Swimming performances of four California stream fishes: temperature effects

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Synopsis

The critical swimming velocity (U_{crit}) of four California stream fishes, hardhead, *Mylopharodon conocephalus*,
hitch, *Lavinia exilicauda*, Sacramento pikeminnow, *Ptychocheilus grandis*, and Sacramento sucker, *Catostomus*
occidentalis was measured at 10, 15, and 20°C. Hardhead, Sacramento sucker, and Sacramento pikeminnow swim-
ming performances tended to be lowest at 10°C, higher at 15°C, and then decreased or remained constant at 20°C.
Hitch swimming performance was lower at 10°C than at 20°C. There were no significant differences among species
at 10 or 15°C, although pikeminnow and hitch were ca. 20% slower than hardhead or sucker. At 20°C hardhead,
Sacramento sucker, and Sacramento pikeminnow had remarkably similar U_{crit} but hitch were significantly (by 11%)
faster. We recommend that water diversion approach velocities should not exceed 0.3 ms^{-1} for hitch (20–30 cm total
length) and 0.4 ms^{-1} for hardhead, Sacramento pikeminnow, and Sacramento sucker (20–30 cm TL).

Introduction

The endemic fish fauna of the Sacramento–San Joaquin
river system (California) includes a number of unique
cyprinids and catostomids (Brown & Moyle 1993,
Moyle 1976), many of which have experienced declines
in abundance and distribution. Some species, such
as the thicktail chub, *Gila crassicauda*, Sacramento
perch, *Archoplites interruptus*, and Clear Lake splittail,
Pogonichthys ciscoides, are either extinct or extremely
rare throughout their historical ranges. Native fish
population declines are the result of the combined
effects of exotic species introductions (Brown &
Moyle 1993), impoundment construction (Moyle et
al.[1]), large scale water diversion (McEwan & Jackson
1996), and historical fisheries management practices
(Moyle et al. 1983). Fortunately, habitat alterations due
to dam construction, intentional species introduction,
and destructive management practices have largely
ceased. Perhaps the gravest threat still facing native
fishes are the > 1000 screened and unscreened water
diversion intakes along the remaining free-flowing sec-
tions of the Sacramento and San Joaquin river systems
(McEwan & Jackson 1996). Unlike velocity barriers,
which fish like the Sacramento sucker, *Catostomus*
occidentalis, attempt to negotiate with high-velocity,
short duration bursts of anaerobic swimming (Wales
1950), fish may try to negotiate approach velocities of
water diversion intakes at aerobic speeds. Indeed, the
largest diversions are powerful enough to reverse flows
in sizable portions of the Sacramento–San Joaquin sys-
tem, making it very hard for fish to avoid displacement
and/or entrainment (Miller[2]).

[1] Moyle, P. B., R. M. Yoshiyama, J. E. Williams & E.D.
Wikramanayake. 1995. Fish species of special concern in
California. Final Report, 2128IF, Department of Wildlife &
Fisheries Biology, University of California, Davis. 272 pp.

[2] Miller, P.B. 1993. The delta: overview of the Sacramento-San
Joaquin Delta. Report to the California Urban Water Agencies.
49 pp.

The risk of entrainment and severe injury or death at an intake may be exacerbated by the drastic alteration of the natural flow and thermal cycles in the Sacramento–San Joaquin system's impounded streams (McEwan & Jackson 1996, Miller[2]). Central Valley rivers historically carried large volumes of cold water in winter and early spring and smaller volumes of warmer water at other times. However, flow patterns are now determined by the agricultural, urban, and industrial demands. Currently, flows are generally reduced during the winter months, increased flows of cold water are provided in late spring and summer, and reduced flows of warm water are provided in fall and early winter. Because fishes' aerobic swimming performances can be affected by water temperature (Johnston & Ball 1997) and season (Kolok 1991), it is possible that the risk of entrainment is increased by these unnatural flow regimes.

Until recently, most research on California's native fishes' temperature effects focused on the economically valuable chinook salmon, *Oncorhynchus tshawytscha*, and steelhead, *Oncorhynchus mykiss irideus* (Castleberry et al.[3], McEwan & Jackson 1996). Increased awareness of the critical status of native non-game delta smelt, *Hypomesus transpacificus*, and splittail, *P. macrolepidotus*, and the magnitude of the threats facing them led to their protection under federal endangered species legislation. These species' environmental tolerances and swimming performance under different conditions have been investigated recently (Swanson et al. 1998, Young & Cech 1996). Native fishes that are not currently protected under state or federal endangered species legislation demand more study because they often dominate the fish fauna in both biomass and absolute numbers (Moyle et al. 1983).

