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Synopsis

Spawning of razorback suckers, *Xyrauchen texanus*, in Lake Mohave occurred from 10–22° C and larvae were collected at water temperatures from 10–15° C in 1982 and 1983. In the laboratory, hatching success was similar from 12–20° C, but reduced hatching success was found at 10° C while none hatched at 8° C. Development rate and oxygen consumption were positively related to incubation temperature. Direct effects of ambient Lake Mohave water temperatures on hatching success of razorback sucker embryos are considered minimal. Historical spawning temperatures for the species are hypothesized based upon successful incubation temperatures and comparison to the white sucker, *Catostomus commersoni.*

Introduction

Lower-than-historic water temperatures from hypolimnetic discharges of dams on the Colorado River have been implicated as a factor contributing to the decline of razorback suckers, *Xyrauchen texanus* (Vanicek et al. 1970, Johnson & Rinne 1982, Marsh 1985, Tyus 1987). Thermal cycles under which native species evolved have been altered by these discharges, which increase winter temperatures and decrease those in summer (Paulson et al. 1980a). Reduced temperatures during incubation may directly result in egg mortality or increase the length of exposure of embryos and larvae to other sources of mortality such as water level fluctuations, predation, and severe wave action.

Initiation of spawning by fishes is usually timed with optimal survival temperatures. Naturally-spawned eggs should be expected to emerge as larvae at ambient temperatures as long as seasonal thermal trends continue (McCormick et al. 1977, Alabaster & Lloyd 1980). Spawning of razorback suckers has been documented in nature at water temperatures from 6–22° C (Douglas 1952, McAda & Wydoski 1980, Bozek 1984, Tyus 1987). In the laboratory, Marsh (1985) found that 20° C was the optimal incubation temperature for razorback suckers, with lower hatching success at 15° C and complete mortality at 5 and 10° C. It appears, therefore, that poor reproductive success in the Colorado River may be due to incompatible incubation temperatures from cold hypolimnetic discharges of reservoirs.

Lake Mohave contains the largest known population of razorback suckers (Minckley 1983, Bozek 1984). The species is rare in other lower river

locations (Minckley 1983), and rare in the upper Colorado River (Holden 1978, Holden & Stalnaker 1975, Tyus 1987). Spawning by razorback suckers is widespread in Lake Mohave, and while successful reproduction and emergence of larvae have been repeatedly documented (Paulson et al. 1980b, Bozek 1984, Marsh & Langhorst 1988), there has been no evidence of recruitment (McCarthy & Minckley 1987).

Inappropriate temperature regimes have been suggested as one reason for the poor reproductive success of the razorback suckers (Johnson & Rinne 1982, Marsh 1985). In Lake Mohave, spawning occurs from 10–22° C (Bozek 1984), a temperature regime which appears largely incompatible with the optimal incubation temperature of 20° C obtained by Marsh (1985). This suggests that successful embryonic development and emergence may not occur or may be reduced during a large part of the spawning season, and contribute to recruitment failure. The purpose of this study was to determine temperature ranges under which razorback sucker larvae emerge in Lake Mohave and describe hatching success, development rates, and oxygen consumption in the laboratory under corresponding temperatures.

Methods

Larvae were collected from Lake Mohave at night in known spawning areas using hand-held dive lights during 1982 and 1983. The lights were held stationary, 0.25 m above the water surface, and larvae entering the illuminated area during 15 min sample periods were netted by hand. Collections were usually made in water approximately 1 meter deep, but three water depths were sampled in the Six Mile Coves area in February 1983. Species identification and interval of development was determined for each larvae following Snyder (1981) and Fuiman (1979), and by using laboratory-cultured razorback sucker larva as reference material. Early and late protolarvae correspond to free embryos while early mesolarvae correspond to larvae (Balon 1984). When collections at a site exceeded 300 individuals, only 50% were processed to determine stages of development.

