SWIMMING PERFORMANCE OF DELTA SMELT: MAXIMUM PERFORMANCE, AND BEHAVIORAL AND KINEMATIC LIMITATIONS ON SWIMMING AT SUBMAXIMAL VELOCITIES

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Summary

Swimming performance, measured as critical swimming velocity (U_{crit}) and endurance, and swimming behavior and kinematics were measured in delta smelt *Hypomesus transpacificus*, a threatened estuarine planktivore. Most fish (58 % of the U_{crit} test group) were capable of achieving and sustaining moderately high velocities: mean U_{crit} was 27.6±5.1 cm s^{-1} (S.D.). U_{crit} was not affected by either acclimation temperature (12–21 °C) or fish size (3.2–6.8 cm standard length) and was generally comparable with values measured for other similarly sized fishes. The remaining 42 % of the fish failed to swim at velocities above 10–15 cm s^{-1}. Interestingly, of the fish that provided a U_{crit} measurement, 62 % experienced at least one temporary swimming failure between 10 and 20 cm s^{-1}. Endurance was highly variable and, for all velocities, not normally distributed; the only significant decrease, from 6 h to 64 min, occurred between 10 and 15 cm s^{-1}. Kinematic analyses of stroke frequency, stroke amplitude, stride length, glide frequency, glide duration, proportion of time spent stroking and the number of strokes between successive glides showed that delta smelt employed three velocity-dependent swimming gaits: a discontinuous 'stroke-and-glide' swimming behavior below 10 cm s^{-1}; a continuous swimming behavior above 15 cm s^{-1} and up to U_{crit}; and a discontinuous 'burst-and-glide' swimming behavior at velocities above U_{crit}. Swimming failure at velocities between 10 and 20 cm s^{-1} coincided with the transition from 'stroke-and-glide' swimming to continuous swimming; delta smelt were unable or unwilling to swim steadily in the flume within this transition velocity range. These results underscore the importance of monitoring and quantifying behavior in experiments intended as physiological performance tests of whole animals.

Key words: fish, delta smelt, *Hypomesus transpacificus*, swimming, kinematics, behavior.

Introduction

For many fishes, maximal swimming performance delineates the range of hydrodynamic environments that the fish is capable of occupying (Webb, 1988) and has obvious selective value for activities such as predator avoidance and migration (Videler, 1993). However, most fishes rarely operate at maximal activity levels. Routine swimming activity, usually associated with foraging, is generally low-velocity and unsteady, but the survival value of efficient performance at these activity levels may be equally important (Videler and Wardle, 1991). Therefore, swimming behavior and the performance envelope of the fish represent the balance between requirements for efficient routine locomotion for foraging and the predation and migration pressures for high-level performance (Webb, 1982, 1988). If the strongest selection is for activity levels at either end of the performance range, how do fish perform and behave at intermediate swimming velocities, activity levels that may not be commonly utilized by the fish for foraging, migration or escape? This question may be particularly relevant for fishes that live in altered and managed environments where flow-management strategies and regulations for fish passage and/or exclusion are usually based upon swimming performance at intermediate levels (Clay, 1995). In the present paper, we describe our studies on the swimming performance and behavior of an osmerid fish, the delta smelt (*Hypomesus transpacificus*), and relate our findings to the fish's ecology and management.

The delta smelt is a selective planktivore restricted to the Sacramento–San Joaquin estuary (Moyle *et al.* 1992), a large, complex and highly altered system which drains into San Francisco Bay (California, USA) (Nichols *et al.* 1986). Delta smelt are small (<10 cm standard length), physically delicate and short-lived; most fish live for only 1 year. Spawning occurs in the upper reaches of the estuary in the late winter or early spring. Larvae and juveniles are transported downstream to (usually) brackish water (mean salinity 2 ‰, range 0–14 ‰; Moyle *et al.* 1992) where they reside until the following winter when, as maturing adults, they migrate 10–100 km upstream to spawn and die. In addition to their foraging and migration

activities, delta smelt are exposed to artificial flow regimes associated with more than 1800 urban, industrial and agricultural water diversions located throughout their habitat (Nichols *et al.* 1986; Jassby *et al.* 1995). Entrainment losses are thought to have contributed to the drastic population decline experienced by the fish during the past 15 years (Moyle *et al.* 1992; USFWS, 1994), and the species is now protected under both federal and state Endangered Species Acts. One application of swimming performance research on this previously unstudied fish would be to assist in establishing velocity criteria for water diversions that minimize harm to this threatened species.

Materials and methods
Fish collection and care

Delta smelt *Hypomesus transpacificus* McAllister were collected from the Sacramento–San Joaquin estuary during the summer and autumn of 1993, 1994 and 1995 using methods described in Swanson *et al.* (1996). All fish were held in flow-through circular tanks (diameter 1 m; depth 0.25 m; inflow 300–800 ml min^{-1}, water velocity 0–5 cm s^{-1}) supplied with temperature-controlled, air-equilibrated, non-chlorinated well water. For the first 4–8 days following collection, water temperature was maintained approximately 1–3 °C below collection temperature and salinity at 2–8 ‰ by the continuous addition of a concentrated salt solution made from rock salt (Leslie solar salt, 99.6 % pure, Cargill Salt, Minneapolis, MN, USA). Beginning 2 days after collection, fish were treated on alternate days for 2–6 days with an antibacterial solution (nitrofurazone, 2–10 mg l^{-1}) and an antifungal treatment (formaldehyde, 0.1 ml l^{-1}) for 1 h. Following this prophylactic treatment, salinity was decreased to 0 ‰ and water temperature adjusted by 1–2 °C day^{-1} to predetermined experimental levels.

The fish were maintained under a simulated natural photoperiod regime (latitude 38°N) and fed a combination of live *Artemia* nauplii (Argent Chemical Laboratories, Redmond, WA, USA) and a commercial diet (BioKyowa, Inc., Cape Girardeau, MO, USA). All tanks were cleaned daily to remove fecal material and uneaten food, and shielded with semi-opaque screens to minimize disturbance of the fish.

Because delta smelt spawn seasonally and complete their life cycle in a single year, fish age, size, developmental stage and seasonal temperature regimes tend to be strongly correlated (Moyle *et al.* 1992; Mager, 1996). We therefore acclimated the fish to seasonally appropriate temperatures which represented, for each life history stage, a low and high level. During the summer and autumn, for juvenile (3.0–4.4 cm standard length, *SL*) and subadult (4.5–5.9 cm *SL*) fish, we used 17 and 21 °C; during the winter and spring, for subadult and adult fish (≥6.0 cm *SL*) we used 12 and 17 °C. All fish were held for a minimum of 7 days at the specified temperature prior to use in the experiments.

Delta smelt are extremely delicate and very sensitive to stress (Swanson *et al.* 1996); even careful handling can cause temporary loss of equilibrium. Therefore, handling

immediately prior to and at the completion of experiments was accomplished quickly (<1 min between holding tank and experimental apparatus) with minimal disturbance and mechanical trauma to the fish. Water in the transfer containers was maintained at the acclimation temperature and treated with rock salt (8 ‰) and NovAqua, a commercial water conditioner that contains polymers (dose 2–5 ml l^{-1}; Kordon Co., Hayward, CA, USA), to reduce osmotic imbalance associated with stress (Wedemeyer, 1972; Mazik *et al.* 1991). Transfer between holding tanks, buckets and the experimental apparatus was accomplished using 250 or 500 ml glass containers rather than mesh nets to minimize air exposure and abrasion of skin and scales. Any fish that exhibited prolonged or repeated loss of equilibrium was not used in the experiments and, for each type of experiment, an individual fish was used only once.

