MASTER

Thermal Limits for Growth and Reproduction
in the Desert Pupfish, Cyprinodon n. nevadensis¹

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ABSTRACT

The thermal limits for growth of the desert pupfish (Cyprinodon n. nevadensis) were determined in seven-week laboratory feeding experiments at three rations (1.5, 3.0 and 4.5% body weight day) of Tetra-min prepared food and seven temperatures (12, 16, 20, 24, 28, 32, and 36 C). Curves of specific growth rates (% dry weight gain/day) as related to temperature were skewed to the left at the three rations. Growth was inhibited at 12, 16 and 36 C. Fish at the lower two temperatures were torpid and lacked appetite; the higher temperature fish did not eat sufficient food to match the high metabolic cost.

The thermal scope for growth was narrowed as ration decreased and as age/size increased. Taking these factors into account, the thermal limits for growth of immature pupfish feeding at moderate to high rates were 17.5 to 31.0 C with optimum growth achieved at 22.0 C. Successful reproduction depends on egg production and egg viability. Based on these criteria, the thermal limits for reproduction are 25.0 to 31.0 C with an optimum at 28-29 C. Thus, the reproductive limits are narrower than those growth. Some degree of flexibility should be allowed in these limits due to variability in the measurements. Nevertheless, the optimum temperature and the lower limits for reproduction are both higher than their counterparts for growth. Growth can be accomplished at temperatures about 7 C below those for successful reproduction.

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The implications of this temperature differential are discussed.

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INTRODUCTION

The objective of this research is to compare the thermal limits for growth with those for reproduction in the desert pupfish, Cyprinodon n. nevadensis. The reproductive tolerance limits for this species have already been established (Shrode and Gerking 1977; Gerking et al. 1979), while the tolerance limits for growth are the subject of the present investigation. The limits for both growth and reproduction reflect the high temperature adaptation of the pupfish which lives in the Death Valley, California, region (Brown and Feldmuth 1971; Otto and Gerking 1973; Naiman et al. 1973). Nevertheless, the relative sensitivity of these two important life functions to temperature should be helpful in defining the thermal conditions suitable for other self-sustaining fish populations.

MATERIALS AND METHODS

Pupfish. A stock of desert pupfish, Cyprinodon n. nevadensis was collected in 1974 from the marsh at Saratoga Springs, Death Valley, California, and served as the progenitors of the seventh generation inbred fish used here. The fish were in a fast-growing period in their lives (3-4 months old) and varied in weight from 40 to 467 mg.

Design of the experiments. Individual fish were placed in 400-600 ml of water in 1000 ml beakers. The beakers were covered with watch glasses and arranged on shelves in controlled environmental rooms at temperatures of 12, 16, 20, 24, 32, and 36 C (photoperiod = 16L 8D). The 28 C group was placed in an aquarium room maintained at the same photoperiod. In order to avoid any possible differences in growth response to different rations caused by variations in light, air movement, temperature, and proximity of fish eating the same ration, the beakers were randomized as to their position on the shelf at each temperature.

The daily rations were 1.5, 3.0, and 4.5% of the live body weight/day adjusted each week to keep pace with growth. This schedule was kept from 20 to 32 C, but the 36 C group could not survive on the 1.5% ration. Therefore, the feeding rates were raised for this group to 3.0, 4.5, and 6.0% of the body weight/day. Both the 12 and 16 C groups fed very little at all rations. Ten fish were assigned to each ration, making a total of 30 at each temperature.

The feeding period was seven weeks for most temperatures and five weeks for 20 C. One week was allowed at each temperature-ration combination for the fish to acclimate before the growth trial began. Most of the experiments were performed in the summer of 1977, but the 12 and 16 C groups were fed in the fall of 1978 in order to establish the lowest temperatures at which the fish would grow.

Food. The fish were fed Tetra-min, prepared by Tetra Werke, W. Germany. It is shipped in flakes which are ground to particles of smaller size. The food was weighed in sufficient quantities to feed an individual fish for a week and then parcelled out in approximately equal daily amounts.

Growth measurements. Each week the fish were removed from the beakers, blotted on filter paper, and weighed to 0.1 mg. If a fish died during the experiments, it was usually replaced by another of approximately the same size. The fish were then transferred to beakers with fresh water.