To assess development under controlled thermal regimes, razorback sucker eggs were inseminated in the field with the sperm from ripe adults netted from Arizona Bay and the Six Mile Coves area. Gametes were collected from 6 adult pairs during 1982 and 8 adult pairs in 1983. Sperm was collected and mixed prior to stripping females to insure maximum genetic variability. All fish used were naturally ripe individuals. No hormonal injections were used to induce egg maturation.

Fertilized eggs were transported at ambient lake temperature immediately following insemination. In the laboratory, fertilized eggs were randomly placed in experimental chambers at lake temperature. Total time from insemination to placement of eggs into chambers was approximately 4 h. Eggs were then acclimated at the rate of 1° C per hour to experimental temperatures (8, 10, 12, 15 and 20° C depending upon experiment) in 18.9 liter aquaria. Temperatures were held within 1.5° C of reported temperature during the duration of the experiment. All acclimation was completed prior to the morula stages of development. Temperature was regulated using a Masterline Model 2095 closed-system, water recirculating and cooling unit, with individual offsetting thermostatic heating units. Water supply was dechlorinated municipal water from Lake Mead.

In 1982, eggs were dispersed over cobble substrates in individual aquaria. During these experiments, fungus developed on some eggs in interstitial pockets that were adjacent to non-developing eggs. To alleviate this, in 1983, eggs were placed in individual chambers on 80-μm-mesh *Nitex* netting and suspended from a rocker-arm assembly having a rocking amplitude of 5 cm and periodicity of 7 cycles per minute. Rocking action provided water movement through the netting and furnished oxygenated water to the eggs. This design prevented fungus from developing on the eggs and precluded treatment of the eggs with fungicide. Experiments between years were not combined because we did not know how the increased water flow associated with the rocker arm assembly would affect oxygen

diffusion rates through the egg envelopes and therefore affect hatching success and development rates. Temperatures used in 1982 were 10, 15, and 20° C while those in 1983 were 8, 12, 15, and 20° C in the first experiment, and 8, 10, 15, and 20° C in the second.

Eggs were examined, state of development determined, and dead eggs removed three times daily. The time in hours for 5, 50, and 95% of the individuals to attain a particular state of development was recorded at each temperature. Only viable offspring were enumerated to determine percent of successful hatching.

Oxygen consumption was measured using a Gilson, differential, single-valve-style respirometer. Eggs, embryos and larvae used in the respirometry experiments were separate from those used in the hatching success. Test chambers contained 8 ml of water and 0.2 ml of 10% KOH in the center well and were temperature controlled by submersion in a self-contained, thermostatically-controlled water bath. Amplitude of rocking during the experiment was 4 cm with periodicity of 60 cycles min^{-1}. Chambers were allowed to equilibrate at test temperatures for 15 minutes prior to starting and were adjusted for barometric pressure.

Respiration rates could not be determined for individual eggs, embryos and larvae at lower temperatures and earlier life stages, so 30 eggs or 15 larvae were used per chamber and measurements were recorded hourly. Oxygen consumption was expressed as μl O_2 15 $individuals^{-1}$ h^{-1}. Three to eight replicates were made at each temperature and life interval. Intervals of development were based upon Minckley & Gustafson (1982): morula/blastula (stages 10–11), pre-tailbud (stages 18–19), pre-hatch (stages 24–26), immediate post-hatch (stages 27–29), swim-up (stage 31), and yolk depletion (stage 33–34).

Results

Field collections

Razorback sucker larvae were collected in Lake Mohave at 9.5–15.0° C, indicating successful incubation of eggs at these temperatures (Table 1). Diel variation in temperature at collection sites was as

Table 1. Lake Mohave razorback sucker larvae collections.

