Changes in Bluegill, *Lepomis macrochirus*, Life History in Response to Thermal Extremes

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INTRODUCTION

Our present day knowledge of life history evolution stems from the early contributions of Cole (1954), Lack (1954) and Williams (1957, 1966a,b) which enhanced our understanding of the relationship between natural selection and life history traits. Life history patterns have been shown to vary considerably among populations of the same fish species and can provide information for assessing patterns and mechanisms of microevolutionary change. The divergence of life history characteristics among populations may be caused by the direct influence of environmental factors on phenotypic variation, or may be the outcome of genetic adaptations to local environmental conditions

Extreme environments can provide opportunities to evaluate divergences in life history traits among populations. One such extreme environment that has been exposed to both chronic and acute thermal perturbation is the Par Pond Reservoir System located on the Savannah River Site near Aiken, South Carolina. Nuclear production reactors began operation on the Savannah River Site, in the late 1950s and continued until the late 1980s. During the 35 year period, a single nuclear production reactor (P-reactor) produced water that was heated to more than 50 ºC and then released into the Par Pond reservoir system. The Par Pond System is a partially closed loop system of canals and reservoirs that includes Par Pond (1100 ha; normothermic site that is characteristic of most southeastern reservoirs;) and Pond C (67 ha; the heated site, which was almost completely devoid of emergent vegetation. Water loss from the system is supplemented with water pumped from the Savannah River.
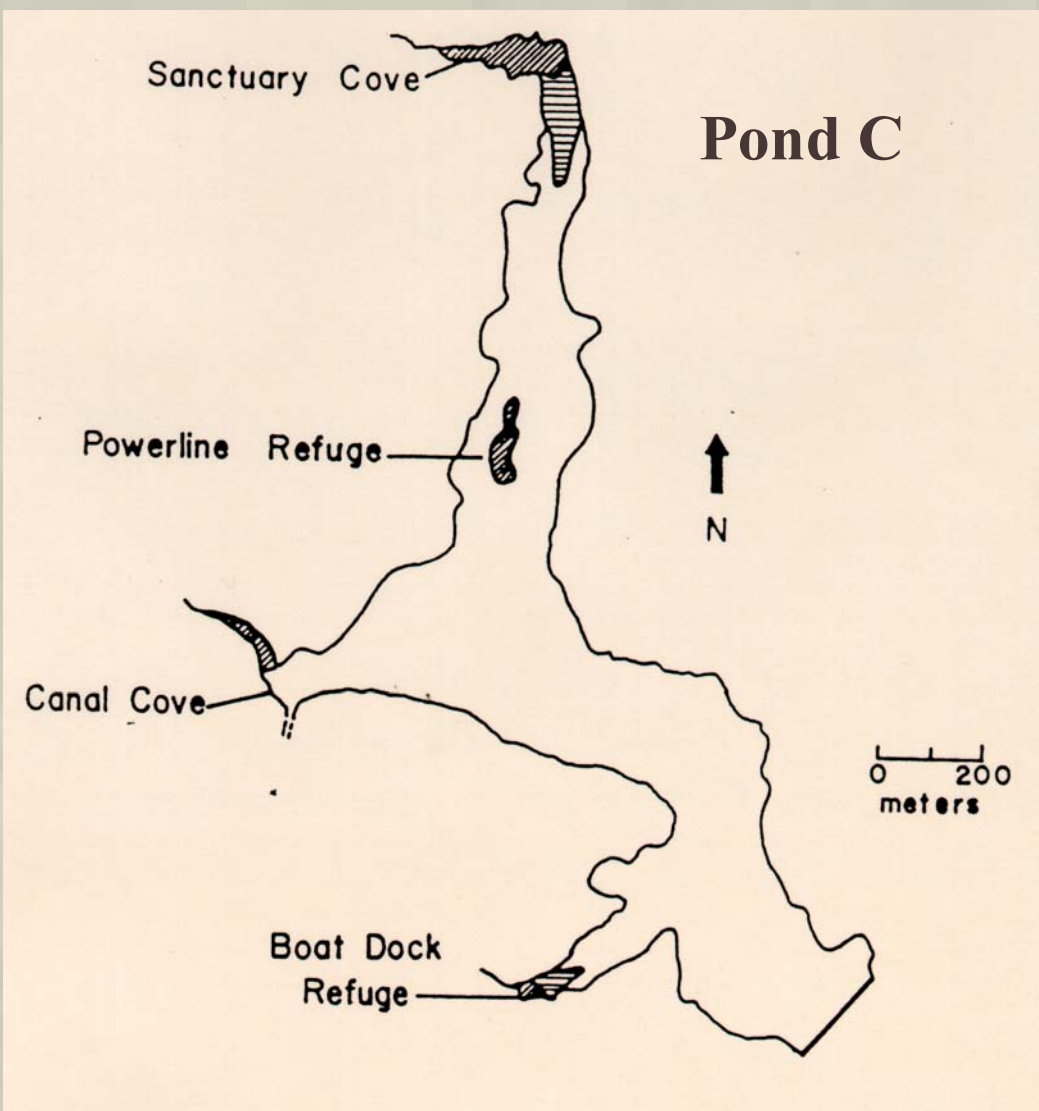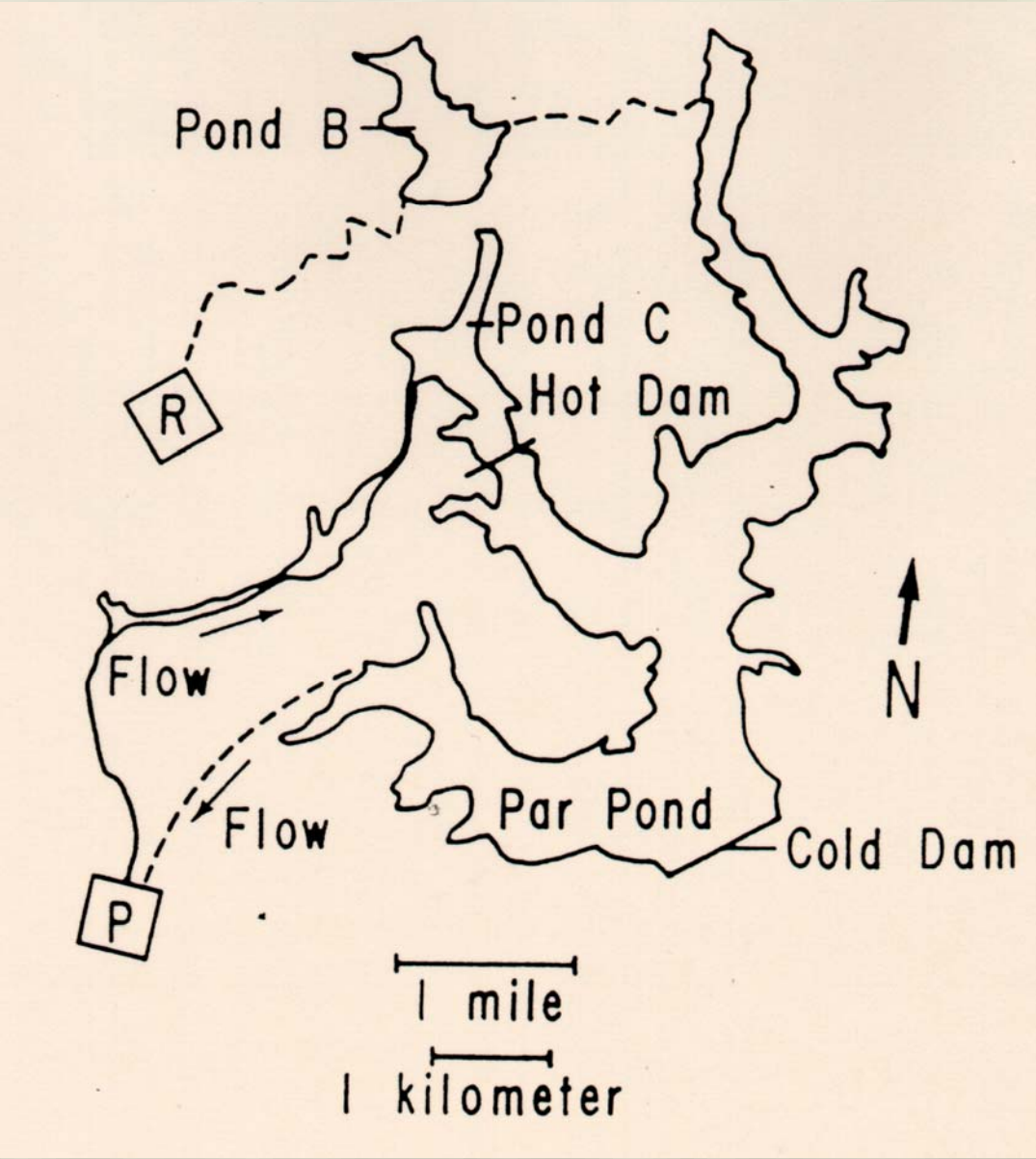