Our objectives were: (1) to measure swimming performance of wild-caught, endemic hardhead, *Mylopharodon conocephalus*, hitch, *Lavinia exilicauda*, Sacramento pikeminnow, *Ptychocheilus grandis*, and Sacramento sucker, *Catostomus occidentalis* at 10, 15, and 20°C, and (2) compare their swimming ability with that of the sympatric rainbow trout. These temperatures are seasonally found in the altered parts of the Sacramento–San Joaquin system where remnant populations remain.

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[3] Castleberry D. T., J. J. Cech, Jr., M. K. Saiki & B. A. Martin. 1993. Growth, condition, and physiological performance of juvenile salmonids from the lower American River: February through June, 1992. Report to the East Bay Municipal Utilities District. U. S. Fish and Wildlife Service. 128 pp.

Material and methods

Fish capture, transport, and holding

Fish were collected from Cache Creek (Yolo and Lake Co.), Putah Creek (Yolo and Solano Co.), and the Pit River (Shasta Co.), all tributaries of the Sacramento River. Sacramento suckers were collected via seining or electrofishing, while all other fishes were line fished using artificial lures with barbless hooks. Seasonal, weather, and flow-driven fluctuations in fish distribution and abundance prevented use of large, equal sample sizes for each species × temperature treatment. Fish were transported to the University of California, Davis, in insulated, oxygenated 120 to 250 liter containers. Sodium chloride (3 g l^{-1}) and MS-222 (25 mg l^{-1}) were added to the water to minimize transport and handling stresses (Carmichael et al. 1984).

Species were segregated in insulated, shaded, round 500-liter fiberglass tanks receiving a constant supply of air-equilibrated, active carbon-dechlorinated well water. Dissolved oxygen levels always exceeded 90% of air saturation. Angled spray bars created a 0.2 to 0.3 m s^{-1} orientation current. Fish were initially held at the collection site temperature (7 to 23°C) for 1 to 2 days before being acclimated at 1°C d^{-1} to test temperatures of 10, 15, and 20°C. Fish were acclimated to the test temperature closest to their collection temperature to avoid acclimation to unseasonal temperatures. Fish were never held for > 4 weeks. Hardhead, hitch, and Sacramento suckers were fed commercial trout pellets and frozen adult *Artemia*, and Sacramento pikeminnows were fed live goldfish, *Carassius auratus*, and mosquitofish, *Gambusia affinis*. Individual fish were randomly selected and transferred to a separate flow-through holding tank and fasted for 48 h prior to swimming experiments.

Swimming experiments

We measured the four species' maximum sustainable aerobic swimming velocity (critical swimming velocity; U$_{crit}$) (Beamish 1978) in a 120-liter Brett-type swimming flume (Brett 1964) with a velocity range of 0.1 to 0.8 m s^{-1}. Fish were transferred to the swimming chamber after being lightly anesthetized (25 mg l^{-1} MS-222; 3 g l^{-1} NaCl). Fish were exposed to the anesthetic treatment for < 3 min to reduce stress associated with capture and handling and never exceeded the first stage of anesthesia (Iwama & Ackerman 1994).

Fish recovered for 1 h in a 0.1 m s⁻¹ orientation current. Fish that did not orient to the current within 5 min were removed and not tested (3 hardhead, 2 hitch). After recovery, water velocity was increased in 0.1 m s⁻¹ steps every 30 min until the fish fatigued. We defined fatigue as the point when a fish became impinged on the rear swimming chamber screen and refused further swimming despite temporary flow reductions and gentle prodding with a rod. Fatigued fish were lightly anesthetized, weighed to the nearest gram, measured (total length, TL, in cm) and marked with a dorsal fin clip. Fish were held for 1 week to monitor post-experimental mortality (no mortality occurred) and were then released at the collection sites.

Data analyses

Critical swimming velocities (m s⁻¹) were calculated (Brett 1964) for each fish. Differences among treatment mean morphometric and swimming performance data were tested for using t-tests and ANOVA. Student–Newman–Keuls and Dunn's post-hoc tests were used. We used backward stepwise regression analyses to test for relationships between each species' U_{crit}, TL and water temperature.