Date	Location[1]	Diel H_2O temp Max/Min	Water depth (m)	# Larvae per minute	Developmental[2] stage (%) EP	LP	EM
20.2.1982	YC	11.0/10.0	1.0	0.52	*	*	*
20.2.	AB	12.0/10.0	2.5	0.60	*	*	*
25.2.	SM	12.0/10.0	0.3	0.33	*	*	*
26.2.	YC	12.0/10.0	0.3	0.40	*	*	*
23.1.1983	YC	11.0/ 9.5	1.0	0.20	75.0	25.0	0.0
25.1.	SM	11.0/ 9.5	1.2	0.47	57.1	42.9	0.0
19.2.	SM	12.0/10.5	1.1	9.85	13.9	71.1	14.9
19.2.	SM	12.0/10.5	2.8	4.69	6.2	66.8	27.8
19.2.	SM	12.0/10.5	4.9	0.77	0.0	82.6	17.4
29.2.	NS	12.0/10.5	1.1	3.53	29.2	63.2	7.6
25.3.	SM	15.0/15.0	1.1	0.0	–	–	–
25.3.	SM	15.0/15.0	2.8	0.0	–	–	–
25.3.	SM	15.0/15.0	4.9	0.0	–	–	–
26.3.	TC	15.0/15.0	1.1	0.84	23.7	65.8	10.5
26.3.	TC	15.0/15.0	6.1	0.0	–	–	–

Total number of larvae collected = 1205

[1] YC = Yuma Cove; AB = Arizona Bay; SM = Six Mile Area; NS = North Six Mile Area; TC = Tequila Cove

[2] EP = Early protolarvae; LP = Late protolarvae; EM = Early mesolarvae; * = indicates developmental stage not determined

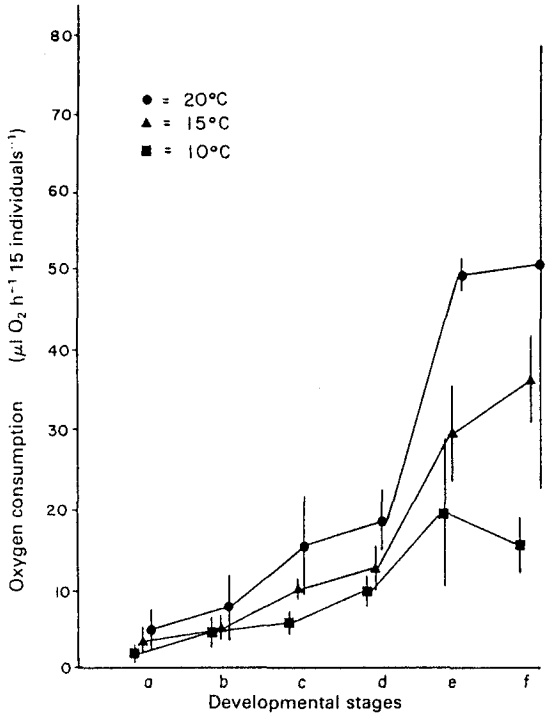

Fig. 1. Oxygen consumption of egg, embryo and larva stages of razorback sucker, *Xyrauchen texanus*, at three developmental temperatures (10, 15, and 20° C). Developmental stages correspond to Minckley & Gustafson (1982) and are: a – morula/bastula, b – pre-tailbud, c – pre-hatch, d – post-hatch, e – swim-up, and f – yolk depletion. Oxygen consumption values are the means and corresponding 95% confidence intervals.

high as 2° C occurring in February 1982. Based upon developmental rates at 10° C, larvae collected in January 1982 probably were the result of spawning in early December or late November 1981. November through January are the coldest seasonal water temperature months in Lake Mohave.

The highest density of larvae was found in the Six Mile Coves area in February 1983 when 10 larvae min^{-1} were collected at a depth of 1.1 m. Larvae were less abundant on that date in deeper water over the spawning area. Water temperatures during collecting were 12.0° C during the day and 10.5° C at night.

Although larvae were abundant in the Six Mile Coves area in February, no larvae were collected from this site in March. Severe winds and heavy wave action preceding the collection dates disrupted and likely decimated redds in the spawning area. Spawning in this area was abandoned for the remainder of the year following the storm but continued in other areas of the reservoir that presumably were more protected as evidenced by larvae collected from Tequila Cove.