When P- reactor was operational, heated effluent flowed through four cooling ponds and then entered Pond C at approximately 50 ºC. At least 90% of the water in Pond C reached lethal limits for almost all-living organisms during long periods of reactor operation. Fish in Pond C survived the unpredictable periodic heating of the reservoir by occupying one of four relatively small and distinct refuges which contained cooler water from springs or streams. The refuges were smallest and best defined during the summer and larger and less well defined during winter. Temperatures in the refuge areas ranged from 30ºC in the deepest areas to 35ºC along the shoreline. In addition to the elevated temperatures within the refuge areas, bluegills experienced high fish density (increased interspecific interactions), low food availability, and reduced habitat structure (Block et al. 1984, Fischer et al., 1987; Taylor and Mahoney 1988).

Over 35 years of reactor operation, a total of 218 reactor down periods occurred on an unpredictable schedule of which 89% were less then 21 days in duration (short reactor down period), while only 11% were greater than 20 days long (long reactor down period). Pond C was able to return to approximately normothermic conditions when reactor down periods exceeded 15 days or more, which occurred about once every 18 months. During extended reactor down periods phytoplankton and zooplankton populations were able to become established and fish were able to occupy the entire reservoir.

Bluegill are one of the most common fish species inhabiting the Par Pond Reservoir system and are the descendants of natural stock present at the time of construction of the dams. The acute and chronic exposure of bluegill to stressful and/or extreme environments may provide an opportunity to test life history theories as well as document the extreme condition over which an organism can adapt. Environmental perturbations acting as stressors may become strong selective agents that result in rapid life history evolution within a population.
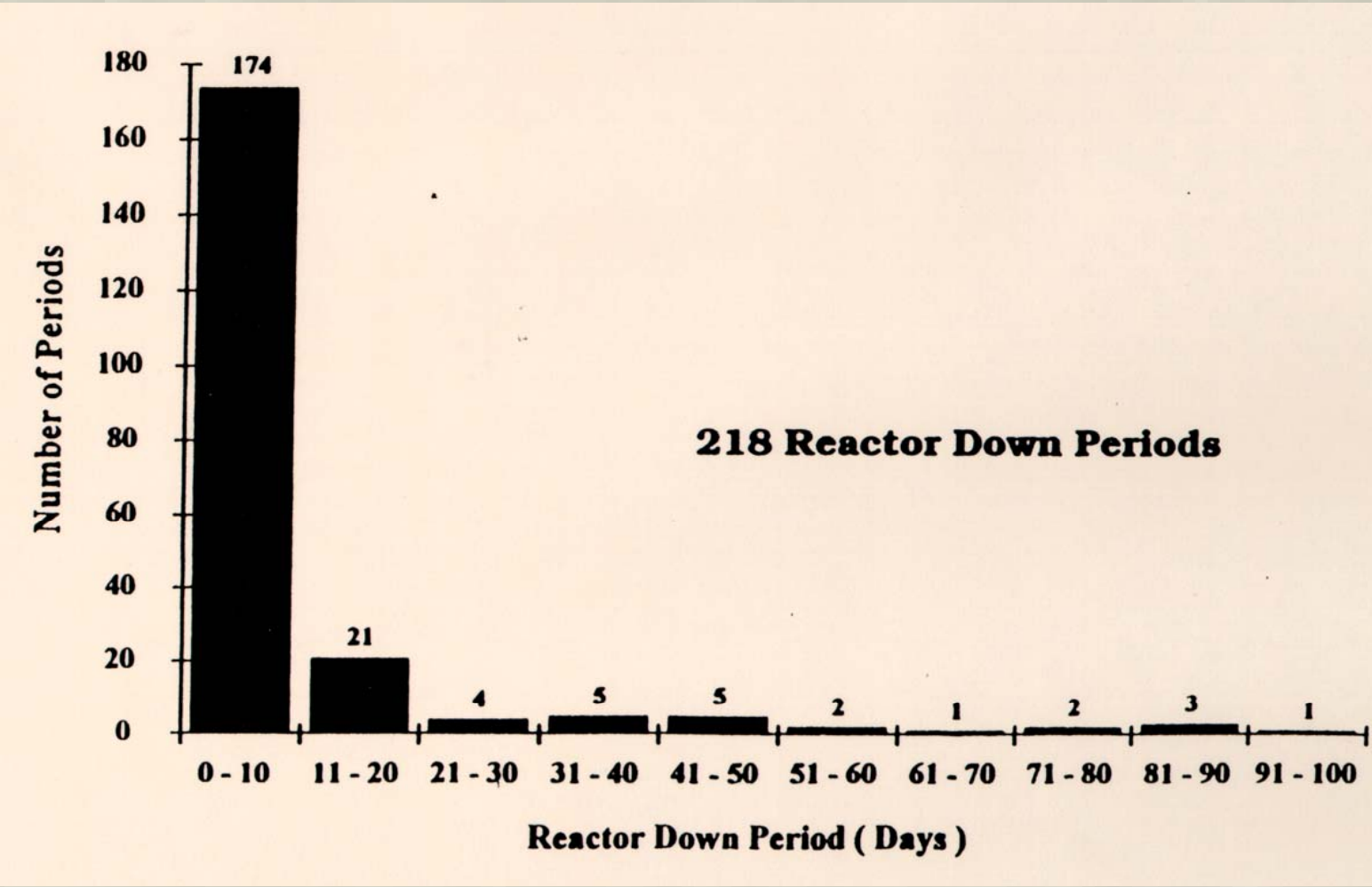
Thus, a comparison of the life history traits of 1) growth rate, 2) age and size at first reproduction, and 3) egg size and egg number between bluegill from the normal site (Par Pond) and the altered site (Pond C) should provide us with an understanding of how an organisms life history traits may diverge in response to the stressors of elevated temperature and its associated covariates of increased interspecific interaction, reduce food availability, and reduced habitat structure.