Swimming performance and behavior

Swimming performance of individual delta smelt was measured in terms of critical swimming velocity (U_{crit}), the maximum velocity a fish can maintain for a specified amount of time, and endurance, the length of time a fish can sustain swimming at a constant velocity (Brett, 1964). Measurements were made using a modified Brett-type, recirculating swimming flume (total volume 9 l; swim chamber diameter 9.1 cm; swim chamber length 24 cm) calibrated using an electronic flow meter (Marsh-McBirney, model 201D, Frederick, MD, USA). Flow through the swim chamber was relatively uniform; for example, at 28 cm s^{-1}, velocity measurements made at ten locations within the chamber, including within 1 cm of the chamber wall, varied by less than 10 % (S.D.). Observations of fish swimming in the chamber indicated that there were no low-velocity areas that were consistently selected by the fish. Water velocity measurements were not corrected for solid blocking (Brett, 1964) because the maximum cross-sectional area of the largest fish used in the experiments was less than 5 % of the cross-sectional area of the swim chamber. Prior to the introduction of a fish into the apparatus, the salinity of the water in the flume was increased to approximately 4 ‰ to reduce handling-stress-related osmotic imbalance. Beginning 5–10 min after the fish was introduced, the flume was flushed with fresh water (95 % washout in 40 min). All experiments were conducted in fresh water (0 ‰) at the acclimation temperature (±0.5 °C) of the tested fish.

Each U_{crit} experiment consisted of a 50 min pre-test recovery/flushing period (water velocity U=1–3 cm s^{-1}, depending on fish behavior in the swim chamber) followed by stepwise increases of 3.5±0.4 cm s^{-1} (mean ± S.D.) in water velocity at 10 min intervals until the fish fatigued. The duration of the recovery period represented a compromise between adequate time to recover from handling and further stress resulting from prolonged confinement in the swim chamber. Many investigators do not allow any recovery time (e.g. Bainbridge, 1960; McLeod, 1967; Young and Cech, 1993), and Glova and McInerney (1977) found no significant differences in swimming performance of juvenile coho salmon

(*Oncorhynchus kisutch*) allowed 1 and 12 h recovery periods prior to testing. Fatigue was indicated by the failure of the fish to swim and hold its position in the chamber, repeated (more than three) impingements on the downstream barrier screen and the inability of the fish to reorient to the current and swim following impingement. An impingement was defined as contact by at least 75 % of the fish's length with the downstream screen. U_{crit}, expressed as cm s^{-1}, was calculated, using the equation from Brett (1964), as:

$$U_{crit} = U_i + [U_{ii}(T_i/T_{ii})],\tag{1}$$

where U_i is the highest velocity maintained for the prescribed time (cm s^{-1}), U_{ii} is the velocity increment (e.g. 3.5 cm s^{-1}), T_i is the time elapsed at fatigue velocity (s) and T_{ii} is the prescribed swimming time (10 min).

Each endurance experiment consisted of a 50 min pre-test recovery/flushing period (U=1–3 cm s^{-1}, depending on fish behavior in the swim chamber) followed by a gradual increase in water velocity (rate of increase 5–20 cm s^{-1} over 1 min) to the predetermined experimental level. The maximum duration of the experiment was 6 h. Fatigue was defined by three impingements within a 10 min period. Endurance is expressed as the time (min) of the third impingement within the 10 min period. Experiments in which the fish failed within 30 s at the prescribed experimental velocity were not included in our analyses. This protocol generally excluded burst or sprint swimming, a maximum activity level that requires the fish to recruit anaerobic white muscle and is characterized by very short endurance times (<15 s; Brett, 1964, 1967; Videler, 1993).

During all experiments, visual observations were made on swimming behavior, including rheotaxis, discontinuous *versus* continuous stroking behavior and all incidences of impingement. Delta smelt which failed to orient to the current and swim at low velocities (U<10 cm s^{-1}) without repeated touching, bracing or impingement against the downstream screen (U_{crit} experiments) or failed to achieve the prescribed velocity (endurance experiments) were categorized as non-swimmers, removed from the swimming flume, and no measurement was recorded. Delta smelt frequently became impinged at low and moderate velocities, prompting an immediate temporary reduction in current velocity by the investigator (during which the timer for the U_{crit} interval or endurance measurement was stopped) to allow the fish to reorient to the current. Reorientation of the fish and reinstatement of the current at the appropriate experimental level was accomplished by a gradual increase in water velocity timed to coincide with periods when the fish was oriented in the upstream direction in the swim chamber. After reorientation and re-establishment of the experimental velocity (maximum allowed duration 3 min), the experiment continued until the fish fatigued. In U_{crit} experiments, fish that exhibited rheotaxis and willingness to swim at low velocities but were unable to swim consistently and required frequent current reductions and reinstatements at moderate velocities (U=10–15 cm s^{-1}) and were unable to achieve higher velocities

were categorized as transition velocity failures, removed from the apparatus, and no measurement was recorded. For delta smelt from which a U_{crit} measurement was obtained, the velocity at which the fish experienced its first incidence of impingement unrelated to fatigue, U_{imp1}, at velocities at least two increments or 6–8 cm s^{-1} slower than the velocity at which the fish ultimately fatigued, was also recorded. In endurance experiments, the first incidence of impingement was recorded as T_{imp1} (min).

After each experiment had been completed, the fish was removed from the apparatus, anesthetized (tricaine methanesulphonate, MS-222; dose 70 mg l^{-1}), weighed (±0.01 g), measured (*SL*, ±0.1 cm) and released into a holding tank. Standard length, the length from the tip of the snout to the end of the vertebral column, was used in all calculations, analyses and data presentations because it was easily and accurately measured and, in video records, the caudal peduncle was more clearly visible than the caudal fin. The conversion between standard length (*SL*) and total length (*TL*) (P. S. Young and J. J. Cech, Jr, unpublished results) is described by the equation:

$$SL = 0.003 + 0.840TL\tag{2}$$

(N=244, r^2=0.997, P<0.001).

All fish used in the experiments were visibly healthy. However, some incidences of a systemic bacterial disease (*Mycobacterium* spp.) were detected among adult fish in some of the holding tanks during the winter and spring of 1994 and 1995. Following experiments using fish from these tanks, each fish was killed and sent for diagnosis to the Fish Pathology Laboratory, School of Veterinary Medicine, University of California, Davis, USA. Swimming performance results from fish found to be infected were not included in the analyses.