Results

Hardhead, hitch, and Sacramento pikeminnow swam steadily over the tested velocity and temperature ranges but Sacramento sucker did not. At low velocities, the sucker remained stationary on the bottom of the swimming chamber with their paired fins

angled, possibly creating downward-oriented lift to resist downstream displacement. Suckers transitioned to intermittent swimming at moderate velocities and only used steady swimming at velocities approaching their impingement velocity. The maximum velocity at which suckers could avoid impingement was defined as the critical holding velocity and is held to be functionally similar to the U_{crit} (Rimmer et al. 1985).

Size

Fishes used in the experiment were generally similar in size (Table 1), possibly resulting from the size-selective collecting techniques. However, the 10°C hardhead and hitch were significantly longer than the 10°C suckers and pikeminnows, and the pikeminnows were in turn significantly longer than the 10°C suckers. The 10°C hardhead were similar in size to the 15°C hardhead, but were significantly longer than the 20°C hardhead. Hitch used at 20°C were significantly shorter than those used at 10°C. Because of the small range of sizes used, the only species for which size was a significant independent variable in the regression equations was the hitch. Curiously, larger hitch (albeit at the cooler temperature) swam more slowly:

$$U_{crit} = 1.85 + TL(-0.055).$$ Body weight variation generally followed the TL pattern.

Temperature

The relatively narrow temperature range ($\Delta T = 10$°C) did not significantly affect U_{crit}, with the exception of

Table 1. Native non-gamefish mean (±SE) total lengths, weights, and critical swimming velocities when acclimated to different temperatures. The same superscripted letters in one column denote statistical similarity between species at the same temperature (p > 0.05). Identical superscripted numbers in one column denote statistical similarity within a species at the different temperatures.

Temperature (°C)	Species	n	Total length (cm)	Weight (g)	Critical swimming velocity (m s⁻¹)
10	hardhead	10	28.5 ± 0.95[a1]	194 ± 20.1[a1]	0.47 ± 0.03[a1]
	hitch	5	26.0 ± 0.68[a1]	164 ± 11.3[a,b1]	0.39 ± 0.07[a1]
	Sacramento pikeminnow	9	22.9 ± 0.43[b1]	87 ± 5.5[b,c1]	0.40 ± 0.06[a1]
	Sacramento sucker	7	19.1 ± 0.87[c1]	60 ± 9.1[c1]	0.47 ± 0.05[a1]
15	hardhead	7	24.4 ± 1.61[a1,2]	124 ± 25.9[a1,2]	0.57 ± 0.02[a1]
	Sacramento pikeminnow	10	24.7 ± 0.69[a1]	104 ± 9.2[a1]	0.57 ± 0.04[a1]
	Sacramento sucker	8	20.0 ± 1.12[b1]	79 ± 17.8[a1]	0.48 ± 0.06[a1]
20	hardhead	12	22.5 ± 1.32[a2]	102 ± 22.2[a2]	0.51 ± 0.04[a1]
	hitch	8	23.7 ± 0.53[a2]	116 ± 10.2[a2]	0.57 ± 0.03[b2]
	Sacramento pikeminnow	8	23.3 ± 1.04[a1]	88 ± 10.7[a1]	0.50 ± 0.06[a1]
	Sacramento sucker	8	20.9 ± 1.47[a1]	93 ± 20.6[a1]	0.51 ± 0.05[a1]

hitch, where those swimming at 10 C were ca. 0.8 m s^{-1} slower than hitch swimming at 20°C. This difference may have resulted from the size difference (equation above). The other species' swimming performances tended to be lowest at 10°C, higher at 15°C, and then decreased or the same at 20°C, but perhaps due of the small sample sizes and high variability, these were not significant trends.

Interspecies comparisons

There were no significant performance differences among the species at 10 or 15°C, although the pikeminnow and hitch were approximately 20% slower than hardhead and sucker. At 20 C, hardhead, Sacramento pikeminnow and Sacramento sucker swam at remarkably similar velocities, but hitch were significantly (by 11%) faster.

Discussion

Despite differences in microhabitat use (Brown & Moyle 1991), hardhead, hitch, Sacramento pikeminnow, and Sacramento sucker showed similar levels of station-holding (i.e., swimming) performance over the 10 to 20°C range. Although hardhead swimming performance did not significantly vary with temperature, the highest mean U_{crit} occurred at 15°C (Figure 1a). The 17 to 26% larger hardhead at 10°C (slowest mean U_{crit}) may have been restricted by the swimming chamber, although their cross-sectional areas did not exceed the recommended maximum of 10% of the swimming chamber's cross-sectional area (Webb 1993). Alternatively, the smaller hardhead could have derived some hydrodynamic advantage from occupying the boundary layer, though hardhead tended to swim in the middle of the swimming chamber. Cech et al. (1990) reported that hardhead resting routine oxygen consumption rates only increased by 33% over the 10 to 20°C range, far less than the 2 to 3-fold increase typically seen in poikilothermic vertebrates (Schmidt-Nielsen 1990). Recent studies have reported that fish show decreased physiological thermal sensitivity at temperatures approaching their optimum, which may explain our hardheads' 15°C swimming optimum (Jobling 1997, Taylor et al. 1997). The lack of a significant relationship between hardhead size and swimming performance may have resulted from the narrow range of sizes used.