METHODS

Bluegill were collected during over a two year period, form both Pond C (heated site) and Par Pond (normothermic site) for determination of reproductive status, age, and the reproductive parameters of egg number and egg size. Fish were collected using an electroshocking boat and then frozen and returned to the lab for later analysis. Total length (mm), mass (to nearest 0.01g), and reproductive condition were recorded for each fish. Sagittal otoliths were also removed from each bluegill and stored dry for determination of age. In addition, gonads from spawning females were removed and stored in Gilson fluid for later analyses of reproductive parameters. Size at first reproduction was determined as the size range over which more than half the adult bluegill were reproductively active.

Stored otoliths were immersed in ethyl alcohol and examined whole against a dark background using a dissecting scope and reflected light. Otolith radius and the distance to each annulus were measured along the long axis from the center using an ocular micrometer. Ages of bluegill were determined by counting otolith annuli. Growth of bluegill was back calculated from otolith measurements using a modified Fraser-Lee method:

$$Lx = Lo + (Lc - Lo)(Rx - Ro) / (Rc - Ro)$$

Where Lx is estimated total length at age x, Rx is otolith radius at age x, Lc is length at capture, and Rc is otolith radius at capture. Lo is estimated length at swim-up (6 mm), and Ro is estimated otolith radius at swim-up (0.04). Mean length at each age was back calculated for the various age groups.

Gonadal tissue was removed from the Gilson solution and egg number determined by counting the total number of ovulated eggs in the ovaries of 25 and 17 female bluegills from Pond C and Par Pond, respectively. In addition, the Morphosys Video Imaging System was used to measure the diameter of 10 eggs/female bluegill. Egg size of each female was considered to be the average of the 10 egg diameter measurements.

RESULTS and DISCUSSION

Bluegill collected from both Pond C (heated site) and Par Pond (normothermic site) ranged from 1-6 and 1-9 years in age and ranged from 69.7-207.8 and 78.0-285.0 mm TL, respectively. An analysis of variance indicated a significant difference in mean bluegill length ($F_{1,215}$ = 554.23; P < 0.0001) between the two sites with Par Pond (= 211 $\pm$ 4.0) having a mean TL length 24 mm larger than that observed for Pond C bluegill (= 187 $\pm$ 3.2). In addition, Par Pond bluegill grew faster and therefore obtained a significantly larger TL at all age classes ($F_{8,215}$ = 1191.23; P < 0.0001; Fig. 3.). Within each pond no An analysis of significant difference was observed in either growth rates or age specific body sizes of male and female bluegill from Par Pond and Pond C.

