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EFFECTS OF CONSTANT AND FLUCTUATING TEMPERATURES ON REPRODUCTIVE PERFORMANCE OF A DESERT PUPFISH, *CYPRINODON N. NEVADENSIS*¹

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Reproductive temperature tolerance tests were performed in the laboratory on an inbred stock of Amargosa pupfish, *Cyprinodon n. nevadensis*. Egg production was optimal at constant temperatures 24 through 32 C and at fluctuating temperatures 32–28 and 36–28 C. The reproductive tolerance range, defined as the range of optimal egg production with at least 50 percent hatchability, was 24 through 30 C, which is one-fifth of the range for normal activity and one-seventh of the critical thermal tolerance range. Temperature also affected the quality of eggs produced; temperature and yolk diameter were inversely related. The tolerance limits for oogenesis were narrower than the limits for successful hatching of healthy eggs exposed to temperature stress after spawning.

INTRODUCTION

Upper and lower lethal temperatures have been used as a criterion of survival for many species of fish. However, fish rarely encounter lethal temperatures either in nature or in areas of thermal pollution. This observation coupled with

the fish's ability to avoid extreme temperatures leads us to believe that the outright elimination of local populations from thermal death is rare. Temperature affects all life processes, and survival of populations depends on their response to a range of temperatures well within the lethal limits. Therefore, we have chosen to examine the range of temperatures over which reproduction can be successfully accomplished, because survival of populations depends on their ability to reproduce. We have called this

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study reproductive temperature tolerance.

The effects of various constant and daily fluctuating temperature regimes on reproductive performance have been investigated in a eurythermal fish, the Amargosa pupfish, *Cyprinodon n. nevadensis*. This species occurs in the drainage system of the Amargosa River extending from southern Death Valley, California, to the southwestern border of Nevada. We chose the Amargosa pupfish as an experimental animal because it is hardy in the laboratory, it breeds over the whole year, and the females release their eggs individually. Thus, the pupfish provides us with the advantages of year-round observations and an unusual measure of reproductive effort, i.e., eggs laid per unit time.

The genus *Cyprinodon* has attracted attention because it is widely distributed throughout the deserts of the southwestern United States and several of its species are endangered. The critical thermal maximum (CTM), or short-term temperature tolerance, of adult pupfish from several springs and marshes from Arizona and the Death Valley region has been determined: *C. macularius* (Lowe and Heath 1969), *C. nevadensis*, *C. salinus*, and *C. diabolis* (Brown and Feldmuth 1971), and *C. milleri* (Otto and Gerking 1973). Studies have also been conducted on the production of a pupfish population (*C. nevadensis amargosae*) in a thermal stream (Naiman 1976a, 1976b), social organization and life history (Soltz 1974), and temperature effects on growth and metabolic efficiency in *C. macularius* by Kinne (1960) and in *C. n. nevadensis* by Raush (1976). The effect of temperature on development rate and upper and lower limits for egg incubation have been determined under constant temperature conditions for *C. macularius* (Kinne and Kinne

1962), *C. rubrofluvialis* (Echelle, Hubbs, and Echelle 1972) and under constant and daily cycling temperatures in *C. n. nevadensis* (Shrode 1975).

Several conclusions have emerged from our research. First, the temperature range for successful reproduction is narrower than the upper and lower critical thermal limits by a considerable margin. Next, our results show that the upper and lower thresholds (about 24–32 °C) for optimum egg production parallel the temperature range for successful hatching (about 24–30 °C). Also, the maximum daytime temperature for egg production under fluctuating temperature regimes is slightly greater than the maximum achieved under constant temperature conditions. Last, the design of our experiments revealed that oogenesis is the most temperature-sensitive phase of the life cycle, whereas eggs and larvae have been viewed as the most sensitive stages heretofore.

MATERIAL AND METHODS

A breeding stock of *Cyprinodon n. nevadensis* was collected from the marsh of Saratoga Springs, Death Valley National Monument, California. A breeding pair from the field stock produced the sibling F₁ parental stock. Breeding pairs of this sibling parental stock were separated in 17 20-liter aquaria by a perforated clear plastic divider which was removed for 30 min daily to allow spawning. Eggs were laid on a yarn mop from which they were removed and incubated in petri dishes. These F₂ sibling fish became the experimental stock.