Swimming kinematics

A subsample of U_{crit} experiments was video-taped for analysis of swimming kinematics at different water velocities. The fish were filmed from above using a video camera (Hitachi, model VM1700A, 30 frames s^{-1}) suspended 55 cm above the swimming chamber. Video recordings were analyzed manually in slow motion (1–10 frames s^{-1}) and, for some parameters, using a computer-assisted video capture and motion analysis system (Peak Performance Technologies, Inc., Englewood, CO, USA). Measurements were made on stroke frequency (Hz), stroke amplitude (*L*, measured as the total lateral excursion of the caudal peduncle and expressed as a proportion of *SL*), stride length (*Ls, SL* stroke^{-1}), calculated as:

$$Ls = U/(SL \times fs),\tag{3}$$

where U is velocity (cm s^{-1}), *SL* is standard length (cm *SL*$^{-1}$) and *f*s is stroke frequency (Hz). Glide frequency (Hz), glide duration (s), the proportion of time spent stroking (calculated as the proportion of a 20–60 s interval spent stroking) and the number of strokes between successive glides (counted, 5 cm s^{-1} only, and calculated as stroke frequency/glide frequency) were also measured. A glide was indicated by the fish holding its

body rigidly straight with no lateral undulations of either the trunk or caudal fin (minimum detectable duration 0.04 s or two frames). All measurements were made on three occasions during each velocity interval, usually during the first 3 min, the middle 4 min and the final 3 min of each 10 min interval, and only during periods of consistent swimming by the fish. For stroke amplitude and glide duration, at least three strokes or glides were measured during each of the three measurements within each velocity.

Statistical methods

Comparisons among appropriate treatment groups (e.g. temperature, life history stage, swimming velocity) were made using analyses of variance (ANOVAs) and two-tailed t-tests. Nonparametric tests (e.g. Mann–Whitney rank sum tests) were used to compare treatment groups for which the data were not normally distributed. The effects of continuous variables such as fish size and velocity were examined using regression analysis and, for some swimming kinematic parameters, piecewise regression analysis (Neter et $al.$ 1985). To account for individual variation in maximal swimming capacity, velocity was expressed as a proportion of the U_{crit} value measured for that fish (U/U_{crit}; i.e. physiologically equivalent velocity; Drucker and Jensen, 1996a,b) for some of the analyses of swimming kinematics. Proportions were subjected to angular transformation prior to statistical analyses. All data are expressed as the mean ± S.D. unless otherwise noted. All statistical procedures were conducted using Systat and Sigmastat software.

Results

Critical swimming velocity

U_{crit} measurements were obtained from 63 (58 %) of 109 fish tested in the swimming flume (3.2–6.8 cm SL; 18 juveniles, 23 subadults and 22 adults; at 12 °C, $N=20$; at 17 °C, $N=33$; at 21 °C, $N=10$). Among fish that failed to swim adequately, 20 (18 %) were classified as non-swimmers and 26 (24 %) as transition velocity failures. Although these fish were not weighed or measured, the percentages of fish that failed to swim in the experiments did not change with fish age or season (both tests, $P>0.1$). Of the fish that swam to fatigue, U_{imp1} measurements were made on 39 fish (62 %) that were temporarily impinged at water velocities substantially below their critical swimming velocities. The proportion of fish that experienced non-fatigue-related swimming failure was not significantly affected by size ($P=0.08$) although, in general, more small fish (3–4 cm SL, 88 % impinged) were impinged at low velocities than large fish (6–7 cm SL, 54 % impinged).

Delta smelt U_{crit} and U_{imp1} (Fig. 1) were not affected by acclimation temperatures from 12 to 21 °C (ANOVA, both tests, $P>0.5$; t-tests within life history stages, all tests, $P>0.2$). Therefore, for subsequent analyses, the results from all three temperatures were pooled. Neither fish size (regression, all temperatures pooled, $P>0.3$; 17 °C only, $P>0.5$) nor life history stage affected U_{crit} (ANOVA, $P>0.1$). The mean critical
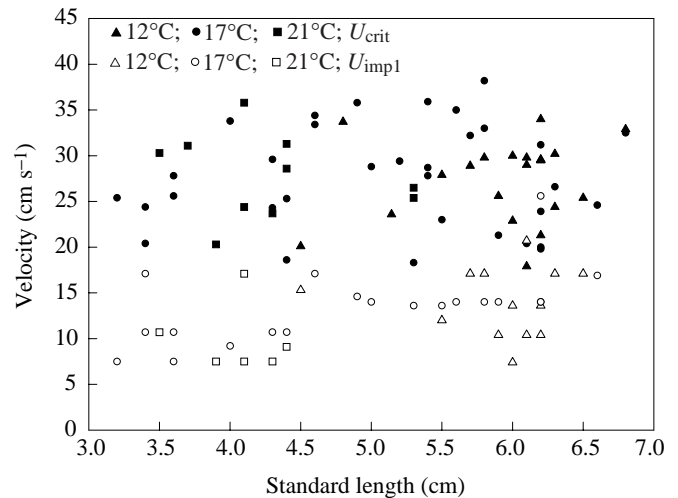

Fig. 1. Critical swimming velocity (U_{crit}, filled symbols) and velocity at first impingement (U_{imp1}, open symbols) of delta smelt acclimated to three temperatures.

swimming velocity of delta smelt was 27.6±5.1 cm s^{-1}. U_{imp1} increased significantly with increases in fish size (regression, all temperatures pooled and 17 °C only, both tests, $P<0.01$); small fish experienced non-fatigue-related swimming failure at slightly lower velocities than large fish. The regression of U_{imp1} on size was: $U_{imp1}=3.8+1.8SL$ ($N=39$, $r^2=0.228$, $P<0.01$).

Endurance

Endurance measurements were obtained from 81 (71 %) of 114 fish tested (3.6–7.3 cm SL; 20 juveniles, 31 subadults and 30 adults; at 12 °C, $N=24$; at 17 °C, $N=37$; at 21 °C, $N=20$). The remaining 33 fish (29 %) failed to orient to the current and swim or were unable to achieve the prescribed experimental velocity. The percentage of non-swimmers did not change with fish age or season (both tests, $P>0.2$). Of the fish that completed the experiment, 32 (40 %) experienced at least one incidence of non-fatigue-related swimming failure and impingement where the difference between endurance and T_{imp1} was greater than 10 min. Fish size did not affect the proportion of fish that experienced early impingement ($P>0.1$).

Endurance and T_{imp1} were highly variable (Table 1). Both decreased significantly with increases in velocity (both regressions, $P<0.001$), but significant effects of temperature, life history stage and size were not detected (all tests, $P>0.1$). Among velocity levels ($U\pm2.5$ cm s^{-1}), nonparametric analyses indicated that both endurance and T_{imp1} decreased significantly between 10 and 15 cm s^{-1} (both tests, $P<0.05$), but velocity had no significant effect on either response between 5 and 10 cm s^{-1} or from 15 to 30 cm s^{-1} (all contrasts, $P>0.05$; Table 1). Regression analysis of endurance and T_{imp1} at velocities above 10 cm s^{-1} also indicated that there was no change in either response over this velocity range (both tests, $P>0.1$). Within velocities, endurance time was significantly greater than T_{imp1} only at 10 cm s^{-1}. At this velocity, fish experienced temporary swimming failure substantially sooner than fatigue or the end

Table 1. *Endurance, the time of the first impingement, (T_{imp1}), and the proportion of fish that experienced non-fatigue-related impingement of delta smelt at different velocities ($U\pm2.5\,cm\,s^{-1}$)*

	Velocity ($cm\,s^{-1}$)					
	5 (9)	10 (17)	15 (13)	20 (20)	25 (15)	30 (7)
Endurance (min)						
(Median)	360	360	64	51	50	11
(Range)	254–360	3–360	2–360	2–360	1–360	2–360
T_{Imp1} (min)						
(Median)	223	150	16	16	49	6
(Range)	5–360	2–360	1–196	2–200	1–360	2–360
Impinged (%)	44	47	60	40	13	14

Endurance and T_{imp1} results, pooled among temperature and fish size, were not normally distributed and so are presented as medians and ranges.