Mean bluegill length and growth rates of age I-IV bluegill from Pond C were considerably lower than those observed for bluegill from Par Pond.   However, the mean body size and growth rates of Pond C bluegills were similar to data obtained for bluegill from reservoirs in the southeastern United States. The increased growth rate and associated increase in mean body length of Par Pond bluegill may be an outcome of increased resource productivity. Even though primary productivity is intermediate in Par Pond compared to other southeastern reservoirs, per capita resource availability may be high. The high amount of resources per capita may be due to decreasing densities of juvenile bluegill resulting from heavy predation. The difference between Par Pond and other reservoirs, including Pond C, is the abundant population of predators in Par Pond, largemouth bass are about 3-4 times more abundant and 25% larger in Par Pond as compared to other reservoirs. Thus, if heavy predation is decreasing juvenile bluegill densities in Par Pond, the resultant increase in per capita resource availability may lead to increased bluegill growth rates.
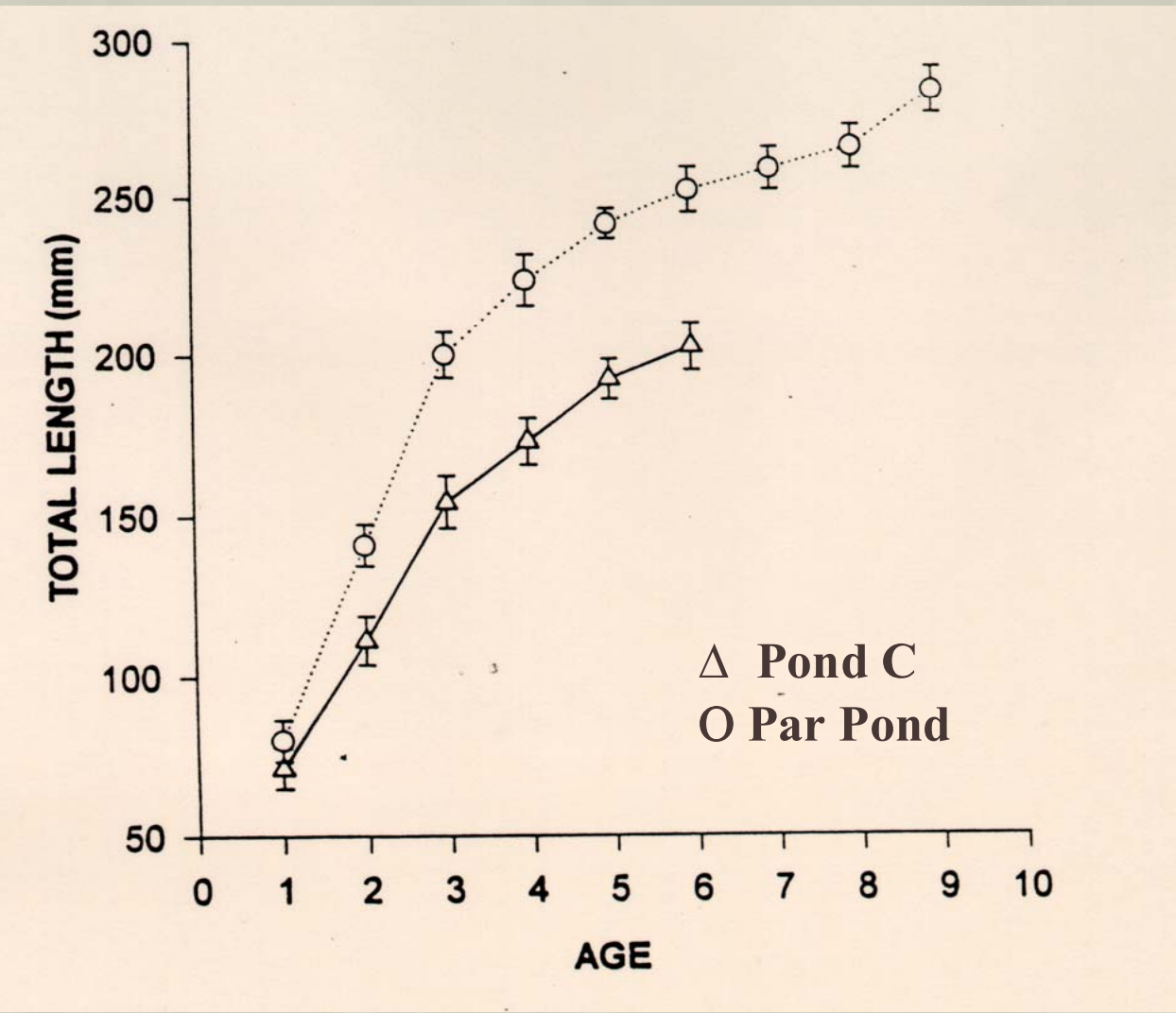
Bluegill from both Pond C and Par Pond grew rapidly until about age IV (attained TL of 173.4 in Pond C and 224.4 mm in Par Pond), after which body growth was reduced in both ponds. Mean Annual growth increments before age IV of bluegill from Par Pond were significantly higher (based on non-overlap of the standard errors) than growth increments obtained for Pond C bluegill. However, mean growth increments after age IV did not differ for bluegill from both sites. Bluegill from the heated site (Pond C) became