Breeding pairs, eggs, and larvae were maintained at 28 °C under a photoperiod of 16L 8D with incandescent and fluorescent lights. Fish were fed commercial fish food and brine shrimp daily.

Reproductive performance tests were

conducted with the F_2 fish at age 4–5 mo. For each test, males and females were acclimated at least 21 days to the test temperature in separate tanks. Breeding pairs were then placed in divided 20-liter aquaria in a controlled environment chamber which maintained the test temperature within 0.5 C and a photoperiod of 16L 8D. After a 3-day adjustment period, the divider was removed from each aquarium at 0800 h for 30 min each day for 21 days to allow spawning. Egg laying was completed within the half-hour period; if the female was not ready to spawn, she swam toward the surface as the male approached. Eggs were collected from spawning mops, the yolk diameter was measured with an ocular micrometer at the two- to eight-cell stage along the axis perpendicular to the animal-vegetal pole. Eggs were then counted and placed in petri dishes in controlled environment rooms for incubation.

On the twenty-second day, before spawning, female fish were weighed and measured (total length). The ovaries were removed, weighed, and preserved in Gilson's fluid.

Reproductive tolerance experiments were conducted at constant temperatures 18, 20, 22, 24, 26, 28, 30, 32, 34, and 36 C and at daily fluctuating temperatures 24–16, 32–28, 36–28, 38–28, and 39–30 C. The low temperature occurred at 0800 h and the peak at 2000 h (fig. 1). Spawning occurred at the lowest temperature of the cycle. In natural situations spawning occurs early in the morning, at the lowest temperature period, in warm months (Soltz 1974). All tests were conducted between March and October.

Thermal tolerance of adult fish was determined as the critical thermal maximum (CTM). CTM tests were conducted on male fish from the reproductive

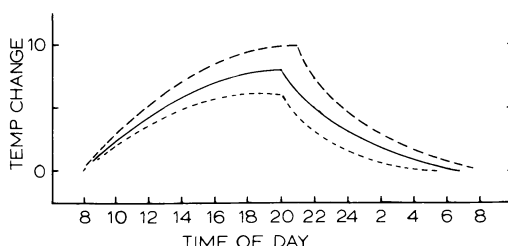


FIG. 1.—Daily cycle of fluctuating temperature regimes. 10 C daily temperature change = dashed line, 8 C = solid line, 6 C = dotted line. Spawning occurred at 0900 h.

tolerance tests. At the termination of the reproductive experiments, the males were transferred to 22-liter test tanks at the acclimation temperature. At 1000 h the next day, the temperature was increased 0.3 C/min with a 600-watt thermostatically controlled heater. The temperature at which each fish appeared to lose equilibrium was recorded; the mean represented the CTM.

RESULTS

An attempt was made to use fish within as small a size range as possible for the reproductive tolerance test; however, during acclimation and testing, fish at intermediate temperatures, 28 and 30 C, grew faster and were slightly larger by the end of the test period (table 1). In a control experiment, egg production of 57 4- and 5-mo old fish ranging in weight from 0.31 to 1.45 g (\bar{x} = 0.78, SD = 0.22) and TL from 28 to 42 mm (\bar{x} = 34, SD = 3) was monitored for 3 wk at 28 C. Within this size range there was no correlation between body weight and percentage of days on which eggs were laid (r = .16, r^2 = .03, P = .2), eggs per spawning (r = .02, r^2 = .00, P = .9), or mean number of eggs laid per day (r = .07, r^2 = .00, P = .6).

