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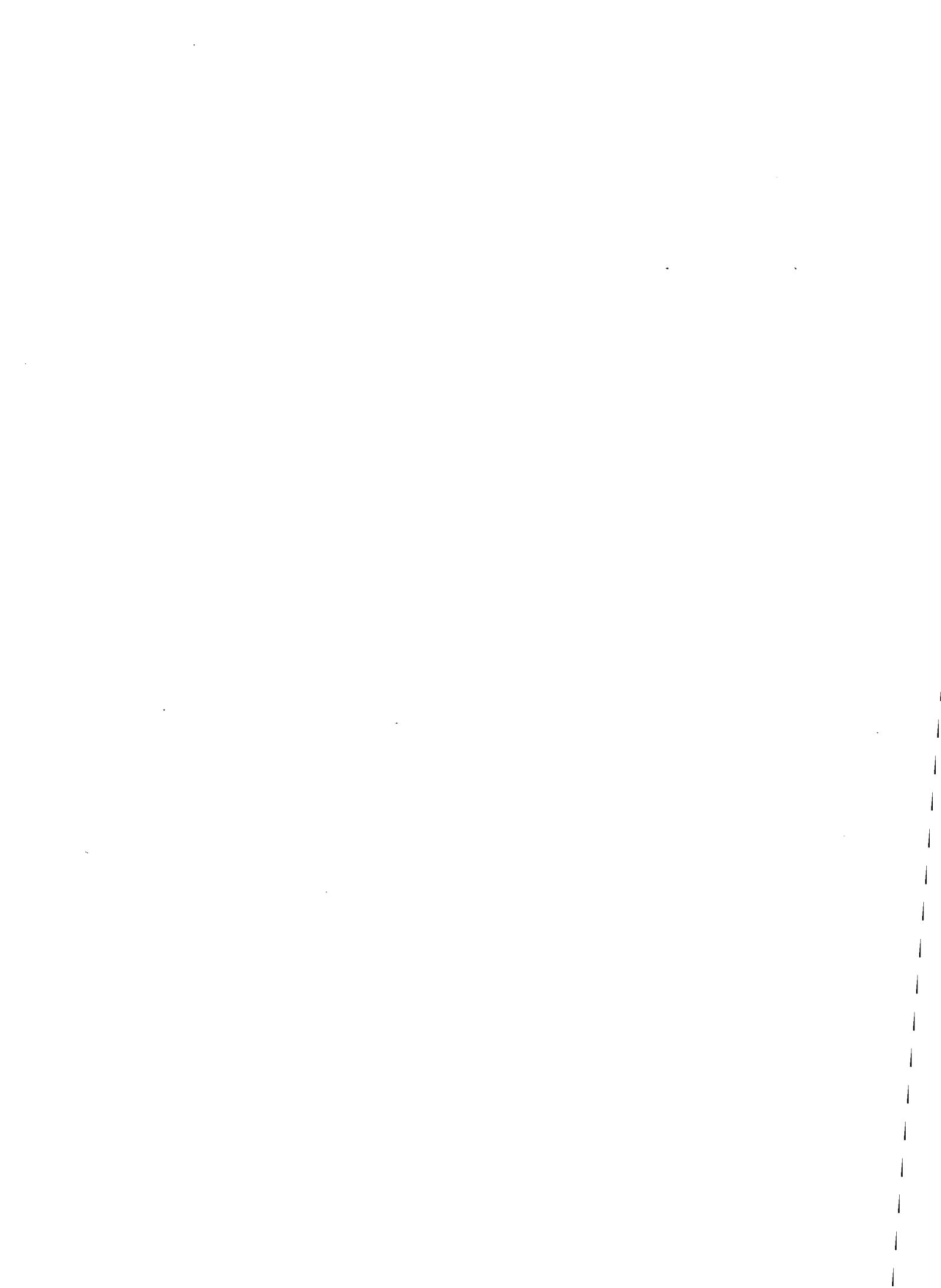