Medians not connected by an underline were significantly different ($P<0.05$, Mann–Whitney rank sum test).

Sample sizes are given in parentheses.

of the experimental period. The proportion of fish that experienced early, non-fatigue-related impingement was not significantly related to velocity ($P=0.07$), although a decreasing trend with increases in velocity was suggested (Table 1).

Swimming behavior

Visual observations and analyses of video recordings of delta smelt swimming during U_{crit} and endurance experiments indicated that the fish, a subcarangiform swimmer (Breder, 1926) that uses only body–caudal fin propulsion, used three distinct swimming behaviors. At velocities below $10\,cm\,s^{-1}$, the fish swam discontinuously, alternating active stroking with passive gliding, but they generally maintained their position within the chamber and swam in a consistent manner. At moderate to high velocities, above $15–20\,cm\,s^{-1}$, the fish swam steadily by stroking continuously and maintained their position in the chamber. At high velocities, usually exceeding $25–30\,cm\,s^{-1}$ and during the penultimate and/or final (i.e. fatigue) velocity interval in the U_{crit} experiments, swimming became less steady. The fish alternated continuous stroking swimming, during which they were usually unable to maintain their position in the chamber, with darting 'bursts' during which the fish rapidly moved forwards in the chamber before resuming continuous stroking swimming. Examination of this behavior in slow motion revealed that the forward movement consisted of one rapid, large-amplitude stroke, during which the head and anterior trunk were substantially displaced laterally, followed by a short-duration glide. In U_{crit} experiments, this swimming behavior was usually a reliable indicator of impending fatigue. At intermediate velocity levels, $10–20\,cm\,s^{-1}$, and during one or two of the U_{crit} velocity intervals within this range, virtually all of the fish that were willing to swim exhibited agitation and erratic swimming behavior. Specific behaviors included shifting between continuous and discontinuous swimming,

long-duration glides during which the fish drifted backwards with the current and frequently contacted the downstream screen with its caudal fin or became impinged, swimming from side to side in the chamber (i.e. 'zig-zagging'), temporary failures of rheotaxis during which the fish swam directly towards the chamber sides, and refusal to swim by bracing with the caudal fin against the downstream screen. In the U_{crit} experiments, of the fish that were willing to swim (includes transition velocity failures, $N=26$, and fish from which a U_{crit} measurement was obtained, $N=63$), 73 % (65 fish) experienced at least one impingement and temporary or total swimming failure within this velocity range. For transition velocity failures, the mechanical and physiological stress resulting from repeated impingements (which occurred both during attempts to reorient the fish and re-establish the current, and after current re-establishment during the continuation of the velocity interval) usually culminated in loss of equilibrium. Those fish that were able to continue the experiment after one or more impingements (mean 2.2 ± 1.3 impingements) within this velocity range usually swam without further incident for the remainder of the experiment, exhibited the darting behavior indicative of fatigue at high velocities, and yielded a U_{crit} measurement similar to those obtained from fish that did not experience any non-fatigue-related impingements ($P>0.05$).

Swimming kinematics

Swimming kinematics were measured in nine fish (three juveniles at 17 °C; three subadults at 17 °C and three adults at 12 °C). Mean U_{crit} of these fish was $28.9\pm6.1\,cm\,s^{-1}$ (range $18.6–33.8\,cm\,s^{-1}$). There were no consistent significant relationships between any of the kinematic parameters and the time when they were measured in the velocity interval. Therefore, for each fish, the results from each velocity interval were pooled for analyses. Fish size significantly affected several of the measured parameters. For those parameters, data

were analyzed by life history stage. For all stages, the kinematic responses to velocity differed depending on how velocity was expressed. The results are therefore presented in relation to absolute velocity (cm s^{-1}; Fig. 2) and velocity as a proportion of the measured U_{crit} value for each fish (U/U_{crit}; Fig. 3).

Stroke frequency (Figs 2A, 3A) increased with increases in velocity for all life history stages (all regressions, $P<0.001$), but was generally more closely related to absolute swimming velocity than to velocity as a proportion of U_{crit}. At all velocity levels, stroke frequency was significantly affected by size (all tests, $P<0.05$); juvenile fish had higher mean stroke frequencies than adults, and values for subadult fish were intermediate. For juvenile and subadult fish, but not for adults, stroke frequencies approached a maximum at velocities exceeding 25–30 cm s^{-1} and did not increase with further increases in velocity (both stages, $P>0.05$).

Stroke amplitude (Figs 2B, 3B) did not differ significantly among life history stages at any velocity level, but there were differences in the relationship between stroke amplitude and velocity for the three stages. For juveniles and subadults, stroke

amplitude increased with increases in velocity up to $0.8U_{crit}$ and then decreased with further increases in velocity (both regressions, $P<0.05$). For adult delta smelt, stroke amplitude did not vary with velocity (i.e. the slope was not significantly different from 0; $P>0.05$).

Stride length (Figs 2C, 3C) was not significantly affected by life history stage at any velocity up to 35 cm s^{-1} (all tests, $P>0.05$); the results were therefore pooled for some analyses. At 5 cm s^{-1}, stride length was generally high but, with increases in velocity to 10 or 15 cm s^{-1}, it decreased significantly (both tests, $P<0.05$). Between 20 and 30 cm s^{-1}, stride length increased with increases in velocity for juvenile and subadult fish (both stages, $P<0.05$), but not for adults ($P>0.5$).