At test temperatures 24 through 34 C males were in vivid breeding color with bright blue sides, yellow forehead, and

TABLE 1
LENGTH AND WEIGHT OF FEMALES USED IN REPRODUCTIVE TOLERANCE TESTS

TEMPERATURE	N	MEAN WEIGHT (g)	± SD	RANGE		MEAN SL (mm)	± SD	RANGE	
				Min (g)	Max (g)			Min (mm)	Max (mm)
18 C.....	7	0.875	0.301	0.487	1.294	30.4	2.9	27	36
20 C.....	14	0.818	0.278	0.424	1.351	30.1	3.1	24	35
22 C.....	7	0.617	0.101	0.431	0.724	28.9	1.3	27	31
24 C.....	10	0.794	0.095	0.622	0.930	30.3	1.1	28	31
26 C.....	10	0.896	0.178	0.619	1.142	31.3	1.6	29	34
28 C.....	12	1.059	0.158	0.882	1.450	32.5	1.9	30	37
30 C.....	10	1.194	0.215	0.806	1.623	33.6	1.9	30	36
32 C.....	10	0.832	0.250	0.587	1.369	29.2	1.8	27	33
34 C.....	9	0.734	0.182	0.402	1.036	28.8	2.7	24	33
36 C.....	10	0.759	0.108	0.591	0.896	29.4	1.0	28	31
24-16 C.....	10	1.013	0.245	0.699	1.458	32.7	2.3	30	37
32-28 C.....	11	0.754	0.082	0.614	0.882	29.5	1.4	28	32
36-28 C.....	11	0.773	0.110	0.634	1.028	30.2	1.1	29	32
38-28 C.....	8	0.763	0.094	0.555	0.860	29.5	1.5	26	31
39-30 C.....	10	0.793	0.184	0.400	1.043	29.8	2.6	24	32

NOTE.—SD = standard deviation, SL = standard length.

strong black bands on posterior margins of anal, caudal, and dorsal fins (see table 2 for male lengths and weights). They immediately began pursuing females when the divider was removed and maintained their interest throughout the allocated spawning period. At 22 C both male and female were often hidden under the spawning mop. Occasionally both would swim around and at times the males chased the females. Males were in pale breeding color except one which was medium blue. At 20 C pale breeding colors were seen only on one male; the others showed no breeding coloration. All activities were slow at 20 C; the fish often remained on the bottom or hidden in the mop and showed little interest in each other. At 36 C the color of the males was usually very pale, but they pursued the females vigorously.

There was no pattern to the sequence of days on which spawning occurred or in the sequence of number of eggs per spawning at any test temperatures. The proportion of days on which eggs were laid ranged from 2% at 36 C to 72% at 30 C, with a mean of 38% (fig. 2). At

28 C, eight of 12 females laid eggs at least two-thirds of the days. At 30 C, seven of 10 females spawned at least two-thirds of the time and four fish missed 2 or less days out of 21. Differences between temperatures in the proportion of days on which eggs were laid were significant in an analysis of variance test with arcsin transformation of data ($F = 4.3$ with 14 and 134 df; $P < .01$). Performance was optimum at

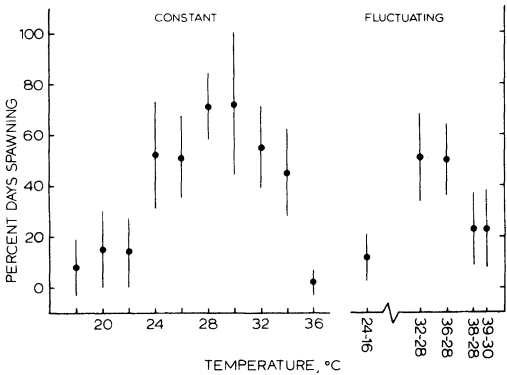


FIG. 2.—Mean (± SD) proportion of days on which spawning occurred for breeding pairs of *Cyprinodon n. nevadensis* acclimated and then bred for 21 days at test temperatures 18 through 39 C. Number of individuals at each temperature can be found in table 1.

constant temperatures 24 through 32 C and fluctuating regimes 32-28 and 36-28 C.

The number of eggs per spawning was also affected by temperature. An analysis of variance on log transformed data was highly significant ($F = 9.7$ with 14 and 134 df; $P < .01$). The mean number of eggs per spawning for all temperatures was four and the maximum was 10 at 30 C (fig. 3). The number of eggs per spawning was greatest at constant temperatures 24 through 32 C and at fluctuating temperatures 32-28 and 36-28 C.