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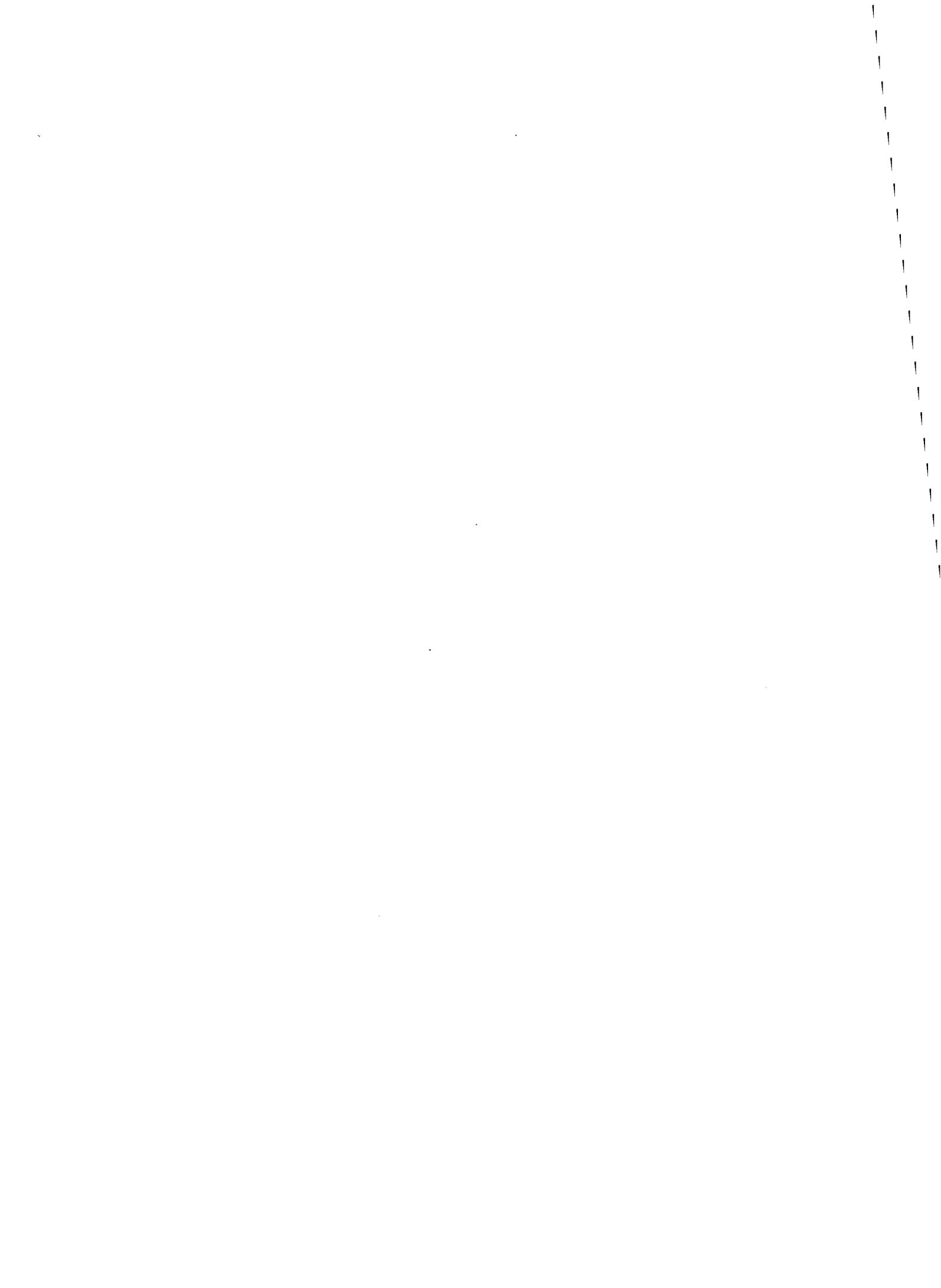
McMahon, Thomas Elwood