Glide frequency (Figs 2D, 3D) was not affected by size at any velocity level (all tests, $P>0.05$); the results from the three life history stages were therefore pooled for all analyses. Glide frequency was generally more closely related to absolute velocity at low and moderate velocities and to proportional velocity at velocities approaching and above U_{crit}. It decreased significantly from approximately 1 Hz at 5 cm s^{-1} to near zero at 20 cm s^{-1} ($P<0.001$), remained low between 20 cm s^{-1} and
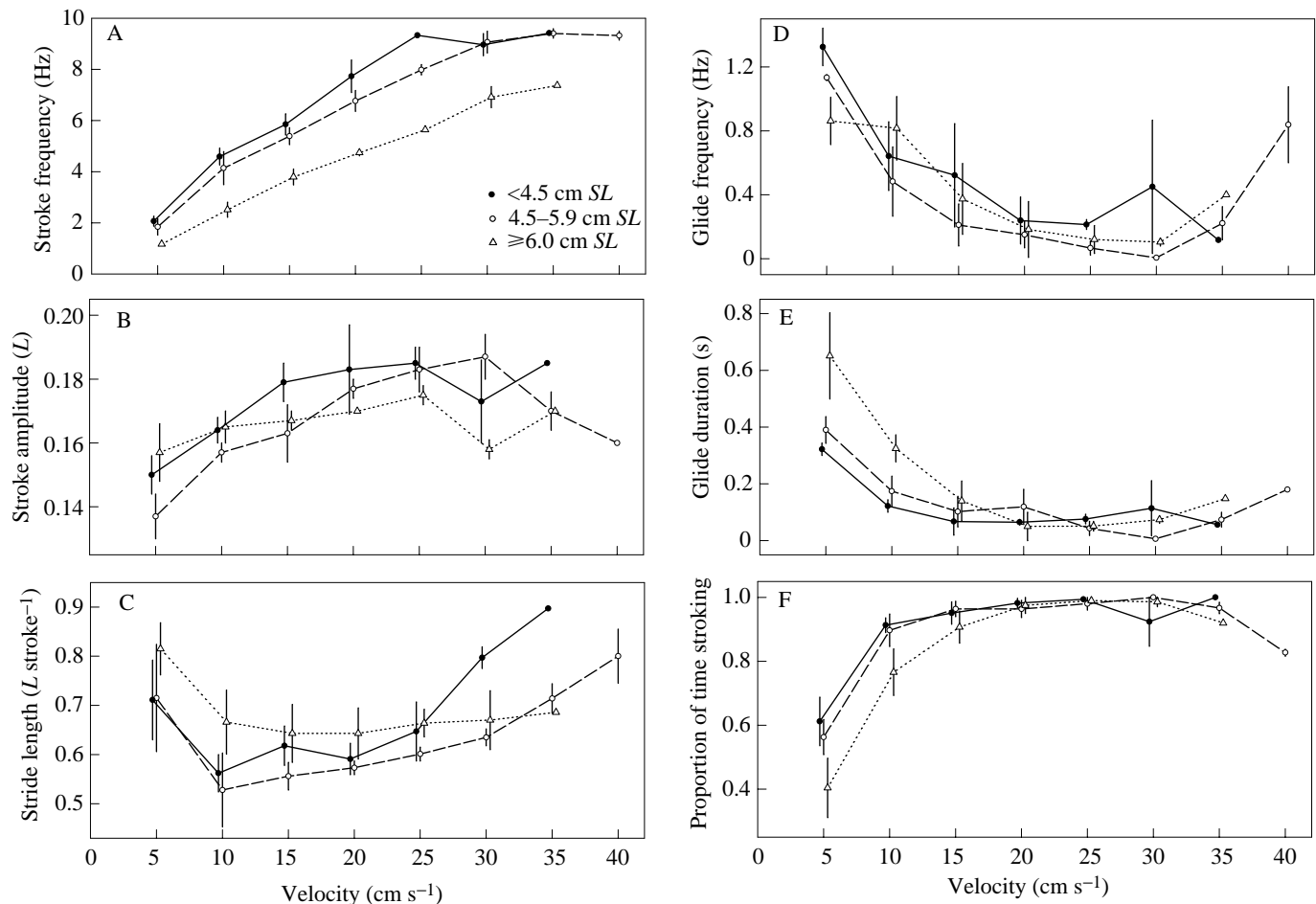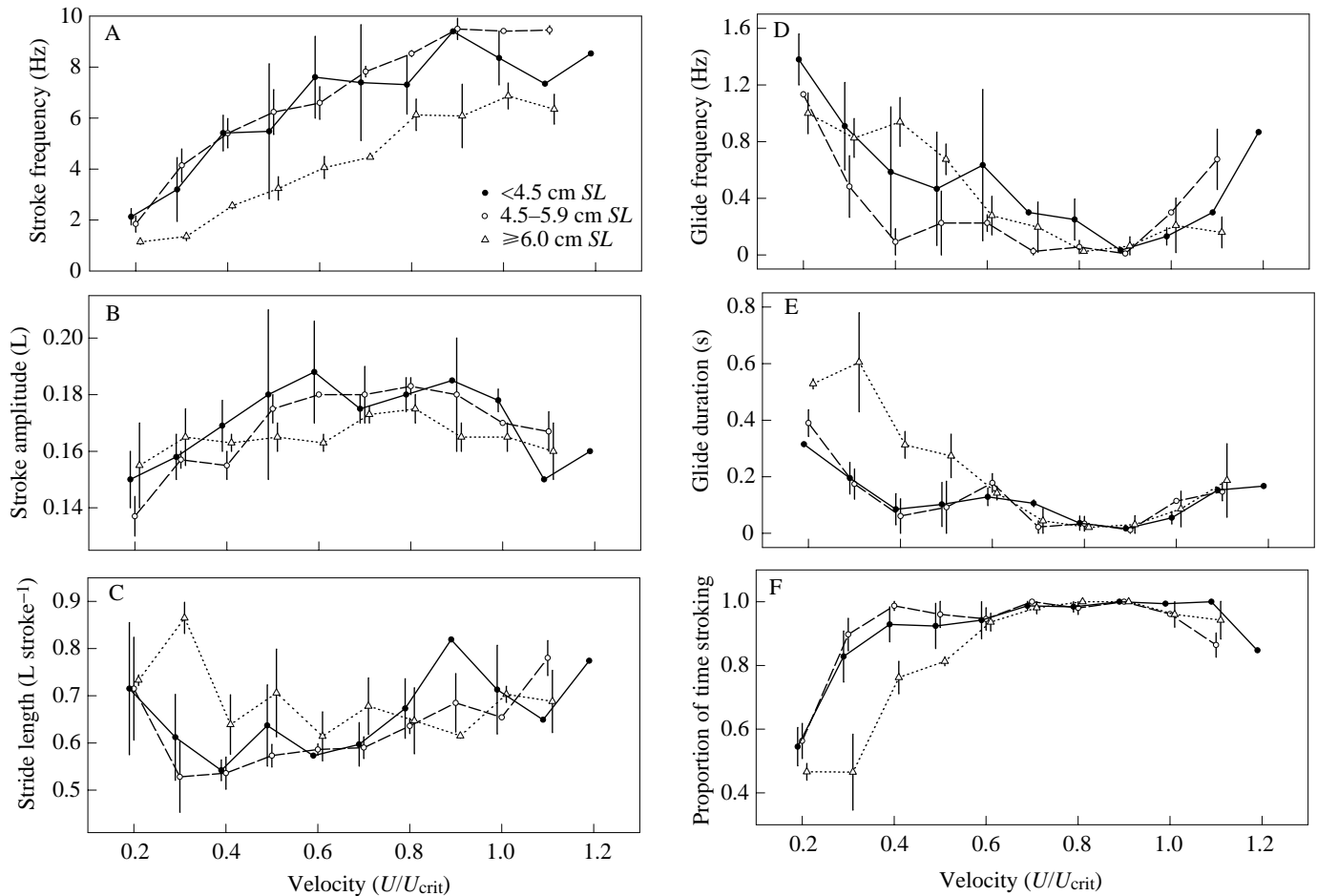

Fig. 2. Swimming kinematics (A, stroke frequency; B, stroke amplitude; C, stride length; D, glide frequency; E, glide duration; F, proportion of time spent stroking) of delta smelt from three life history stages in relation to swimming velocity (cm s^{-1}). Points are means ± S.E.M. ($N=3$) for each life history stage at each velocity level ($U±2.5$ cm s^{-1}) and have been slightly offset on the x-axis to improve visual clarity for error bars.

Fig. 3. Swimming kinematics (A, stroke frequency; B, stroke amplitude; C, stride length; D, glide frequency; E, glide duration; F, proportion of time spent stroking) of delta smelt from three life history stages in relation to velocity calculated for each fish as U/U_{crit} (where U is velocity in $cm\,s^{-1}$ and U_{crit} is critical swimming velocity in $cm\,s^{-1}$). Points are means ± S.E.M. (N=3) for each life history stage at each proportional velocity level (U±$0.05U_{crit}$) and have been slightly offset on the x-axis to improve visual clarity for error bars.