The number of eggs laid per gram of female per day followed a pattern similar to that of number of eggs per spawning (fig. 4). An analysis of variance on log transformed data was highly significant ($F = 14.8$ with 14 and 134 df; $P < .01$). The range of temperatures at which egg production per gram body weight was greatest occurred at constant temperatures 24 through 32 C and at fluctuating temperatures 32-28 and 36-28 C. Production dropped sharply above and below these temperatures.

When egg production among the first,

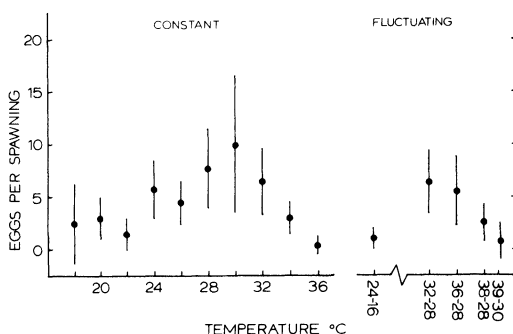


FIG. 3.—Mean (\pm SD) number of eggs per spawning for breeding pairs of *Cyprinodon n. nevadensis* acclimated and then bred for 21 days at test temperatures 18 through 39 C. Number of individuals at each temperature can be found in table 1.

second, and third week of each constant temperature experiment was compared, no significant differences were observed at 20, 22, 26, 28, and 30 C. At 24 and 32 C, the third week was better than the second, which in turn was better than the first (analysis of variance; $F = 6.1$ with 2 and 27 df; $P < .01$). At 34 C the order was second, third, and first ($F = 7.8$ with 2 and 21 df; $P < .01$).

Egg production under a daily fluctuating temperature regime was comparable to egg production at the constant tem-

TABLE 2

LENGTH AND WEIGHT OF MALES USED IN REPRODUCTIVE TOLERANCE TESTS

TEMPERATURE	N	MEAN WEIGHT (g)	\pm SD	RANGE		MEAN SL (mm)	\pm SD	RANGE	
				Min (g)	Max (g)			Min (mm)	Max (mm)
18 C.....	7	1.27	0.50	1.06	1.85	40.3	6.2	40	46
20 C.....	14	1.16	0.49	0.53	2.10	38.9	4.1	33	45
22 C.....	7	0.57	0.16	0.37	0.81	31.6	3.0	28	36
24 C.....	10	0.91	0.21	0.61	1.21	36.7	2.7	33	41
26 C.....	10	1.24	0.31	0.86	1.97	40.2	2.6	36	46
28 C.....	12	1.12	0.25	0.76	1.49	39.0	2.4	35	43
30 C.....	10	1.34	0.34	0.75	1.86	41.1	4.3	31	46
32 C.....	10	0.84	0.18	0.58	1.18	35.9	1.9	34	40
34 C.....	9	0.93	0.19	0.69	1.33	36.4	3.1	32	42
36 C.....	10	1.94	0.24	0.66	1.31	37.1	2.0	35	40
24-16 C.....	10	0.90	0.25	0.60	1.43	36.5	4.4	31	47
32-28 C.....	11	0.99	0.26	0.69	1.49	37.9	3.3	33	44
36-28 C.....	11	0.95	0.29	0.63	1.46	37.0	3.0	33	42
38-28 C.....	8	0.76	0.25	0.47	1.31	34.5	3.1	31	41
39-30 C.....	10	0.83	0.23	0.56	1.35	35.5	1.6	32	37

perature equivalent to the mean of the fluctuating regime when the maximum or minimum temperature of the regime did not exceed the optimal constant range of 24 to 32 C (figs. 2, 3, and 4). However, at temperature regimes in which the peaks fell above or below this range, egg production was slightly reduced in comparison with performance at constant temperature equivalent to the mean of the fluctuating regime. Performance was slightly better than that at the constant temperature equivalent to the maximum temperature of the fluctuating regime.

Ovary weights (table 3) and number of yolked oocytes per ovary were determined at the end of each breeding experiment. High variation in both measures occurred at all but extreme temperatures. There was no indication of accumulation of eggs or of atretic eggs at any temperature.