reproductively active at 1-2 years, and at a mean total length of 91 $\pm$ 3.5 mm as compared to Par Pond bluegill which became reproductive at 2-4 years, and at a mean total length of 213 $\pm$ 3.0 mm. An analysis of variance indicated a significant difference in mean total length at first reproduction ($F_{1,107}$ = 151.94; P < 0.0001) between bluegill from the heated and normothermic sites.
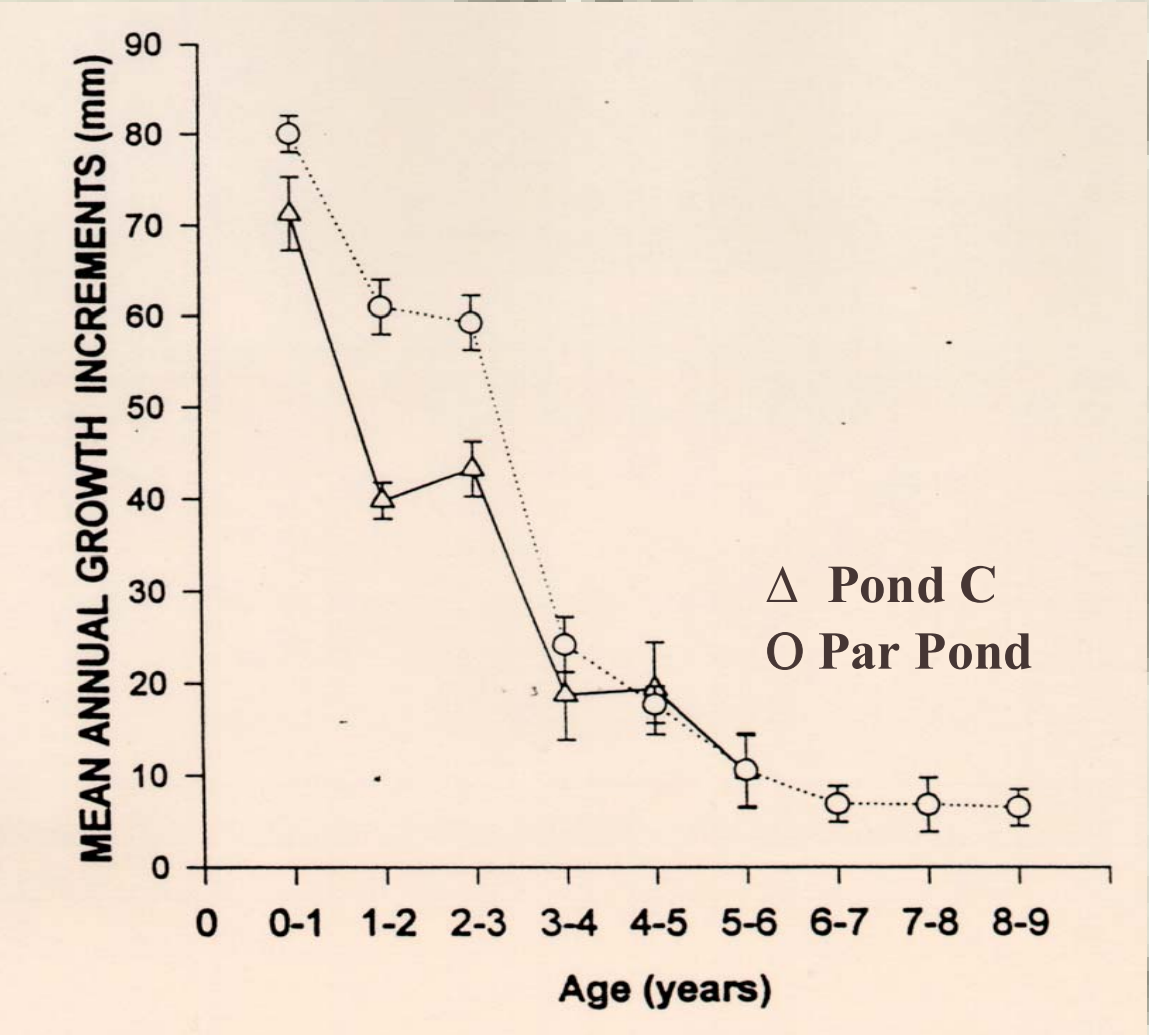
Differences in growth patterns observed for bluegill from both Par Pond and Pond C may be due to differences in energy allocation between the competing compartments of growth, maintenance and reproduction. Individuals that mature at a smaller size allocate resources to reproduction at the expense of growth, leading to a reduced growth rate. Bluegill in Pond C matured approximately 1-2 years earlier and 122 mm smaller mean TL than bluegill from Par Pond. However, the age (1-2 years) and size (mean TL of 91 mm) at maturation of Pond C bluegill is similar to data obtained for bluegill from both thermal and normothermic reservoirs in the southeastern United States. Thus, the differences observed in growth rates in Pond C bluegill compared to Par Pond bluegill may be due to the differences observed in age and size at first reproduction and the corresponding trade-off in energy allocation. Age and size at first reproduction can be influenced by size-or age- specific mortality. In Par Pond the circumstances of a high juvenile bluegill mortality due to an increased predator population, coupled with low adult mortality due to lack of fishing, should favor a larger size (older age) at maturity, and thus allow for rapid growth for a longer period of time.