Aeration. The beakers were not aerated since oxygen content remained high for a week's feeding period. Three separate tests were made with fish fed at 4.5% body weight/day in 500 ml water at 36 C where respiration and decomposition would be expected to be the greatest. Dissolved oxygen averaged 87% saturation at the end of a week.

RESULTS

Variability. A large amount of variability was encountered. For example, the coefficient of variation among the growth measurements of the 30 individuals at 24 C averaged 229% over all of the observations made during the seven-week feeding period. In view of this variability, it is surprising that the average growth response is so sensitive to ration (Fig. 1). The 24 C - 1.5% ration-group lost weight over six of the seven weeks, while the 3.0 and 4.5% daily rations produced progressive increases in weight. This pattern of response was characteristic of all temperatures except 12 and 16 C at which the fish fed very little. The consistency of the average weight changes gave us confidence that differences in growth among temperatures and rations could be detected if indeed they did exist.

Specific growth rate. The initial live weights varied from one feeding trial to another (Table 1). Although the mean live weights for the three rations were about the same (range = 144 to 159 mg), considerably more variation resulted when weights were classified by temperature (range = 85 to 214 mg). The smallest weight (85 mg) at 20 C was due to the fact that this was the first feeding trial, and consequently the fish were the first to be drawn from the fast-growing stock.

Specific growth rate was expressed as a percentage change in dry weight per week over the initial dry weight (Wurtsbaugh and Davis 1977). This expression yields greater values for small fish than for large fish growing the same absolute amounts. The bias in favor of specific growth of small specimens can be taken into account by using covariance in the statistical treatment of the data which allows for the correlation between initial weight and specific growth rate. The results of a covariance analysis of arc-sin transformed values (adjustment for using percentages) involving the four temperatures from

20 to 32 C yields a significant difference among the three rations ($F = 66.7$, d.f. = 108 and 2, $P < 0.01$) and among the temperatures ($F = 2.87$, d.f. = 108 and 3, $P < 0.05$). When the adjusted specific growth rates from the covariance analysis are plotted against temperature, they are skewed to the left (Fig. 2). All three rations have this same characteristic. The low values at 24 C compared with those at 20 and 28 C are noted, but we are unable to explain this inconsistency.

Failure to grow at extreme temperatures. The thermal limits for growth can be demonstrated by relating specific growth rates at the various temperatures to the amount of food assimilated (Fig. 3). The 20 to 32 C lines are curvilinear and shifted to the right, indicating that the maintenance cost rises as temperature increases. The 12, 16 and 36 C lines also show the same curvilinear relationship but never reach a positive growth rate. Apparently none of the three groups assimilate enough food to equal the maintenance requirement. The 12 and 16 C groups ate little of the food that was offered to them and had low assimilation rates of 17 and 33%, respectively, of the dry weight of food consumed (Gerking and Lee in prep.). The fish were inactive, nearly torpid, at both temperatures. The 36 C fish assimilated food at the same rate as those from 20 to 32 C (mean = 74%) but did not consume enough food, even at 6% of the body weight/day, to match their maintenance requirements. This group was hyperactive, swimming much more vigorously than any other group.

A significant mortality paralleled the failure to grow at the extreme temperatures. At 12, 16 and 36 C, the fish experienced mortalities of 63, 60 and 60%, respectively, during the seven-week feeding period. These values compare with an average of 12% at the other temperatures, thereby implicating temperature stress as a contributing factor.

DISCUSSION

Growth Curves

Shape of the growth curves. Curves relating specific growth rate and temperature rise sharply from 16-17 C to a maximum at 20-22 C and decrease at higher temperatures. The curves are skewed to the left. This pattern is repeated in some but not all species that have been investigated in this regard. Both Brett et al. (1969) and Elliott (1975a) obtained similar results in sockeye salmon (Oncorhynchus nerka) and brown trout (Salmo trutta), respectively. Curves which are skewed to the right have been noted in the channel catfish (Ictalurus punctatus) by Andrews and Stickney (1972a) and in a model of yellow perch (Perca flavescens) growth developed by Kitchell et al. (1977).

The upper thermal limits for positive growth vary from 35 C at the 4.5% ration to 23 C at 1.5%. This is a typical response indicating that metabolic rate, and therefore maintenance ration, is temperature dependent (for examples see Brett et al. 1969; Wurtsbaugh and Davis 1977). The lower limit is about 17 C for all three rations. No growth was achieved at 12 and 16 C.