The temperature at which fish were maintained affected not only the number of eggs produced, but also the quality. There was an inverse relationship between temperature and the yolk diameter

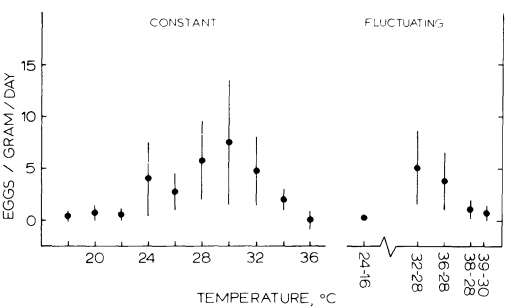


FIG. 4.—Mean (\pm SD) number of eggs (per gram of body weight) per day for *Cyprinodon n. nevadensis* acclimated and then bred at test temperatures 18 through 39 C for 21 days. Number of individuals at each temperature can be found in table 1.

of eggs; the differences in yolk diameters at the test temperatures were significant (analysis of variance: $F = 240.6$ with 8 and 1,719 df; $P < .01$, table 3).

A number of small, soft eggshells containing no yolk were produced at 32 C and above. These were not included in egg production or hatchability counts. They were not included in yolk diameter measurements, which may explain the larger mean yolk diameters at these temperatures.

Eggs which were exposed to identical temperatures during oogenesis and incu-

TABLE 3
YOLK DIAMETER OF EGGS LAID AND GONOSOMATIC INDEX (GSI)^a

Temperature	Mean Yolk Diameter	\pm SD	N	Mean GSI	\pm SD	N
18 C.....	1.07	0.09	40	0.05	0.02	7
20 C.....	1.08	0.09	64	0.08	0.04	14
22 C.....	1.07	0.04	16	0.09	0.03	77
24 C.....	1.06	0.05	335	0.13	0.06	10
26 C.....	1.02	0.08	212	0.14	0.05	10
28 C.....	1.01	0.05	187	0.10	0.03	12
30 C.....	1.00	0.05	375	0.07	0.04	10
32 C.....	1.02 ^b	0.07	373	0.09	0.05	10
34 C.....	1.04 ^b	0.08	126	0.05	0.02	9
36 C.....	0.02	0.02	10
24-16 C....	0.09	0.03	10
32-38 C....	1.01	0.06	266	0.09	0.04	11
36-28 C....	1.00	0.06	203	0.09	0.04	11
38-28 C....	0.98	0.07	44	0.04	0.02	8
39-30 C....	0.93	0.08	51	0.04	0.02	10

^a Gonosomatic Index = ovary weight/(body weight — ovary weight).
^b Does not include measurements of large numbers of small, fragile eggs laid at these temperatures.

bation had greater than 50% normal hatch at test temperatures between 24 and 30 C and at 32–28 and 36–28 C (fig. 5). This corresponds to the optimum range for egg production, except at 32 C where egg production was high but hatching success was low. This range was much narrower than that for successful hatching of eggs which underwent oogenesis and were spawned at 28 C and then were transferred to test temperatures from 18 to 39 C. Under these conditions, greater than 50% normal hatch occurred at constant temperatures 20 through 36 C and at fluctuating temperatures 28–20, 36–28, and 38–30 C. The two hatching success experiments were conducted at different times and in different laboratories in the same building. The experiments where oogenesis and incubation were performed at identical temperatures were a part of the present series; those where the eggs underwent oogenesis and were spawned at 28 C, subsequently being transferred to test temperatures from 18 to 39 C,

were a part of an earlier reported series (Shrode 1975). The lack of strict comparability of the two series of experiments probably accounts for the difference of 26% in the maximum hatching success obtained under optimal temperature conditions. On the other hand, the difference of about 70% at 20 C and at 32 C can be attributed to differences in experimental treatment, i.e., temperature during oogenesis. Thus, the tolerance limits for oogenesis were narrower than the range of temperatures for successful hatching of healthy eggs subjected to the temperature stress at an early stage (two to eight cell) of development.

