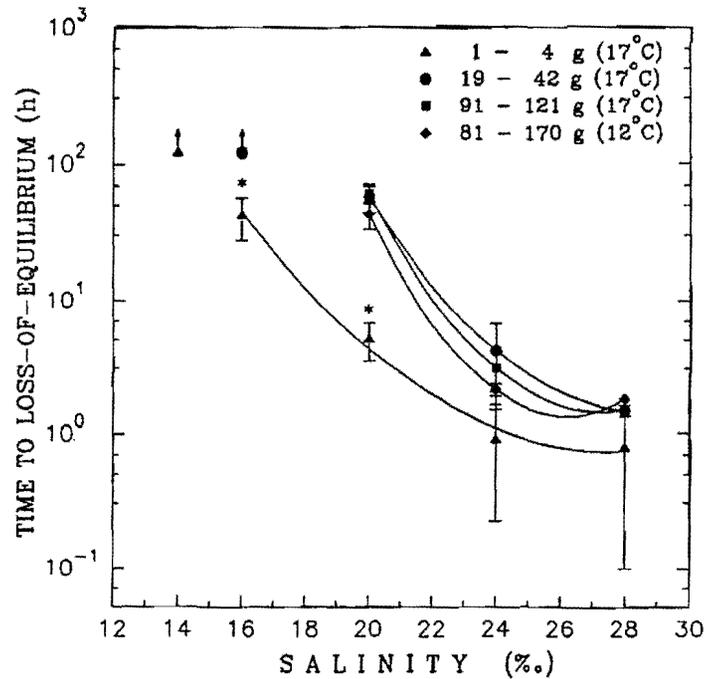


FIGURE 3.—Mean (\pm SE) times to loss of equilibrium (TLE, \log_{10} scale) in relation to salinity level in different age-groups of splittail. Sample sizes range from three to four; asterisk indicates a significantly lower TLE value at the same salinity level ($P < 0.05$); arrow indicates survival for more than 120 h.

1971; Jobling 1981) and is also more economical with respect to materials and human effort (Hutchison 1976; Kilgour and McCauley 1986). In the ILT method, fish are abruptly transferred to different temperatures; this procedure not only subjects the fish to heat or cold shock but also incorporates the effects of transfer stress. Although at some temperatures the thermal shock and transfer stress might be sublethal, the combined effect is believed to compound the effect of starvation and quickly lead to death (Itzkowitz et al. 1983).

The thermal limit values obtained here are the most conservative estimate of CTM because the rate of increase ($0.1^{\circ}\text{C}/\text{min}$) or decrease ($0.08^{\circ}\text{C}/\text{min}$) precludes thermal acclimation. If the rate is too slow (e.g., $1^{\circ}\text{C}/\text{h}$) a significant partial thermal acclimation would occur; if the rate is too fast

(e.g., $1^{\circ}\text{C}/\text{min}$) the lag between bath temperature and fish body temperature would lengthen. Both rates would result in decreased CT_{min} values or increased CT_{max} values (Kilgour and McCauley 1986). Furthermore, Becker and Genoway (1979) observed that at the rate of $0.1^{\circ}\text{C}/\text{min}$, the CT_{max} values nearly equal the upper ILT values.

The splittail's high thermal tolerance (mean $\text{CT}_{\text{max}} \approx 9\text{--}14^{\circ}\text{C}$ above acclimation temperatures) fits well within some of the widely distributed freshwater California cyprinids, which have CT_{max} $6\text{--}20^{\circ}\text{C}$ above acclimation temperature (e.g., Sacramento blackfish *Orthodon microlepidotus*, California roach *Hesperoleucus symmetricus*, hitch *Lavinia exilicauda*, and Sacramento squawfish *Ptychocheilus grandis* [Knight 1985]; fathead minnow *Pimephales promelas*, Klamath tui

TABLE 2.—Regression equations showing relationship between salinity (S , ‰) and time to loss of equilibrium (TLE, h) for different splittail age-groups.