U_{crit} and then increased at velocities above U_{crit} ($P<0.05$). For all life history stages, glide frequency was markedly more variable at intermediate velocities (10 and $15\,cm\,s^{-1}$) than at lower or higher velocities.

Glide duration (Figs 2E, 3E) was affected by size at low velocities ($5\,cm\,s^{-1}$, $P=0.08$; $10\,cm\,s^{-1}$, $P<0.05$) and exhibited a pattern similar to that of glide frequency. For all stages, it decreased significantly with increases in velocity ($P<0.001$), from 0.3 to 0.6 s at $5\,cm\,s^{-1}$ to near zero at velocities between $15\,cm\,s^{-1}$ and U_{crit}. At velocities above U_{crit}, glide duration increased significantly (pooled results, $P<0.01$). For all stages, glide duration at velocities above U_{crit} was significantly lower than that at $5\,cm\,s^{-1}$ (all tests, $P<0.01$).

The proportion of time spent stroking (Figs 2F, 3F) was not significantly affected by size at any velocity level (all tests, $P>0.05$) so the results were pooled for analyses. At low velocities, fish stroked for only approximately half of the time. The proportion of time spent stroking increased with increases in velocity up to $15\,cm\,s^{-1}$ ($P<0.001$), when the fish swam by stroking continuously. At velocities above U_{crit}, the proportion of time spent stroking decreased ($P<0.05$).

During discontinuous swimming when the fish interspersed glides with active stroking, the number of strokes between successive glides differed among velocities and, for some velocities, among life history stages. At $5\,cm\,s^{-1}$, there was no effect of size on the number of strokes per glide ($P<0.5$); all fish used 1–6 strokes/glide (counted range; mean 1.8±1.2 strokes/glide counted; 1.6±0.4 strokes/glide calculated). With an increase in velocity to $10\,cm\,s^{-1}$, the number of strokes per glide increased significantly for all life history stages ($P<0.01$) and was highly variable. It was significantly greater for juvenile (19.1±31.2 strokes/glide) and subadult (20.8±32.3 strokes/glide) fish than for adults (5.4±6.3 strokes/glide) ($P<0.05$). At $15\,cm\,s^{-1}$, the number of strokes per glide was still highly variable and, for adult fish only, significantly higher (45.5±80.3 strokes/glide) than at $10\,cm\,s^{-1}$ ($P<0.01$). At velocities above U_{crit}, significant differences among the three stages were not detected, although a trend towards a higher number of strokes per glide for adult fish was suggested (juvenile, 17.2±10.4 strokes/glide; subadult, 17.9±10.3 strokes/glide; adult, 70.7±63.2 strokes/glide). For all life history stages, the number of strokes per glide was

significantly higher at velocities above U_{crit} than at $5\,cm\,s^{-1}$ (all tests, $P<0.05$).

Discussion

Maximal swimming performance

Critical swimming velocities of delta smelt were comparable to or somewhat lower than those of other similarly sized fishes acclimated to similar temperatures (Table 2). In contrast, their endurance–velocity relationship did not conform to the pattern reported for other fishes (e.g. a logarithmic decay in endurance with increasing velocity; Brett, 1964, 1967; Videler, 1993). Delta smelt endurance was extremely variable, only weakly related to velocity and, for all velocity levels, not normally distributed. The only significant decline in performance occurred at velocities less than half of U_{crit}, but some fish were able to swim for up to 6h at velocities approaching mean U_{crit}. These unusual results, combined with the large proportion of fish that experienced temporary or total swimming failure at submaximal velocities in the U_{crit} experiments (discussed below), probably indicate behavioral and/or kinematic impediments to swimming at certain velocities. However, they may also reflect limitations and biases in the experimental protocol we used for these experiments, including the relatively short experimental duration (6h compared with 16.7h used in some other studies; Brett, 1964) and the endpoint used to indicate fatigue. This arbitrary endpoint was chosen because of the delta smelt's demonstrated susceptibility to non-fatigue-related swimming failure in the flume. In most instances, it corresponded to physiological fatigue (e.g. following impingement, the fish were quiescent in the chamber and incapable of swimming further). However, at low to moderate velocities, the fish were usually active following impingement and, if they could be reoriented to the current, were usually capable of swimming at the prescribed velocity.

Unlike findings for some other fishes (Fry and Hart, 1948; Griffiths and Alderdice, 1972; Brett and Glass, 1973; Videler and Wardle, 1991; Young and Cech, 1996), U_{crit} and endurance were not affected by acclimation temperature, at least within the range tested. The lack of significant effects of temperature on swimming performance may have resulted from the large variances in the results or from the fish achieving, during acclimation, complete thermal compensation in metabolic and/or neuromuscular function (Schmidt-Nielsen, 1979; Hazel, 1993). The results of other physiological studies with delta smelt (thermal tolerances, salinity tolerances and routine metabolism; C. Swanson and J. J. Cech Jr, unpublished results) also suggest thermal compensation by this fish. Such independence of physiological responses to long-term or seasonal fluctuations in temperature could be a selective advantage to this species, which is restricted to moderately shallow estuarine habitats (usually less than 4m deep; Moyle et al. 1992).

Absolute U_{crit} ($cm\,s^{-1}$) and endurance at specific velocities generally increase with fish size (Brett and Glass, 1973; Webb, 1977; Webb et al. 1984; Videler and Wardle, 1991; Young and Cech, 1996). This was not the case with delta smelt, perhaps because of their small size range. In addition, delta smelt begin sexual maturation at 5–6cm in standard length, with greater increases in body volume than in length (Mager, 1996). Reduced swimming performance of maturing fishes has been reported for other species (Blaxter, 1969) and may contribute to the absence of a size effect in our data. Physiological and morphological changes associated with gonadal development could have affected maximum aerobic capacity (scope for activity; Fry, 1957), body flexibility or, possibly, the fish's behavioral responses to flowing water or confinement in the flume. These ontogenetic changes may underlie the significant differences in swimming kinematics and reduced kinematic plasticity of adult fish compared with juveniles and subadults. Adult delta smelt did not exhibit the attenuation in stroke

Table 2. *Comparison of critical swimming velocities (U_crit) of delta smelt and other small fishes*

Species	Acclimation temperature (°C)	Body length (cm)	U_{crit} ($cm\,s^{-1}$)	U_{crit} ($L\,s^{-1}$)[a]	Reference
Delta smelt	12	4.5–6.8	28±4	4.7±0.8	This study
Hypomesus transpacificus	17	3.2–6.8	28±6	5.6±1.5	
	21	3.5–5.3	28±5	6.6±1.6	
Splittail	17	3–5[b]	20–30	5.7–8	Young and Cech (1996)
Pogonichthys macrolepidotus	20	3–5[b]	20–30	5.7–8	
Sockeye salmon	15	5.3–6[c]	38–43[e]	7.1–7.3	Webb and Brett (1973)
Oncorhynchus nerka					
Emerald shiner	12	6.5[d]	59	9.1	Jones et al. (1974)
Notropis athernoides					

[a]Lengths $(L)\,s^{-1}$ calculated as $(U_{crit},\,cm\,s^{-1})$ (body length, cm)$^{-1}$.
[b]Body length measured as *SL*.
[c]Body length measured as total length (*TL*).
[d]Body length measured as fork length (*FL*).
[e]U_{crit} ($cm\,s^{-1}$) values calculated as $(U_{crit},\,L\,s^{-1})$ (*FL*, cm) by the authors.

frequencies, large increases in stroke amplitudes and the concomitant increases in stride lengths observed among smaller, younger fish at velocities approaching U_{crit}. Adult fish were also apparently less capable of shifting to high-velocity discontinuous swimming (see below) than were immature conspecifics. A possible decrease in body flexibility would be indicated by lower stroke amplitudes in mature fish, but amplitude values were comparable for all three size classes. These kinematic differences could also be associated with the lower acclimation temperature for adults, although temperature did not affect U_{crit} or endurance of adult delta smelt. Other studies have reported effects of temperature on at least one kinematic parameter, stroke frequency, to be absent (Smit *et al.* 1971; Rome *et al.* 1984, 1990) or minimal (Sisson and Sidell, 1987; Stevens, 1979).