Although hardhead often occur sympatrically with rainbow trout in relatively cool (10 to 15°C) reaches
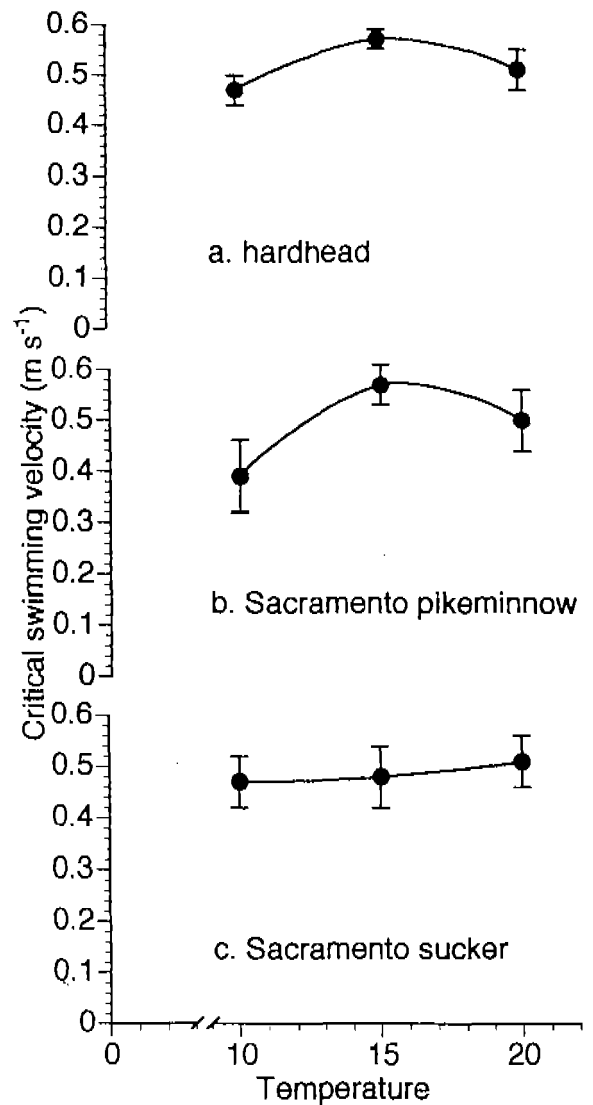

Figure 1. Effects of temperature on the critical swimming velocities of hardhead, Sacramento pikeminnow, and Sacramento sucker.

of the Sacramento–San Joaquin system, they are also found at temperatures of 26 to 28 C (Cooper 1983), higher than the incipient lethal limit for rainbow trout (Cherry et al. 1977). Future measurements of hardhead swimming performance at these higher temperatures would be of interest.

Hitch were the only tested species that showed a significant difference between U_{crit} at different temperatures, although, this difference may have been influenced by the larger size of the 10°C fish (see equation).

This relationship between U_{crit} and TL was unexpected, because U_{crit} (cm s^{-1}) generally increases with TL (reviewed by Beamish 1978. Yates 1983). We suspect that our observation results from a negative effect of the swimming chamber on the larger hitch, though their swimming movements appeared to be unimpaired. We can only draw tentative conclusions regarding our hitch results because of the lack of statistical robustness conferred by the small sample size. The impressive swimming performance of hitch at 20°C would serve them well in the warm, low-elevation lakes, sloughs and slow-moving river reaches where they are typically found.

Sacramento pikeminnow enjoy the second largest distribution of the species studied, being found throughout the low- to mid-elevation reaches of the Sacramento–San Joaquin system. Although Sacramento pikeminnow swimming performance was not significantly affected by temperature (Figure 1b), the highest mean U_{crit} at 15°C may indicate an optimal temperature. Cech et al.'s (1990) findings regarding Sacramento pikeminnow metabolism support this hypothesis. Cech et al. (op. cit.) found that their oxygen consumption rates were generally independent of temperature from 15 to 25°C, with a significant increase between 10 and 15°C.