Age-group	Acclimation temperature	N	Equation	R^2	P
Age 0	17°C	15	$\log_{10}(\text{TLE}) = 13.720 - 1.087(S) + 0.021(S^2)$	0.836	<0.001
Age 1	17°C	11	$\log_{10}(\text{TLE}) = 5.946 - 0.210(S) - 0.0001(S^2)$	0.999	<0.001
Age 2	17°C	12	$\log_{10}(\text{TLE}) = 9.473 - 0.520(S) + 0.007(S^2)$	0.971	<0.001
	12°C	10	$\log_{10}(\text{TLE}) = 10.346 - 0.613(S) + 0.009(S^2)$	0.944	<0.001

TABLE 3.—Mean critical salinity maxima ($CS_{max} \pm SEM$) and estimated salinity tolerance levels (%) for different time to loss of equilibrium (TLE) periods of different splittail age-groups. Salinity tolerance levels were estimated based on TLE regression equations from Table 2.

Criterion	Age 0	Age 1	Age 2	Age 2
Acclimation temperature (°C)	17	17	17	12
CS_{max} (‰): mean (SE)	22.4 (1.0)	23.7 (2.1)	27.4 (1.2)	28.8 (0.5)
Salinity (‰) for				
6-h TLE	20	24	24	23
12-h TLE	19	23	24	22
24-h TLE	18	22	22	21
48-h TLE	17	21	21	20
72-h TLE	16	20	20	20
96-h TLE	16	19	19	19

chub *Gila bicolor bicolor*, speckled dace *Rhinichthys osculus*, and blue chub *Gila coerulea* [Castleberry and Cech 1992]). As estuarine fish, splittails are subject to thermal fluctuations associated with tidal cycles as well as diel and seasonal fluctuations (Moyle 1976; Moyle et al. 1982; Daniels and Moyle 1983). Their high thermal tolerance might partly explain their survival in dead-end slough and marsh environments.

Of concern, however, are thermal discharges

from electrical power generating plants such as those in the Sacramento–San Joaquin Delta, which sometimes discharge water 13–15°C warmer than the intake water (Finlayson and Stevens 1977; Pacific Gas and Electric 1992). In the vicinity of the power plants, splittails make up 4–12% of the total fish composition (Pacific Gas and Electric 1992), and larvae are common (Wang 1986). If a warm-water discharge suddenly increases the ambient temperature by 9–14°C, all splittails in the vicinity will die if they do not swim away. Although adult fish might be able to escape, young fish probably cannot. In addition, even if CT_{max} is not exceeded, temperature just below the CT_{max} may cause structural anomalies (review by Reynolds and Casterlin 1980) that would increase the vulnerability of young splittails to predation (Elliot 1981).

Power plant operations during winter might pose a greater problem. Our results showed that in spring, summer, and fall, a 12°C increase would be lethal, but in winter, an increase of only 9°C would be lethal. However, in some cases, lower ambient temperature may mitigate impact. For example, Bridges (1971) found that juvenile spot *Leiostomus xanthurus* were not killed by the increased temperature from power plant discharges