The corrected mean number of eggs (corrected for differences in total length) from both Pond C and Par Pond bluegill were 1121 $\pm$ 10 and 1041 $\pm$ 13 respectively. A regression analysis indicated that egg number increased with total length for bluegill from both sites (Pond C: egg number = 464.6 + 3.70 TL, $F_{1,23}$ = 33.25, P < 0.0001, R^2 = 0.59: Par Pond: egg number = 666.9 + 2.12 TL, $F_{1,15}$ = 55.1, P < 0.0001, R^2 = 0.78; Fig. 5.). An analysis of covariance (total length as the covariate) showed a statistically significant difference in egg number due to location ($F_{1,39}$ = 10.01; P < 0.0030) with Pond C bluegill exhibiting a increased egg number compared to Par Pond bluegill.

Egg size averaged 1.26 $\pm$ 0.02 and 1.28 $\pm$ 0.02 for bluegill from Pond C and Par Pond respectively. Egg size of bluegill from either site was not influenced by total length ($F_{1,39}$ = 0.52; P = 0.47). An analysis of variance showed no significant difference in egg size among locations ($F_{1,39}$ = 0.86; P = 0.36).

CONCLUSIONS

The patterns observed in Pond C and Par Pond bluegill can be explained in terms of a life history "strategy". In the predictable, normothermic site (Par Pond), once adults reach reproductive size (no longer vulnerable to predation), individuals have a high likelihood of surviving to the next generation period, and may invest a smaller proportion of available resources into each reproductive bout, thereby reducing the associated "cost of reproduction" in terms of higher mortality. In an unpredictable and harsh environment such as Pond C, with higher adult mortality due to thermal stress and an unpredictable prey base, it seems unlikely that a reduction in current reproductive investment would result in an increase in future reproduction. The findings of reduced longevity, and increased reproductive investment in Pond C bluegill lend credence to the life history scenario presented above and may indicate that the life history divergences have a genetic basis.