In both the U_{crit} and endurance experiments, swimming performance even among those fish that swam to fatigue was highly variable. We have observed similarly high levels of variation in other physiological studies with this fish (C. Swanson and J. J. Cech Jr). We consider the variations in behavior and performance observed among delta smelt non-swimmers, transition velocity failures and successful swimmers to represent a continuum of behavioral, physiological and stress responses associated with forced swimming in a flume. However, it is possible that these fish represent distinct subpopulations with different performance and/or behavioral capacities within the species, a phenomenon that has been reported among some other fishes (e.g. juvenile coho salmon *Oncorhynchus kisutch*, Puckett and Dill, 1985). Several lines of evidence argue against delta smelt subpopulations. First, recent genetic analyses indicate that the entire species is a single panmictic population (P. C. Trenham, H. B. Shaffer and P. B. Moyle, unpublished results). Second, detailed morphological analyses of delta smelt collected over several years, including fish used in our experiments, found no different morphotypes within the species (P. S. Young and J. J. Cech Jr, unpublished results). Third, the available ecological and behavioral data on the species, from both field and laboratory studies (excluding this study), provide no evidence for either ecologically or behaviorally distinct subpopulations. For example, delta smelt are consistently found in open, turbid waters of moderate depth, a relatively homogeneous environment, but they are not found in more structured environments closer to shore (except during their spawning season; Mager, 1996). Finally, the proportions of unsuccessful and successful swimmers were not related to fish size, age or season, suggesting that the performance and behavioral parameters we observed are characteristic of the species throughout most of its life cycle. We believe that the relatively large numbers of fish that were unable or unwilling to swim (20–29 % non-swimmers) probably reflect individual variation in the sensitivity of the fish to handling and confinement stress and, despite our careful efforts, unavoidable variations in handling prior to the experiments. In most swimming performance studies, including others conducted in our laboratory, there is usually some fraction of the tested fish that

is unable or unwilling to swim in the flume (although data on these fish are rarely reported). Further, we do not consider the transition velocity failures and the successful swimmers to represent different groups. The large majority of willing swimmers experienced at least one impingement at predictable submaximal velocities. The few fish that avoided non-fatigue-related impingement all exhibited erratic swimming behavior, including contact with the screen and visible distress when forced to swim at velocities within the same velocity range. Compared with the results we have obtained with other fishes (*Morone saxatilis*, Young and Cech, 1993, 1994; *Pogonichthys macrolepidotus*, Young and Cech, 1996; *Oncorhynchus tshawytscha* and *Menidia beryllina*, C. Swanson, P. S. Young and J. J. Cech Jr), the performance and behavior of delta smelt at submaximal velocities were very distinctive. On the basis of these results and observations, the swimming performance of this species in a conventional swimming flume at intermediate velocities appears to depend on behavioral, kinematic and biomechanical factors rather than on morphological and metabolic limits, as it does at high velocities.

Swimming gaits

Kinematic analyses confirmed behavioral observations that delta smelt exhibited three velocity-dependent swimming modes or gaits (Alexander, 1989). Each gait was distinguished by both kinematic and performance characteristics. At velocities below $10\ cm\ s^{-1}$, delta smelt employed 'stroke-and-glide' swimming behavior, alternately swimming and coasting through the water. Using this gait, the fish could swim indefinitely, indicating that aerobic red muscle fibers provided the propulsion (Rome *et al.* 1990; Webb, 1993), and they rarely experienced non-fatigue-related swimming failure. At velocities above 15–$20\ cm\ s^{-1}$ and up to U_{crit}, delta smelt swam by stroking continuously with no intermittent gliding. Most of the fish could sustain swimming using this mode for more than 30 min, suggesting that this activity level was also fueled primarily by aerobic metabolic pathways, and they became impinged infrequently. At velocities near and above U_{crit}, the fish shifted again to discontinuous swimming, using a 'burst-and-glide' gait. We have distinguished this gait from that used by the fish at low velocities for three reasons. First, the kinematics of these two discontinuous swimming modes differed substantially, including the number of strokes per glide and the glide duration. Second, performance, as indicated by endurance, was substantially reduced during 'burst-and-glide' swimming, probably because the fish were utilizing anaerobic white muscles to supplement the power of the aerobic red muscles (Rome *et al.* 1990; Webb, 1993; Jayne and Lauder, 1994). Rome *et al.* (1990) and Drucker and Jensen (1996*a,b*) demonstrated that changes in gaits at high velocities involved recruitment of white muscle to supplement the power of red muscle fibers. Third, the velocity ranges of the different gaits and the transition velocities between gaits were dependent on different characteristics, fish size and stroke frequency at the low-velocity transition and individual performance capacity, as indicated by U_{crit}, at the high-velocity transition.

The size-dependence of the velocity range of 'stroke-and-glide' swimming and the transition velocity between this gait and the next, as indicated by the significant differences in the number of strokes per glide among the life history stages at 10 and $15\,cm\,s^{-1}$ and the size effect on U_{imp1} (discussed below), suggest that the use of this gait may be limited primarily by mechanical or kinematic constraints, such as stroke frequency (and muscle shortening velocity; Rome *et al.* 1990) or body morphology, both of which are size-dependent in delta smelt. Stroke frequencies at mean U_{imp1} for each life history stage were comparable (4.2, 4.7 and 3.7 Hz for juvenile, subadult and adult fish, respectively). In contrast, the transition to 'burst-and-glide' swimming was closely related to individual maximal performance capacity, U_{crit}, a physiologically equivalent level of activity characterized by the recruitment of anaerobic white muscle fibers to support the increased activity level, rather than fish size, absolute velocity or a kinematic parameter such as stroke frequency. This suggests that the transition to this gait may be mediated by metabolic cues as well as mechanical ones (Rome *et al.* 1990). There may be enough qualitative differences among the three types of axial movements exhibited by delta smelt to question whether pattern generators and other neural circuitry are shared, a suggestion also posed by Jayne and Lauder (1994), who studied similar swimming gaits in bluegill sunfish (*Lepomis macrochirus*).