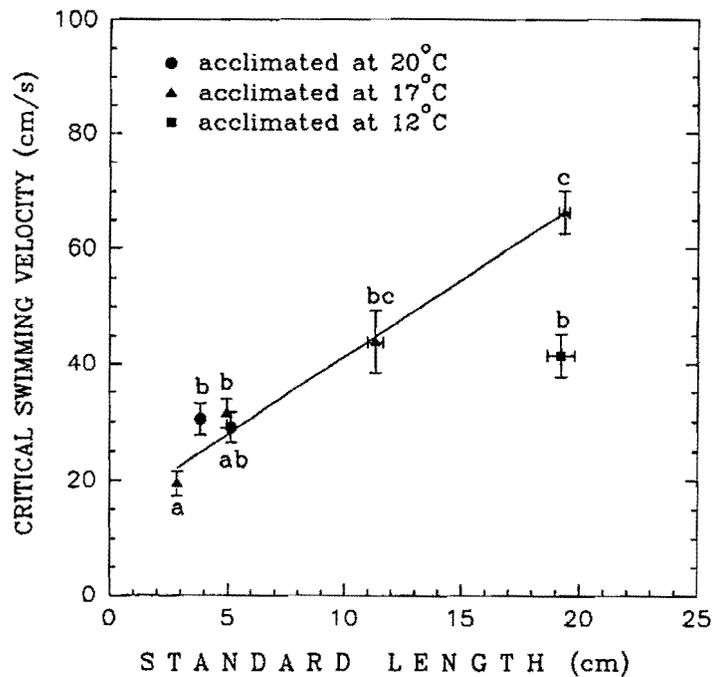


FIGURE 4.—Mean ($\pm SE$) absolute critical swimming velocities of splittails in relation to mean ($\pm SE$) standard lengths. Regression line is plotted for fish acclimated at 17°C only; $N = 8-14$; velocities lacking a common letter are significantly different ($P < 0.05$).

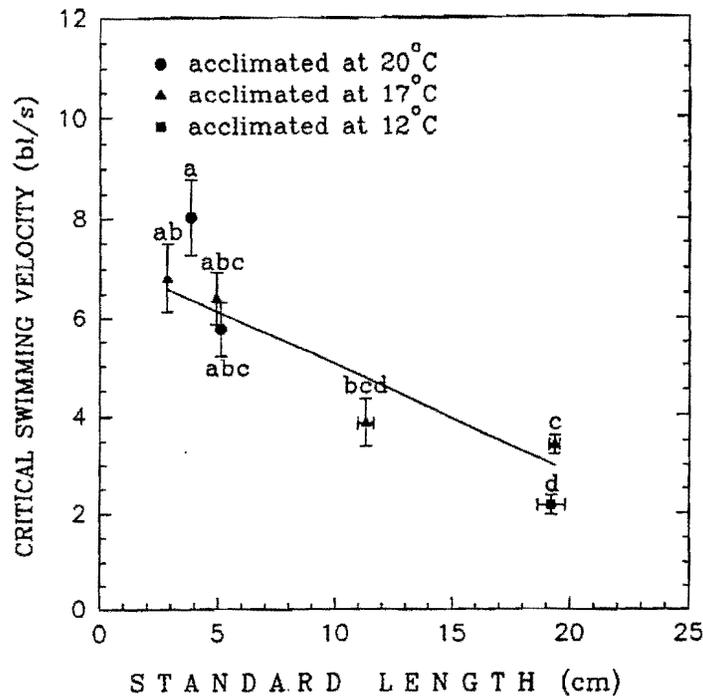


FIGURE 5.—Mean (\pm SE) relative critical swimming velocities of splittails in relation to mean (\pm SE) standard lengths; bl is body lengths. Regression line is plotted for fish acclimated at 17°C only; $N = 8-14$; velocities lacking a common letter are significantly different at $P < 0.05$.

during winter because the ambient water temperature was lower and maximum temperatures never reached CT_{max} .

An additional potential for mortality can occur during winter if power plant operations are shut down. Many fish kills in winter are associated with such shutdowns because exposure to cold after acclimation to warm water is lethal to temperate fishes (Stauffer 1980). If the water temperature in the vicinity of power plants suddenly drops to 7°C due to power plant shutdown, it could be lethal to the splittails in the area because, regardless of thermal acclimation, the lower thermal limit of any splittail age-group tested is 7°C.