The CTM was related to acclimation temperature (fig. 6). The highest CTM attained, at acclimation temperature 36 C, was 43.5 C. The critical thermal minimum for fish acclimated at 28 C was 4.5 C; at 20 C it was 2.8 C. The CTM of fish acclimated to cycling temperatures was near that of fish acclimated to a constant temperature equivalent to the peak of the cycle, with the exception of the low temperature acclimation cycle 24–16 C, where the response was similar to that of fish acclimated to the mean temperature, 20 C. The reproductive tolerance limits fell toward the upper end of the acutely determined limits under which fish can escape unfavorable conditions.

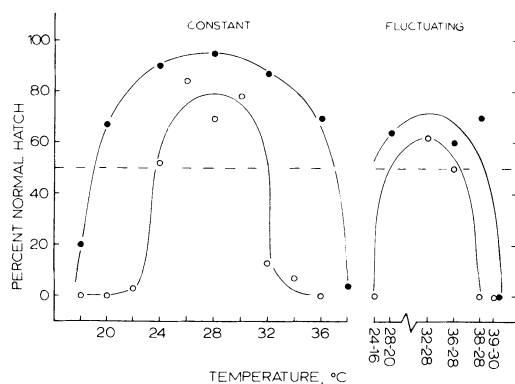


FIG. 5.—A comparison of percentage of eggs hatched between (1) closed circles = eggs exposed to 28 C during oogenesis and transferred at spawning to incubation temperatures ranging from 18 through 39 C, $N = 270$ at each temperature (Shrode 1975); and (2) open circles = eggs exposed to identical temperatures during oogenesis and incubation, $N = 300$ –400 for 24 through 34 C, $N = 50$ –150 for 18 through 22 C, $N = 7$ for 36 C, $N = 50$ –150 for fluctuating temperatures.

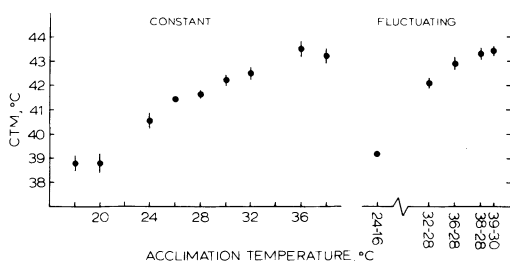


FIG. 6.—Critical thermal maxima (\pm SD) of male *Cyprinodon n. nevadensis* acclimated at temperatures 18 through 39 C. These males had participated in the reproductive tolerance tests.

DISCUSSION

Our results bear on four questions dealing with temperature tolerance. First, the limits for successful reproduction are narrower than either the limits for normal activity or for spawning. Second, the response to cycling temperature acclimation is different for successful egg production than it is for critical thermal limits. Third, acclimation temperature of the female during egg maturation affects the quality of the eggs. Fourth, we suggest that our results have some application to thermal problems concerning fish in general and possibly to other poikilothermal animals.

Although adult pupfish can exist under a wide range of temperature conditions (Feldmuth et al. 1974), our results show that the conditions for successful reproduction are much narrower. The highest constant temperature to which these fish were acclimated with negligible mortality was 38 C and the lowest temperature at which fish remain active was about 10–12 C. The critical thermal limits are about 2 and 44 C. The Amargosa pupfish produces eggs with limited hatching success in the laboratory between constant temperatures 22–34 C. Thus, as determined under constant temperatures, the fish breed over a range which is about one-half the activity range or about one-third the critical thermal tolerance range (fig. 7).

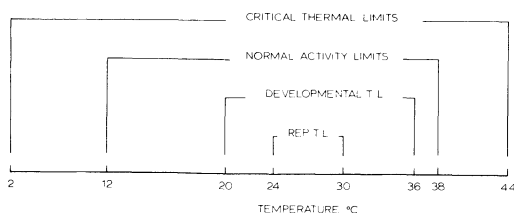


FIG. 7.—Diagrammatic representation of reproductive tolerance, developmental tolerance, normal activity, and critical thermal limits determined under constant temperature laboratory conditions for *Cyprinodon n. nevadensis*.