THE ROLE OF EMIGRATION IN THE DYNAMICS AND REGULATION OF
POPULATIONS OF THE DESERT PUPFISH (CYPRINODON MACULARIUS)

The University of Arizona

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THE ROLE OF EMIGRATION IN THE
DYNAMICS AND REGULATION OF
POPULATIONS OF THE DESERT PUFFISH
(Cyprinodon macularius)

by

Thomas Elwood McMahon

A Dissertation Submitted to the Faculty of the
SCHOOL OF RENEWABLE NATURAL RESOURCES
In Partial Fulfillment of the Requirements
For the Degree of
DOCTOR OF PHILOSOPHY
WITH A MAJOR IN WILDLIFE AND FISHERIES SCIENCE
In the Graduate College
THE UNIVERSITY OF ARIZONA

1984

THE UNIVERSITY OF ARIZONA
GRADUATE COLLEGE

As members of the Final Examination Committee, we certify that we have read
the dissertation prepared by Thomas Elwood McMahon

entitled "The Role of Emigration in the Dynamics and Regulation of Popula-
tions of the Desert Pupfish (*Cyrinodon macularius*)"

and recommend that it be accepted as fulfilling the dissertation requirement
for the Degree of Doctor of Philosophy.

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SIGNED: Thomas Edward McMahon

DEDICATED TO THE MEMORY OF MY NEPHEWS,
MATTHEW AND GARRETT WANTINK

ACKNOWLEDGMENTS

I would like to express my gratitude to Dr. Jerry Tash who stimulated many of the ideas of my research and provided support and encouragement from start to finish. The many hours of discussion and friendship with Dr. Tash will be remembered always; I feel fortunate to have been his student. I also thank Dr. Tash and Dr. William Matter for helping me realize the joys and necessity of critical thinking and intellectual stimulation.

I thank my committee members: William Matter, William Shaw, Lyle Sowls, Jerry Tash, and Chuck Ziebell for their cooperation and for their critical review of this paper. I profited from friendship and discussion with fellow students Steve Holanov and John Menke. I thank Benny Wanjala for help in gaining access to computer funds and Dr. Matter for statistical advice. I wish to express my appreciation to Esther Ayers and Stacey Copley for typing and other assistance that helped greatly to smooth the path to completing my degree.

This study was supported by funds and facilities provided by the Arizona Cooperative Fishery Research Unit. I wish to thank personnel of the Organ Pipe Cactus National Monument for their assistance and cooperation in obtaining desert pupfish. Employment with the Habitat Evaluation Procedures Group, U.S. Fish and Wildlife Service,

Fort Collins, allowed me to continue my studies. I appreciate the continual support and good humor shown by my supervisor, Jim Terrell.

I am most grateful to my wife, Doreen, for her help in all phases of my doctoral studies. Her unwaivering love and patience and her constant moral and financial support made this study possible and certainly more enjoyable. The addition of my son, Adam, during the final phases of my studies made the writing of this paper even more challenging and interesting. My hope is that he, too, will know the pleasure of finding things out. I remain grateful to my parents who have always provided me with love and support throughout my life.

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ABSTRACT

The hypothesis that emigration of individuals in excess of resource carrying capacity acts as a population regulatory mechanism was tested experimentally using the desert pupfish (Cyprinodon macularius).

When emigration was prevented, four pupfish populations monitored from May 1982 to March 1984 were unable to regulate numbers to resources. Numbers increased to a mean peak size 1.4 times greater than four pools open to emigration, followed by high mortality, a decline in body condition, reduced recruitment, and stunting. The pattern of overpopulation was similar to that observed in fenced populations of rodents. In contrast, pupfish in open pools had lower numbers, higher recruitment, better condition and growth, and higher total production. Emigration patterns were similar in all four open pools. Population size, rate of increase, and temperature affected emigration rates. Nearly twice as many males than females emigrated. Emigrant pupfish usually had poorer condition factors than residents. Pupfish showed a rapid and uniform increase in emigration when resources were reduced. Nearly one-half (42.2 and 41.8%) of pupfish populations emigrated from two open pools wherein resources were suddenly reduced by 50%. Many fewer fish emigrated from undisturbed control pools (15.2 and 16.0%). The results suggest that residency-emigratory behavior of pupfish can reliably and precisely effect

changes in numbers to be in consonance with resources. They support emigration as sufficient to regulate pupfish numbers to resources in open systems without the need for other factors or mechanisms.

CHAPTER 1

INTRODUCTION

Population regulation has long been a controversial topic and numerous theories have been developed to account for it (Tamarin 1978). These theories can be divided into four general categories (Krebs 1978): 1) a biotic category wherein population numbers are kept in check by parasitism, predation, interspecific competition, or food shortage (led by Nicholson 1933 but also supported by others including Park 1948; Lack 1954; Huffaker 1958; and Holling 1959), 2) a climatic category wherein weather controls numbers (Andrewartha and Birch 1954), 3) a comprehensive category wherein a combination of all environmental factors controls numbers (Thompson 1929, Lidicker 1978), and 4) a self-regulation category wherein differences in the "quality" of individuals controls numbers (Chitty 1960).