Although acclimation history had no influence on the lower thermal limit of the splittail, it had significant effect on the upper tolerance limit. Increase in thermal acclimation is accompanied by an increase in upper thermal limit, a response common in other cyprinids (e.g., Sacramento blackfish, California roach, hitch, Sacramento squawfish [Knight 1985]; fathead minnow, Klamath tui chub, speckled dace, blue chub [Castleberry and Cech 1992]) and many other fish species (Jobling 1981). In addition to thermal acclimation, fish size

(weight) also had an influence on the splittail upper thermal limit but not on the lower thermal limit. As a splittail grows, its upper thermal limit decreases. Because splittails are spawned in flooded vegetation during late spring and early summer and age-0 fish habitats have peak water temperatures that are presumably warmer, these young fish might be more adapted to higher temperatures than age-1 and age-2 fish.

Seasonal upper safe thermal limits for splittail can be inferred from the estimated upper safe thermal limits of different splittail age-groups acclimated at different temperatures (Table 1). For example, summer upper safe thermal limit would be based on 20°C acclimation, spring-fall upper limit would be based on 17°C acclimation, and winter upper limit based on 12°C acclimation. Until a more detailed study is conducted of the thermal effects on survival, growth, reproduction, and other splittail dynamics, these upper safe thermal limits can serve as the bases for estimating seasonal upper thermal requirements of age-0, age-1, and age-2 fish.

Estimated final temperature preferences and thermal growth optima based on Jobling (1981)

equations were all higher than the acclimation temperatures and very much lower than the upper limits (Table 1). Under certain conditions, physiological processes may have different thermal optima and these may result in changes in the preferred temperature (Crawshaw 1977). For example, Brett (1971) observed that sockeye salmon *Oncorhynchus nerka* normally select 15°C, a temperature at which active metabolism, sustained swimming speed, and cardiac work are maximal. With unlimited food rations, young salmon sustain optimum growth at this temperature. However, if rations are limited, growth optima occur at a lower temperature (Brett et al. 1969; Brett and Higgs 1970), a pattern also found in bluegill *Lepomis macrochirus* (Stuntz and Magnuson 1976), western mosquitofish *Gambusia affinis* (Wurtsbaugh and Cech 1983), and lake trout *Salvelinus namaycush* (Mac 1985). Other nonthermal influences (e.g., season, photoperiod, age, sex, maturity, light intensity, nutrition, health, salinity, disease, pollutants, biotic interactions) can also affect thermal preference (reviews by Reynolds and Casterlin 1980 and Stauffer 1980).

Dissolved Oxygen

California cyprinids that live in warm lentic waters or intermittent, slow-flowing streams are tolerant of low DO levels (0.2–1.5 mg O₂/L; e.g., goldfish *Carassius auratus* [Fry and Hart 1948]; fathead minnow, Klamath tui chub, speckled dace, blue chub [Castleberry and Cech 1992]). The splittail's preferred habitats (slow-moving sections of rivers and sloughs) can have very low DO levels. For example, in Buckley Cove (located in the section of the San Joaquin River known as the Stockton Ship Channel), the DO level can drop to 0.4 mg O₂/L at midday, 92.3 cm below the surface (California Department of Water Resources 1994). Fish generally avoid hypoxic conditions by moving away from them. However, when food abundance is low, fish (especially benthic foragers) readily forage in hypoxic waters (Rahel and Nutzman 1994). Splittails are benthic foragers (Caywood 1974; Daniels and Moyle 1983) and their short-term low DO tolerance may increase survival by permitting foraging for invertebrates with low DO requirements or foraging in hypoxic benthic areas at times of low food availability. This low DO tolerance is enhanced during winter because the lower acclimation temperature results in lower CDO_{min} values (Figure 1). This is probably because at colder temperatures, fish have lower oxygen consumption rates (review by Fry 1970) and

thus can tolerate lower DO levels in the water. Davis (1975) explained that at lower temperature, fish blood oxygen dissociation curves, which relate blood percentage saturation to the PO₂, typically shift to the left (indicating a lower oxygen requirement to fully saturate the blood), decreasing the PO₂ threshold for hypoxia responses.