Total lengths of wild-caught larvae on different sampling dates ranged from 10.4 ± 0.5 to 11.1 ± 0.5 mm (mean ± 1 sd). The largest was 12.6 mm and in the early mesolarval stages of development. No larvae collected were past this stages of devel-

Table 2. Hatching success of razorback suckers as a function of water temperature. Percent viable hatch of normal embryos are expressed as the mean ± one standard deviation.

Experiment	Spawning temperature	Incubation temperature	Number of replicates	No. of ova per replicate	% viable hatch (mean)	% viable hatch (range)
A	11.0	10	2	250	57.3 ± 7.3	(52.2–62.3)
B	12.8	10	1	626	21.9	na
	12.8	15	1	580	32.2	na
	12.8	20	1	601	33.6	na
C	11.0	8	4	50	0.0	na
	11.0	12	4	50	36.0 ± 10.8	(20.0–44.0)
	11.0	15	4	50	39.5 ± 4.9	(34.0–46.0)
	11.0	20	4	50	38.0 ± 4.8	(34.0–44.0)
D	13.0	8	4	70	0.0	na
	13.0	10	4	70	36.3 ± 7.3	(27.0–44.0)
	13.0	15	4	70	64.8 ± 5.0	(59.0–71.0)
	13.0	20	4	70	64.5 ± 3.8	(61.0–70.0)

na = not applicable.

opment. Larvae collected in February 1983 tended to be developmentally older than those in January.

Laboratory studies

Embryos successfully hatched in the laboratory at 10–20° C but there were no viable embryos hatched at 8° C (Table 2). Hatching success ranged from 22 to 57% at 10° C, 32 to 65% at 15° C, and 34 to 65% at 20° C. Optimal hatching temperatures appear to be from 12–20° C where hatching success was similar within experiments. Although success was considerably lower at 10° C than at 15 or 20° C in two experiments, it was remarkably high in the first experiment (57%).

The highest mortality during incubation was at 10° C occurring prior to the morula stages. Almost 30% greater mortality occurred at 10° C in experiment D during these pre-morula stages than at either 15 or 20° C. The effect of vacillating temperatures varying between 8.5 and 11.5° C in experimental chambers is unknown.

Development rate was positively related to temperature (Table 3). Hatching time for 50% of the eggs was 420-556 h at 10° C, 256–298 h at 15° C, and 158–168 h at 20° C. Swim-up for 50% of the larvae took 3 times longer at 10° C than at 20° C. Development rate for larvae through yolk depletion was also positively related to temperature although experiments were usually terminated prior to full yolk depletion for all larvae at 10° C. Oxygen consumption increased with increased temperatures at all developmental stages (Fig. 1). Oxygen consumption also increased with development at each temperature. The largest increase in oxygen consumption was associated with the swim-up development stages. Likewise, variability was also highest among replicates at these stages, possibly due to the different physiological abilities to swim.

Discussion

Comparison of hatching success

Our laboratory data indicate that spawning by razorback suckers is successful at 10–22° C. These temperatures correspond to those occurring in Lake Mohave during their 7-month spawning season, November through May. Larvae collected from Lake Mohave at 10–15° C confirmed laboratory results that lower temperatures did not preclude successful spawning.

Hatching success in the laboratory was similar between 12 and 20° C, but reduced at 10° C in one experiment. Hatching success at 10° C was never less than 50% of the warmer incubation temper-

Table 3. Influence of temperature on hatching and developmental rates. Values are hours since insemination when 50% of the individuals per sample attained a particular developmental interval. Range of development times expressed as 5% and 95% individuals attaining a particular developmental interval are in parentheses.