Ration effect. The growth curves become more skewed as ration decreases, and as a result the optimum temperature shifts from 22 to 20 C. The interaction between ration and temperature is even more pronounced in the sockeye (Brett et al. 1969) and in the brown trout (Elliott 1976). For example, the optimum temperature for sockeye growth dropped from 15 to 5 C as the ration decreased from 6% to 1.5%/day. The same relationship was reported in some of the experiments on rainbow trout (Salmo gairdneri) performed by Wurtsbaugh and Davis (1977). No ration effect was revealed in feeding experiments on the channel catfish (Andrews and Stickney 1972), in which the optimum temperature remained at 30 C at feeding rates from 2 to 6%/day.

The scope for growth, or the temperature range over which growth is positive, is progressively reduced as ration is reduced. The reduction is due to the dependence of maintenance ration on temperature, as mentioned previously. As the growth curves are compressed, the optimum shifts to lower temperatures. This explanation was originally proposed by Brett et al. (1969) and is generally supported by the results of the present experiments.

Age or size effect. The age/size effect on the optimum temperature for growth came to our attention when reviewing Kinne's (1960) results on Cyprinodon macularius. These pupfish made the greatest absolute growth at 30 C in a 24-week feeding trial dating from the hatching date. It was clear, however, that the advantage of the fish at the 30 C temperature was gained primarily in the first two weeks. Later, growth rate was superior at lower temperatures. From 14 weeks onward, the age of the pupfish in the present experiments, the optimum temperature of C. macularius was 20 C, which closely corresponds with our results. Kinne recognized this and noted "the field observations and experiments performed in the laboratory indicate that the temperature optimum shifts downward with age and salinity."

An age/size effect on the optimum growth temperature has been noted in other species as well. The effect is evident in the growth curves of the guppy (Poecilia reticulata) reported by Gibson and Hirst (1955). When Strawn's (1961) growth optimum of 27.5 C for small (hatching to 22 days) largemouth bass (Micropterus salmoides) are compared with the 18-25 C optimum reported for larger fish (Niimi and Beamish 1974), the same decrease of the optimum growth temperature with age/size is apparent. The white sucker, Catostomus commersoni, has an optimum temperature of 26.9 C for the first 4-5 weeks of life (McCormick et al. 1977), while a temperature preference of adults in nature, which would be expected to be optimum for growth, was shown to be

18-21 C (Horak and Tanner 1964). Hokanson (1977) gives the growth optimum for 0.5 g yellow perch as 28 C and for the 5.2-23.7 g group as 23 C. An optimum of 30 C has been cited by Brett (1979) for the 17-40 g pumpkinseed sunfish (Lepomis gibbosus), but Pessah and Powles (1974) state that "the most significant aspect presented here is the trend for fish [pumpkinseed growth] between 15 and 30 C to level off in time to the same relative growth." In general these observations support the view that the growth of young fish is given a thrust by higher temperatures that lasts only a relatively short time. Slower growing fish at a lower temperature may exhibit superior growth somewhat later in life and finally reach a greater length than their faster growing companions at the same age. This experimental data supports the concept of growth compensation that has been demonstrated in numerous species in nature.

Some outstanding exceptions to the age/size effect have also been observed. Elliott (1975) found a 12.5 C growth optimum for brown trout from 1 to 300 g. Shelbourn, et al. (1973) indicated a 15 C growth optimum for 0.3 to 30 g sockeye with a gradual broadening of the optimum temperature with increasing size. No size effect was noticed in channel catfish when they were raised from 25 g to market size (Andrews et al. 1972). Thus, the age/size effect on the growth optimum is not a constant feature of growth experiments that have been performed under rigorous conditions of temperature and ration.

Summary. The pupfish growth curves do not display any features that are unique to the species. The skewed-to-the-left curves and the decrease in optimum temperature for growth with a decrease in ration have been observed previously and have a logical explanation. The departures from this pattern give some reason to believe that we are not yet ready to formulate generalities in this regard. The same is true for the age/size effect on optimum temperature. Most of the evidence favors the interpretation that young and small fish

respond more favorably to higher temperatures than do older and larger fish, but some prominent exceptions exist. It is safe to conclude, however, that in the future the conditions under which optimum temperature are measured should be stated, such as size of the fish, daily ration, season of the year when the fish were collected, and salinity. All of these factors are known to affect optimum temperature for growth in some species.