We cautioned against using the CDO_{min} for establishing DO criteria. These values should be considered as extreme end points, approximating lethal limits. Complete loss of equilibrium by fish (end point) indicates the point that experimental conditions become detrimental to the fish. At this point, the fish becomes disoriented and physically unable to escape the harmful conditions which could lead to its death (Becker and Genoway 1979). It has been recommended that studies on the effects of low DO levels on growth be conducted to determine DO minimum criteria (Tarzwell 1958; Doudoroff and Shumway 1967, 1970; Davis 1975; International Joint Commission 1979; U.S. Environmental Protection Agency 1986).

Salinity

Cyprinids are typically stenohaline freshwater fishes, although a few California species have been reported to tolerate salinity levels of 12–16‰ (e.g., common carp *Cyprinus carpio* [Geddes 1979], goldfish [Threader and Houston 1983], Mojave tui chub *Gila bicolor mohavensis* [McClanahan et al. 1986]). However, the splittail has an unusually high salinity tolerance even when acclimated to freshwater. Native California cyprinids that have refuges in streams are rarely found at salinities greater than 3‰ (P. Moyle, personal communication). It is not known if the remaining splittails represent a more euryhaline genetic subset of the splittail populations that once had a much broader geographic range in California. It is suspected that the salinity tolerance of this species comes from having to survive in alkaline lakes on the valley floor during long periods of drought (P. Moyle, personal communication). Splittails are now mostly found in the estuary, living in environments where salinity fluctuates due to flooding, drought, and tidal and seasonal cycles. For example, salinity levels in Suisun Marsh (where most of the age-1 and age-2 fish were collected) seasonally range over 0–17‰ (Baracco 1980) and can increase 1‰/h over a 6-h tidal change (L. Millet, California Department of Water Resources, personal communication). Splittails reportedly have been captured in waters with salinities as high as 18‰ (Meng and Moyle 1995).

As a splittail grows, its salinity tolerance increases with age (Figures 2, 3). Many other fish species have been found to have better salinity tolerances at more advanced stages of development (e.g., channel catfish *Ictalurus punctatus* [Allen and Avault 1970], roach *Rutilus rutilus* [Schofer 1979], sharp-tooth catfish *Clarias gariepinus* [Britz and Hecht 1989], chinook salmon *Oncorhynchus tshawytscha* [Clarke et al. 1981], rainbow trout *Oncorhynchus mykiss* [Johnsson and Clarke 1988]). This phenomenon is probably related to body surface : volume ratio (Parry 1960), to functional development of the osmoregulatory system (Hoar 1988), or to ontogenic changes in hemoglobin (Perez and Maclean 1976). Given the great differences in size between age-0 to age-2 splittails, the reduced body surface : volume ratio in larger fish may significantly contribute to its increased salinity tolerance. In salmonid species, growth is accompanied by functional development of osmoregulatory organs such as gills, kidneys, urinary bladder, and intestine and development of osmoregulatory hormones (reviewed by Hoar 1988). We did not examine the development of splittail osmoregulatory organs that presumably accompanied their growth. The development of these organs may not be as dramatic as those in anadromous salmonids. In the Mozambique tilapia *Oreochromis mosambicus*, a second hemoglobin appears at 47 d that has a higher affinity for O₂ at higher osmotic pressure and temperature and may aid in tolerance to higher salinity and temperature (Perez and Maclean 1976). This may not be the case for the splittail, because splittail growth is not accompanied by an increase in its upper thermal tolerance.

In nature, adult splittails migrate upstream into freshwater to spawn in flooded vegetation. The larvae remain in shallow, weedy areas, and age-0 fish (probably larger than our age-0 fish) migrate downstream with river flows into shallow, productive waters of the estuary (Wang 1986; Meng and Moyle 1995). Results of the salinity endurance tests confirmed that our age-0 fish were much more sensitive to increased salinity levels than the age-1 and age-2 fish. The longer-term TLE results (Table 3) are recommended for determining splittail salinity requirements.