Experiment	Temp. C°	Hatch	Swim-up	Yolk-depletion
A	10	420 (312–504)	672 (591–855)	879 (654–999)
B	10	449 (253–624)	864 (648–1032)	1032 (984–*)
	15	256 (196–312)	408 (360–504)	552 (520–624)
	20	158 (113–216)	288 (259–334)	408 (360–432)
C	8	–	–	–
	12	444 (370–542)	–	–
	15	298 (241–355)	–	–
	20	162 (150–173)	–	–
D	8	–	–	–
	10	556 (530–624)	840 (744–*)	*
	15	272 (242–336)	506 (482–530)	636 (552–720)
	20	168 (149–183)	288 (264–304)	448 (408–480)

* Experiment was terminated prior to 95% of the individuals reaching these developmental stages.

atures. No hatching occurred at 8° C. Our results differ from Marsh (1985) and Toney (1974) who found total egg mortality occurring at 10° C. Marsh (1985) also reported reduced hatching at 15° C. The development rates we observed were less than those reported by Minckley & Gustafson (1982) and Marsh (1985) at corresponding temperatures. This may have resulted from lower initial spawning and preacclimation temperatures of adults and eggs in our study.

Our success in incubating eggs at lower temperatures may reflect simulation of natural conditions to a greater degree than those of previous investigators. Marsh (1985) and Toney (1974) had higher acclimation temperature gradients (higher preacclimation temperatures), used formaldehyde to control fungus, and hormonally-induced maturation of ova. Eggs used by Marsh (1985) were spawned at 17.5–18° C and those used by Toney (1974) were at 16° C before being acclimated to lower temperatures. Different stages of embryonic development are more sensitive to both negative changes and the degree of change in temperature (Alabaster & Lloyd 1980, Cloud et al. 1988). In both studies, embryos were treated with formaldehyde but the synergistic effects of formaldehyde and reduced temperatures are unknown to us. Minckley & Gustafson (1982) found that hormonally-induced ovulation resulted in razorback sucker eggs averaging 1.8 mm diameter, while naturally-ripened eggs averaged 2.9 mm. Egg diameters in our experiments using naturally-ripened fish (mean = 3.1 ± 0.4 sd) were similar to the latter.

It is difficult to control all external variables and look solely at incubation response to temperature differences. Our use of naturally-ripened adults, lower temperature acclimation, and avoidance of formaldehyde may have contributed to differences between our results and those of others. The variability in hatching success among our experiments may indicate the presence of other factors influencing hatching success. Fluctuations in temperature in the experimental chambers may have increased mortality at 10° C. Temperature buffering in the reservoir may reduce this source of mortality and therefore may not be as significant in Lake Mohave.

Influence of temperature on reproduction

Temperature is an important regulator of metabolic and development rates in fish embryos (Winberg 1956, Hoar & Randall 1969, Colby & Brooke 1973). Embryonic development is faster at higher temperatures, but is confined within some physiological minimum and maximum temperature that is specific to individual species. Optimal ranges of embryonic incubation temperatures of many species of freshwater fish can vary, spanning a range of about 8° C or more (Alabaster & Lloyd 1980). These optimal ranges are often concurrent with temperatures selected by that species in nature for spawning. Spawning also often occurs above and below these optimal temperatures. However, there is an increase in mortalities and abnormalities associated with incubation in these temperature ranges (Alabaster & Lloyd 1980).

Hatching success, largely influenced by temperatures during the spawning season, can ultimately affect year class strength of fish (Serns 1984, Reckahn 1986, Coutant 1987, Kallemeyn 1987). The wider range of optimal incubation temperatures in freshwater fishes relative to marine fishes is believed to be an adaptation to the more variable thermal regimes occurring in freshwater systems (Alabaster & Lloyd 1980, Cushing 1982). Cushing (1982) further suggests that longer spawning periods by some species are a mechanism to reduce year class failure by having at least some larvae emerging during times of optimal environmental conditions.

Razorback sucker–white sucker spawning

Little is known about the pre-impounded riverine spawning, incubation, and ecology of the razorback sucker, particularly in regard to temperature. Reduced temperatures from hypolimnetic discharges of dams are implied as a contributing factor to the decline in distribution and abundance of the species (Johnson & Rinne 1982, Marsh 1985). However, the exact mechanism of this interaction is unknown. Comparison of incubation and rearing temperatures between the razorback sucker and

the related white sucker, *Catostomus commersoni* (McCormick et al. 1977) may allow us to hypothesize on potential pre-historical spawning and rearing temperatures for this species.