The temperatures at which most eggs were laid coincide with those at which successful hatch was greater than 50% with the exception of 32 C. The optimum constant temperatures for egg production, with the greatest number of eggs spawned and greater than 50% hatching success, are from 24 to 30 C, or about one-fifth the activity range and one-seventh the critical thermal range. In spite of the fact that egg hatching was poor above 30 C, breeding coloration and spawning behavior occurred at much higher constant temperatures, up to 36 C. The limits for successful egg production were narrower than the limits at which spawning occurred.

Our laboratory results under fluctuating temperatures coincide with the temperature conditions under which reproductive behavior has been observed in nature. In the Amargosa River, which has both wide daily and seasonal thermal cycles, spawning by *C. n. nevadensis* was limited to temperatures between 18 and 35 C (Soltz 1974). In our study under chosen laboratory cycling temperature regimes, egg production and hatching were also observed at temperatures cycling up to 36 C.

Acclimation to cycling temperatures for successful reproduction apparently differs from that observed for critical thermal limits. It is generally found that poikilotherms acclimate to the maximum, or near maximum, of a cycle in their critical thermal response (fish: Brett 1944, Heath 1963, Feldmuth et al. 1974, Otto 1974; frogs: Hutchinson and Ferrance 1970). Our CTM responses for fish acclimated to cycling temperatures were similar.

However, under the cycling regimes utilized in this study, pupfish responded to a temperature between the extremes in terms of their reproductive performance. For example, when egg produc-

tion was monitored at 36–28 C the fish laid 3.8 eggs per gram per day, close to that at the mean temperature of 32 C (4.7 eggs per gram per day), but far greater than the number laid at 36 C (0.4 eggs per gram per day). The same was true at the low cycling regime. At 24–16 C eggs were laid at a rate of 0.2 per gram per day whereas none were laid at 16 C, 4.1 per gram per day at 24 C, and 0.6 per gram per day at 20 C. Egg production was not diminished by exposure to high temperature for a part of each day such as fish experience during the summer in the natural habitat.

The temperature at which females were maintained affected not only the number of eggs produced but also the quality, as shown by differences in size and hatchability. Over the range of temperatures for 50% hatch or greater, yolk diameter was inversely correlated with temperature. Echelle et al. (1972) also found this to be true for the Red River pupfish, *C. rubrofluvialis*. Since productivity in desert water also varies with temperature, low in winter and early spring and increasing in summer with the mean water temperature (Naiman 1976a), change in egg size may be a facultative response to the availability of food for fry, providing greater yolk reserve under less favorable conditions.

Temperature conditions during oogenesis at 28 C were capable of development with a hatching success greater than 50% when they were transferred after spawning to constant temperatures as high as 36 C, whereas no eggs hatched which both matured in females and were incubated at 36 C. Eggs which underwent oogenesis at temperatures as low as 32 C were not capable of development with a 50% hatching success at the same temperature (see fig. 5). The thermal tolerance for oogenesis is much more limited

than is the tolerance for eggs during the developmental period from spawning to hatching.

Studies on many species of fish have determined the thermal tolerance limits for early life history stages. In many cases the thermal history of the spawning adults, including those conditions during oogenesis, are unknown or unreported. These factors should be taken into consideration, because fish will come into spawning condition within a range of environmental conditions where abiotic factors appear to affect the viability and tolerance of the eggs produced.

The reproductive temperature tolerance limits established for the Amargosa pupfish are skewed toward high temperatures when compared with the probable limits of the majority of temperate zone fishes. Although these limits are species specific, we might predict from our results that the tolerance limits of other species occupy about the same proportion of the temperature range that limits activity and survival—one-fifth of the activity range and one-seventh of the critical thermal range. This narrow range is greatly influenced by the fact that oogenesis is the most sensitive stage of the life history to temperature. As a result, some doubt is cast on the general significance of temperature tolerance tests on eggs and larvae for assessing the affects of localized temperature changes caused by the thermal effluent of various industries.

Finally, this same argument may have some bearing on the question of year-class strength in many fishes. The wide year-to-year variations in year classes that are commonly observed in fish populations are generally conceded to be due to abiotic factors, often considered to be temperature changes during spawning. Since small departures from the

tolerance limits drastically reduce egg production and quality, perhaps the temperature experience of the female during the period of egg maturation may be one of the determining elements in controlling year-class strength.

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