Swimming Performance

Splittail swimming performance is consistent with the species' streamlined body form and deeply forked caudal fin (hence the common name) and might be aided by an unusual station-holding be-

havior. Aleev (1969) analyzed the relationship between maximum body height (H) and standard length (SL), and the ratio (Y) of anterior- H distance (axial distance from the anterior end of the fish to the level of H) to the SL of 156 fish species. He concluded that for the most efficient swimmers (e.g., Atlantic herring *Clupea harengus*, bluefish *Pomatomus saltatrix*), H is 30% or less of SL and Y is between 0.40 and 0.55. The splittail's H of 19% of SL and Y of 0.48 categorize it as an efficient swimmer. Swimming is very important for splittails' survival because the fish migrate during high winter-spring runoff to flooded vegetation for spawning and forage in these periodically flooded habitats as young (Caywood 1974). Daniels and Moyle (1983) observed that the spawning success of splittails was positively correlated with river outflows; Caywood (1974) also observed that a successful year-class was associated with winter run-off sufficiently high to flood the peripheral areas of the estuary. In our swimming tests, many splittails held (or tried to hold) onto the upstream screen of the swimming chamber with their mouths when velocity approached their U_{crit} , and it is possible that splittails hold on to vegetation or other substrate features to maintain station against strong currents.

Mean absolute U_{crit} (cm/s) increased with splittail length, which is typical for many fishes because of the improved efficiency of the caudal fin (Webb 1977). Similarly, mean relative U_{crit} (body lengths/s) decreased with splittail length, as is the case for many other fishes. The decrease in relative U_{crit} with length is probably because the power needed to overcome drag increases exponentially with body length (Weihs 1977); also, the maximum stride frequency is reduced in larger fish due to increased contraction times of swimming muscles with the length of the fish (Wardle 1977).

Increase in temperature resulted in greater swimming performance by small age-0 and age-2 splittails. Increases in acclimation temperature of 3°C for small age-0 fish and 5°C for age-2 fish increased absolute U_{crit} by 11 and 25 cm/s, respectively, and increased relative U_{crit} in age-2 fish by 1.26 body lengths/s. Similar observations of increased U_{crit} with increased temperature have been reported for other fish species. For example, for the fry of four salmonid species, an increase of 7°C resulted in a 5-cm/s (~2-body length/s) increase in U_{crit} (Heggenes and Traaen 1988); for largemouth bass *Micropterus salmoides*, an increase of 11°C resulted in an increase of 0.61–1.47 body lengths/s in U_{crit} (Kolok 1992); for yellowfin

tuna *Thunnus albacares*, swimming speed was positively correlated with red muscle temperature (Dizon et al. 1977). Low temperature generally results in decreased swimming performance, probably as a result of biochemical (e.g., enzymatic) and physiological changes (Wardle 1980). The general increase in fish swimming performance with thermal increase reportedly derives from decreases in swimming muscle contraction times (Wardle 1980) and increased aerobic power output available from red muscle fibers at higher environmental temperatures (Heap and Goldspink 1986). Decreased muscle contraction time at higher temperature increases tail beat frequency, resulting in better swimming performance (Batty et al. 1991). Increase in aerobic power output from red muscles at higher temperatures results in white muscle recruitment at higher speed (Rome et al. 1984; Heap and Goldspink 1986). For example, in common carp at 10°C, white muscle fibers were recruited at 1.25–1.56 body lengths/s, but at 20°C they were recruited at higher speed of 2.0–2.5 body lengths/s before getting fatigued (Rome et al. 1984). As swimming velocity increases, there is a gradual recruitment of red (aerobic) muscle fibers until they are all utilized, after which white (anaerobic) muscle fibers are recruited in proportion to the swimming velocity. At lower temperature, fish will have recruited all their red muscle fibers at lower swimming speed, and the recruitment of white muscle will occur earlier, resulting in the fish reaching fatigue at lower swimming velocity (Randall and Brauner 1991).