Discontinuous swimming has been shown to be energetically and hydrodynamically advantageous at low velocities (Weihs, 1974) as well as during high-velocity burst swimming (Videler and Weihs, 1982). Energy savings are afforded by the reduction in drag during the glide phase, when the body is held rigidly straight, and can be maximized by increasing the ratio of time spent gliding to time spent stroking and by using only one or two propulsive cycles, or strokes, per glide (Weihs and Webb, 1983). This type of intermittent swimming is also most economical for fishes that swim using a relatively large undulatory wave which has higher drag, e.g. anguilliform swimmers compared with more rigid-bodied carangiform swimmers (Weihs, 1974; Weihs and Webb, 1983; Webb, 1988). The delta smelt has an elongated and flexible fusiform body (length/body depth 6–7.5) and more than 75 % of its body length is displaced laterally during the stroke. At low velocities, the glide time to stroke time ratio for delta smelt approached 1, and the fish consistently swam using one or two strokes per glide. The high stride lengths measured at these velocities further support the conclusion that this gait is extremely efficient for delta smelt. In addition to the energy savings resulting from reduced drag, discontinuous swimming at low and high velocities may benefit delta smelt by optimizing muscle fiber power output and efficiency. Rome *et al.* (1990) showed that discontinuous swimming at low and high velocities improved the efficiency of the carp muscle fibers by allowing the fish to maintain V/V_{max}, the ratio of muscle shortening velocity to the maximum velocity of shortening, within the most effective range (>0.2; Curtin and Woledge, 1988). Carp shifted to discontinuous swimming at

low velocities when, as a consequence of low stroke frequency, V/V_{max} fell below 0.17–0.18, a value too low to generate power efficiently if the fish were swimming steadily. At high velocity when white muscle fibers, which have a much higher V_{max}, were recruited, swimming using intermittent, rapid strokes allowed the fish to operate these muscle fibers at a high V and an optimum V/V_{max}.

The use of discontinuous swimming and three distinct velocity-dependent gaits by the delta smelt may explain some of the atypical and complex kinematic patterns we observed. For most fishes (Bainbridge, 1958; Hunter and Zweifel, 1971; Webb *et al.* 1984; Rome *et al.* 1990; Videler and Wardle, 1991), stroke frequency increases linearly with increases in velocity, and amplitude and stride length are generally constant and independent of velocity, at least at velocities above $1–2\,L\,s^{-1}$. For delta smelt, particularly juveniles and subadults, the relationships between stroke frequency, stroke amplitude and stride length and velocity were markedly curvilinear. For example, increases in stride length for juvenile and subadult fish were probably associated with the relatively larger increases in amplitude within the continuous stroking velocity range and, at velocities near and above U_{crit} and roughly coincident with the transition to 'burst-and-glide' swimming, the attenuation of stroke frequency.

Swimming failure at submaximal velocities

The high incidence of swimming failure at submaximal velocities observed for delta smelt, represented by the transition velocity failures, U_{imp1} and the dramatic decline in endurance between 10 and $15\,cm\,s^{-1}$, coincided with the transition from 'stroke-and-glide' swimming to continuous swimming. Forced, constant-velocity swimming in this transition and intermediate velocity range (>10 to <$20\,cm\,s^{-1}$) appeared stressful in that swimming behavior was erratic. Despite discontinuous swimming within this velocity range, stride length, which can be considered an indication of swimming efficiency, was significantly reduced to the lowest values measured over the fish's performance range. However, the endurance of the fish at the transition and higher velocities, while significantly reduced, was still relatively high (>30 min). This suggests that the transition between the 'stroke-and-glide' and continuous swimming gaits did not involve substantial recruitment of anaerobic white muscles. We are not aware of any reports of similar submaximal or transition velocity swimming failures for other fishes. However, Webb (1975) describes a transitional zone between principal activity levels (sustained, prolonged and burst levels; Brett, 1964) that is characterized by extensive variance in swimming behavior. This fits with our observations of the transition velocity for delta smelt which were changing both activity levels and swimming modes, from the sustained activity level (>200 min endurance; Brett, 1964) and 'stroke-and-glide' gait to the prolonged activity level (1–200 min endurance) and a continuous stroking gait. On the basis of the results of these flume studies as well as observations of spontaneously active, undisturbed fish in large tanks (mean swimming velocity of

undisturbed fish, $N=33$, in a 1 m tank with a 3–4 cm s^{-1} flow regime was 6.9±3.6 cm s^{-1} using 'stroke-and-glide' swimming, 1–2 strokes/glide; C. Swanson and J. J. Cech Jr, unpublished results), delta smelt may avoid regular swimming at velocities within this range.

Ecological correlates and potential management applications

The performance range and swimming behavior of delta smelt illustrated by these experiments are consistent with their ecological niche as small-size, pelagic, selective planktivores (Weihs and Webb, 1983; Videler and Wardle, 1991) and their generalist morphology, which allows for both good low-velocity, unsteady swimming performance as well as adequate high-velocity swimming performance (Webb, 1982). However, flume studies and the U_{crit} and endurance protocols test steady, constant-velocity swimming capacity. Our results presented here, as well as our observations on spontaneously active fish, show that delta smelt are not steady swimmers throughout their swimming velocity range. Therefore, evaluations of physiological performance measurements without consideration of the behavioral context, as well as ecological and management-related interpretations, should be made cautiously.

For a selective planktivore in a homogeneous environment, search is the dominant activity phase of feeding (O'Brien, 1979), and the fish must maximize the volume of water sampled while minimizing energy expenditure (Weihs and Webb, 1983). Our swimming performance and behavior results suggest that low-velocity, discontinuous swimming, efficient and sustainable up to 1–2 L s^{-1}, is probably optimal for this activity. Details of the delta smelt's winter migration are not known, although seasonal sampling for population abundance and distribution suggest that it is slow and diffuse (Moyle *et al.* 1992). These fish may use selective tidal stream transport, moving upstream with flood tides and seeking refuge and holding position during ebb tides, a strategy that has been shown to minimize the energetic costs of migration for other fishes (Harden-Jones *et al.* 1978). Delta smelt are known to move with tidal flows; during the summer and autumn, their population is most concentrated in the 1–2 ‰ salinity range, regardless of tidal cycle or geographic location in the estuary (Moyle *et al.* 1992; Swanson *et al.* 1996). Tidal flows in the estuary can exceed 2 m s^{-1} (Herbold *et al.* 1992) and, given their small size, modest maximum swimming velocities and endurance demonstrated in the laboratory, and their preference for low swimming velocities suggested by observational studies, the fish probably do not make this long-distance movement at constant velocity.

Flow criteria for water diversions and fish bypass systems are usually developed using endurance–velocity relationships and U_{crit} results obtained from flume studies such as those described here for delta smelt. The management objective is to determine the maximum velocity that the majority of fish of a given size and under specific environmental conditions (e.g. temperature) can sustain without impingement for a specified period, usually the predicted exposure time to the diversion or bypass. For most fishes, this velocity is U_{crit}. However, delta smelt swimming performance in the flume, as indicated by the ability to avoid impingement, was often limited at submaximal velocities by behavioral, kinematic and (probably) biomechanical factors, not by physiological or metabolic capacity. This is a distinctly different result from those obtained from fishes such as salmonids, shad and striped bass, and which have been applied to develop flow criteria (Kerr, 1953; Kano, 1982; Bates, 1988; Clay, 1995). The direct use of these results for delta smelt would result in unacceptably low allowable velocities, perhaps 0 cm s^{-1}, since a substantial minority of the fish failed to swim at all, and would probably seriously misinterpret the fish's true performance in flowing waters. Delta smelt will require a different experimental approach, which incorporates behavioral preferences, to develop realistic flow management guidelines.

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