The minimum viable incubation temperature of razorback sucker embryos appears to be similar to that of the white sucker. The maximum viable incubation temperature for razorback suckers, however, is warmer. Successful hatching in white suckers occurred from 9.0 to 20.8° C with high percentages of normal embryos hatching from 9.0 to 17.2° C. We found successful hatching of razorback suckers from 10.0 to 20.0° C and Marsh (1985) found the apparent upper limit of razorback sucker hatching success occurring between 25 and 30° C.

White suckers initiate spawning from 7.2 to 11.8° C (Raney & Webster 1942, Geen et al. 1966, Corbett & Powles 1983). The razorback sucker has been reported spawning in free-flowing reaches of the upper Colorado River basin at temperatures as low as 6° C (McAda & Wydoski 1980). This is the lowest temperature reported for spawning by this species. Both species, therefore, seem to initiate spawning below temperatures required for successful incubation. Spawning prior to optimal incubation temperatures is common in freshwater fish (Alabaster & Lloyd 1980). Our comparison of the white sucker with the razorback sucker indicates that spawning is initiated at similar temperatures and that both have similar successful minimal incubation temperatures. Based on this comparison, initiation of spawning for the razorback sucker at 6° C could, therefore, reasonably be near the historical temperatures that initiated spawning in this species.

While incubation is successful at some lower temperatures, higher temperatures appear to be better for larval growth. Growth in white suckers is extremely slow at 10° C but is maximized at 26.9° C (McCormick et al. 1977). Movement to warmer shallow water by white sucker larvae is believed to occur to optimize growth and therefore survival (McCormick et al. 1977). Razorback sucker development is also extremely slow at 10° C but increases with increasing temperature as demonstrated in our experiments. Optimal development temperatures could be higher than 20° C but were not determined because our highest test temperature was only 20° C. As in white suckers, movement to warmer water to optimize growth might be expected in razorback suckers as well.

Synthesis

No one temperature is best suited for all life stages of a given species. McCormick et al. (1977) found an 11.7° C temperature increase from the optimal embryonic incubation temperature to the optimal larval growth rate temperature. They suggested that fish have adapted the timing of incubation and emergence to increase hatching success and larval growth rates to water temperatures in the systems where they occur. Faster development rates of embryos result in earlier hatching which enables larvae to begin foraging earlier, attain greater size, and compete better for available food resources. Increased size of young fish increases their survivability and therefore recruitment into the population (Mason & Chapman 1965, Fausch & White 1986, Chandler & Bjornn 1988).

Temperatures available for larval and juvenile growth in the upper Colorado River may influence survival of the razorback sucker. Kaeding & Osmundson (1988) suggest that recruitment of Colorado River squawfish, *Ptychocheilus lucius,* in the upper river may be limited by temperature that reduces growth rates needed to secure a minimum overwintering size. Minimum size for 0^+ fish is critical to their survival through the first winter (Gutreuter & Anderson 1985, Wicker & Johnson 1987). Similarly, reduced growth in razorback suckers may also reduce their survival in the upper river.

In Lake Mohave, reduced temperatures may be less of a problem. Incubation temperatures in basin areas of Lake Mohave (10–22° C) appear to be compatible with successful incubation temperatures that we found in the laboratory and evidenced in field collections. The protracted spawning season in Lake Mohave also may reduce the effect of lower spawning temperatures that occur during the early season. While this suggests that direct mortality from lower temperatures may be

low, slower development at lower temperatures can expose larvae to other causes of mortality for longer periods. Potential causes of mortality include water level fluctuation and wind wave-wave activity while larvae are still in the gravel, and food availability and predation once they have reached the swim-up stages. The effects of slower development on these causes of mortality, however, are unknown. Because of the precarious situation of this species, more studies on the ecology of this species are needed to quantify causes of mortality and to understand which environmental factors may limit recruitment into the adult stock.

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