Although splittails were shown to be good swimmers by their high U_{crit} values, no swimming endurance tests were conducted. If the criterion for water diversion screen approach velocity is based solely on U_{crit} results, as in the case of other fish species (Clay 1995), then the recommended approach velocities of 6 cm/s and 10 cm/s by the USFWS (1994) for delta smelt *Hypomesus transpacificus* (a threatened native species of the Sacramento–San Joaquin estuary) and 12 cm/s for salmonid fry would pose no problem for splittails more than 2 cm in SL.

Available data on California cyprinids show an overall pattern of similar environmental tolerances, perhaps reflecting genealogy. Like other native California cyprinids, especially those in rivers and lakes, splittails are well adapted to wet and dry climatic cycles (Meng and Moyle 1995), as reflected in their wide tolerances to thermal changes and low dissolved oxygen. Their exceptionally high salinity tolerance probably enhanced

survival in the estuary. Many of the state's native cyprinid populations have declined (e.g., Mojave tui chub), have become extinct (e.g., Clear Lake splittail *Pogonichthys ciscooides*) or have been extirpated from state waters (bonetail *Gila elegans*) due to habitat loss or pressure from introduced species, such as the common carp (Moyle 1976). Abiotic environmental factors including temperature, dissolved oxygen, salinity, and water current do not appear to limit the splittail's distribution and survival during years of high precipitation. However, California's highly regulated river and reservoir system restricts the occurrence and duration of floods. The splittail's high tolerance to thermal change, low dissolved oxygen, and high salinity presumably permit extended occupancy, especially by age-1 and older fish, of the dead-end sloughs that may be an overly harsh habitat for potential predators or competitors. Although their general hardiness probably contributes to their survival, splittails have been found mostly in the estuary, which is less than a third of the species' former range (Meng and Kanim 1994). This indicates that the conditions contributing to their habitat restriction (e.g., extended drought, water diversion, inadequate seasonal flooding, habitat alteration, water pollution, and biotic factors such as predation or competition) are extremely serious or that other life stages (i.e., egg, larvae, and adult spawners) are significantly less hardy. These alternatives deserve additional study.

Acknowledgments

This study was supported by the Interagency Ecological Program for the San Francisco Bay/Delta. This cooperative program includes the California Department of Fish and Game (CDFG), California Department of Water Resources (CDWR), State Water Resources Control Board, the USFWS, the U.S. Bureau of Reclamation, the U.S. Geological Survey, the National Marine Fisheries Service, the U.S. Environmental Protection Agency, and the U.S. Army Corps of Engineers. P. Hergesell (CDFG) and R. Brown (CDWR) facilitated this support. Splittails were collected by S. Matern, L. Hess, S. Siegfried, G. Weis, J. Morinaka, L. Grimaldo, R. Baxter, H. Bailey, T. Hampson, and the CDFG Fall Midwater Trawl Survey and Delta Outflow/San Francisco Bay Survey groups headed by K. Hieb and J. Arnold. We thank P. Lutes and B. Bentley of the University of California, Davis, Aquaculture and Fisheries Program for assistance in the fish maintenance system; L. Grimaldo for identifying and

J. Wang for confirming identifications of the small age-0 fish; H. Zhou for statistical advice; A. Farrell for advice regarding Figure 3; K. Jacobs and H. Proctor (CDWR) for the water quality monitoring data; and P. Moyle, R. Baxter, L. Holland-Bartels, L. Brown, B. Herbold, J. Stauffer, and one anonymous reviewer for their valuable comments and suggestions on the manuscript. We also thank D. Shigematsu, D. Irwin, M. Thibodeau, S. Cummings, C. Porter, J. Lorenzo, J. Heublein, J. Khoo, G. Cech, L. Brink, and P. Moberg for technical assistance.

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Received October 30, 1995
Accepted April 24, 1996