Thermal Limits of Growth and Reproduction

Comarison of performance curves. The thermal limits for growth, outlined above, can be compared with the limits for reproduction already established by Shrode and Gerking (1977). Both reproduction and growth are expressed as a percentage of peak performance so that the shape of smoothed curves and the thermal limits can be compared directly (Fig. 4). We have chosen the temperature limits defining 50% of peak performance, because they may perhaps be meaningful in the environment. Less than 50% of peak performance, say 10%, in reproduction, growth or both would probably not permit a population to be self-sustaining over the long run. Since the curves are steep near the 50% levels, the temperature limits are not materially broadened at 25 or even 15% of peak performance.

The thermal limits for specific growth rate at the 4.5% ration are 17% to 31.0 C. These limits are narrowed to between 18.0 and 26.0 C at a ration of 3.0%/day, thereby showing the ration effect. Also recall that these fish were in a fast-growing period of their lives. Our experients were not designed to show an age/size effect, although that should be taken into account if these limits are to be determined for other species in the future.

The reproductive temperature limits are influenced by two factors, egg production and egg viability. Pupfish lay many eggs, for example, at 32 C but

the viability of these eggs is very low. Using the two criteria, 50% of peak egg production lies between 26.0 and 33.0 C; the same limits for egg viability lie between 24.5 and 31.0 C. These differences between egg viability and egg production are probably due to smoothing and variability encountered at each temperature at which experiments were done. For example, we cannot distinguish statistically between 28 and 30 C for the peak egg production performance. Thus, some degree of flexibility should be attached to the reproductive limits as reported.

Possible acclimation effect. The thermal limits for growth may be affected by acclimation. For example, we have not measured the growth of fish acclimated at, say, 28 and tested at 20 C (and vice versa), largely because the growth experiments require a considerable period of time, and any acclimation effect might be dissipated before the experiment terminated. Thus, the limits quoted above may need to be modified if the previous temperature experience of the fish is shown to affect growth. On the other hand, the reproductive tolerance limits are fixed. Egg production of the pupfish is characteristic of the ambient temperature even though the animals have been exposed to higher or lower temperatures for a whole generation (Gerking et al. 1979).

Summary. The thermal limits for reproduction are narrower than the limits for growth. The lower limit for growth is about 18 C at a moderate to high rate of feeding whereas that for reproduction is about 25 C. The upper limits are considered to be the same, about 30 C. According to our experiments, growth is possible about 7 C below that which is favorable for reproduction with the provision that the fish are of the same size and are feeding at a moderate to high rate of feeding. The optimum growth temperature is 22 C and the optimum reproductive temperature is 28-29 C. The limits for successful reproduction are narrower than any of the other thermal limits that we have measured on the pupfish (Gerking, in press).

Practical Applications

Two practical applications of the results will be mentioned. There is a desire on some occasions to rear adult fish to large size under controlled conditions. This could be done most efficiently by eliminating the metabolic cost devoted to reproduction. According to our results with immature pupfish, good growth can be obtained at 22 C, a temperature where egg production and egg viability are inhibited. Other species may have a similar temperature differential between optimal growth and reproduction in the adult stage. This is suggested by events following the installation of a hydroelectric dam. The tailwaters are usually fed by cold water from the hypolimnion of the reservoir. Under these conditions, the native fauna survives for a time; the individuals grow large and finally disappear. Pfitzer (1954) reports that one-third of the native warm-water fauna on Watauga and South Holston reservoirs in Tennessee disappeared shortly after the dams were completed. These were short-lived species whereas the longer-lived species were not yet affected. The cold tailwater temperature may have killed some species outright while it depressed reproduction in others, allowing them to survive and grow until mortality from other sources gradually eliminated them.

Those who have a special interest in large-scale permanent environmental alterations, such as dams and power plants, may wish to explore the consequences of the view that reproduction may be the most sensitive of the vital functions of fishes to alterations in temperature. As a result, impact studies designed to predict conditions suitable for self-sustaining populations should focus on tolerance limits for successful reproduction, instead of relying on limits that are defined for survival and growth.

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Figure 1 - Gerking

Figure 2 - Gerking

Figure 4 - Gerking

Figure 7 - Gerking