The most widely distributed species in our study, the Sacramento sucker also had the most temperature-independent swimming performance (Figure 1c). We observed no temperature or size-related differences in U_{crit}: the difference between the 10 and 20°C treatments' mean U_{crit} was a remarkably low 0.04 m s^{-1}. This temperature-independent performance may result from the intermittent swimming behavior and use of the paired fins. This swimming mode may be energetically more efficient than steady swimming (Johnson et al. 1994), reserving more energy for use during steady swimming at velocities approaching their impingement velocity. Additionally, the suckers' demersal orientation could allow them to better exploit the flow boundary layers than the other three species, which typically swam in the center of our swimming chamber. Finally, of the species tested, Sacramento sucker are found along the most extensive elevation and thermal gradient (Moyle 1976), including high-velocity microhabitats (Brown & Moyle 1991). Presumably their consistent swimming performance across the 10 to 20°C range facilitates this distributional success.

Based on our data, water diversion approach velocities should not exceed 0.3 m s^{-1} (hitch) to 0.4 m s^{-1}

(hardhead, Sacramento pikeminnow, Sacramento sucker). High levels of swimming performance variation have been reported in other North American cyprinids (Kolok & Farrell 1994) and may reflect the functional and genetic diversity present in wild fish populations. Because Sacramento sucker are so widely distributed, they are more likely to encounter water diversion intakes than the other tested species. To preserve as much of the genetic stock as possible, conservative swimming performance estimates should be used to avoid excluding significant fractions of their populations. Future studies should also measure the swimming performance of juveniles and the semipelagic larvae of native cyprinids and catostomids.

Interspecific comparisons

With the exception of the hitch and hardhead at 10°C and the 15°C Sacramento suckers, the fish used were of similar size, which simplifies the task of comparing their swimming performances. For a given temperature, the four species tested had statistically similar swimming performances, although the sample sizes were relatively small and the intra- and inter-treatment variation mostly large. However, given these species' sympatry, their similar aerobic swimming performances are not an unexpected result. The three cyprinids (hardhead, hitch, and pikeminnow) had similar swimming styles that responded to temperature in a similar manner, possibly due to convergent selective pressures or as traits inherited from a common cyprinid ancestor.

The only resident, native, sympatric gamefish is the rainbow trout (Brown & Moyle 1993). Rainbow trout are less tolerant of high temperatures than the four species studied here with reported incipient lethal temperatures of ca. 26°C and upper critical thermal maxima for California hatchery strains approaching 31°C at high acclimation temperatures (Myrick 1998). Critical swimming velocity values for 20 to 30 cm rainbow trout range from a low of 0.34 to 0.52 m s^{-1} (Duthie 1987) to a high of 0.94 m s^{-1} (Mulchaey 1994). The effects of size on rainbow trout swimming have been well documented (Bainbridge 1958, Webb et al. 1984). The rainbow trout's higher U_{crit} for the same size fish, argues for water diversion approach velocities to be based on the native, non-game species' swimming abilities, rather than those of the gamefish, especially at temperatures < 15°C.

Ecological considerations

We demonstrated that four. sympatric wild fishes have similar swimming performances over a range of temperatures normally encountered (but see Peake et al. 1997). Despite the similar swimming performances. these species manage to avoid serious competitive interactions through microhabitat partitioning (Moyle & Baltz 1985). We were not able to determine if these species' performance variability resulted from inherent (genetic) functional diversity or from their differential responses to handling and the laboratory environment. Some of our recent work with domesticated strains of rainbow trout (Myrick 1998) suggests that the high level of variability is commonplace even among fish accustomed to frequent handling.

Other swimming-related research is warranted on wild California native fishes. Steady swimming is affected by a number of factors. among them light levels (Swanson et al. 1998). dissolved oxygen levels (Bushnell et al. 1984). xenobiotic toxins (Heath et al. 1997), and feeding state (Alsop & Wood 1997), and these factors need to be investigated for these and other California native non-gamefishes. Steady swimming only represents one component of normal fish swimming behavior. and work needs to be done on unsteady and burst-swimming ability, especially since many fishes use these swimming modes to navigate barrier mitigation structures like fishways and fish ladders (Clay 1995). Finally, physiologists have recognized the limitations of extrapolating data from restrictive flume-experiments to wild situations. Because of this, there is a need for more studies integrating laboratory and field telemetry and studies using large-scale swimming flumes.

Acknowledgements

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