In this study, I focus on the self-regulation category. The theory of self-regulation as formulated by Chitty (1960:11) proposes that "all species are capable of limiting their own population densities without either destroying the food resource to which they are adapted, or depending on enemies or climatic accidents to prevent them from doing so." Proponents for self-regulation suggest that, although extrinsic factors such as climate or predation or disease can reduce numbers in a population, these factors do not result directly from changes in levels of resources, and therefore cannot function to keep

numbers consonant with resources. Instead, self-regulation proponents argue that since all species can increase beyond the limits of the resources of their environments, the evolution of mechanisms that can continually and reliably effect changes in numbers in response to resource changes is probably a necessary adaptation for all species to ensure that numbers never exceed the point at which resources are exhausted (Wynne-Edwards 1962; Chitty 1967a; Healey 1967; Taylor and Taylor 1977; Tamarin 1980). This view of self-regulation fits very well within the definition of population regulation given by Packard and Mech (1980:132) as: "...a continual adjustment of numbers to a level determined by critical resources."

A continuing hurdle for Chitty's theory is in finding acceptable mechanisms through which self-regulation is achieved. One of the mechanisms that has been proposed for population regulation in mobile animals (see Krebs 1978 for review) is emigration (Errington 1956; Lidicker 1962; Wynne-Edwards 1962; Taylor and Taylor 1977; Lomnicki 1978). Emigration is viewed as a result of behavioral spacing in relation to resources when individuals in excess of the resource carrying capacity of a given area leave. Emigratory behavioral spacing assumes that individuals have the ability to assess the availability of resources which triggers a response to either obtain a territory and become a resident if resources are available, or emigrate if resources are unavailable (Taylor and Taylor 1977; Lomnicki 1978). Regulation of population numbers to resources is thereby a by-product of individual residency-emigratory responses; group selection is thus not required

to account for the evolution of this self-regulatory mechanism as suggested by Wynne-Edwards (1962) and Van Valen (1971).

Although there exist many field and laboratory observations of emigration in a variety of vertebrates (e.g., Errington 1956; Mason and Chapman 1965; Christian 1970; Gill 1979; Tamarin 1980; Steward and Pough 1983) and invertebrates (e.g., Dethier and MacArthur 1962; Lomnicki and Slobodkin 1966; Way and Cammell 1970; Walton et al 1977; Lomnicki and Krawczyk 1980; Menke 1983) consistent with the hypothesis that emigration can regulate population numbers in mobile animals, it is generally unknown what triggers emigratory behavior and if it is both necessary and sufficient (Chitty 1967a) for population regulation. Currently the strongest support of the regulatory emigration hypothesis has been the aberrant demography and anomalous behaviors (termed "fence effects") observed in populations of rodents in experimental enclosures. "Closed" rodent populations characteristically exhibit abnormally high densities (Krebs et al 1969, 1973; Boonstra and Krebs 1977) followed by habitat destruction (Myers and Poole 1963; Krebs et al 1969, 1973; Boonstra and Krebs 1977), starvation (Myers and Poole 1963; Krebs et al. 1969, 1973; Boonstra and Krebs 1977) decline in reproductive rates (Brown 1953; Strecker and Emlen 1953; Anderson 1961; Krebs et al. 1969; Lund 1970), and increased aggression (Lidicker 1965), cannibalism (Brown 1953; Anderson 1961), and in situ mortality (Louch 1956; Krebs et al 1969; Lidicker 1975). Since fence effects are absent from unfenced controls (Krebs et al 1969, 1973; Boonstra and Krebs 1977) and from fenced populations having outlets

for emigration (Gaines et al. 1979; Beacham 1981), the most likely explanation is that emigration normally adjusts numbers to resources and overpopulation and overutilization of resources results when it is prevented.

Comparisons of open and closed populations can therefore serve as a valuable tool for testing for the importance of emigration as a potential regulatory mechanism (Lidicker 1975), but as yet this experimental technique has not been applied to species other than rodents. Observations of fence effects in enclosed populations or of emigration from open populations alone, however, are not sufficient to definitively support the regulatory emigration hypothesis since the underlying processes that cause emigration can only be inferred. For example, field studies have not been able to clearly establish whether rodents emigrate in response to resource limitation, social pressure, and/or an innate drive (Fairbairn 1978). Thus, tests of population regulation by emigration must be expanded to include controlled experiments that test for a cause-effect relationship between resource availability and emigration rate.

No one of the several theories that have been developed to account for population regulation in animals has received sufficient critical support to displace the others. Until a single theory displaces the others, the controversy concerning which factor(s) regulate population numbers will reduce our ability to effect wise conservation and management policies. Settling this controversy becomes even more imperative if one considers that population regulation is an interface area of ecology and affects the interpretation of most other areas

(Tamarin 1978). Settling this controversy, if Popper (1959) is correct, requires doing carefully controlled experiments designed (through testing null hypotheses) to definitively support or disprove one or another of the various theories. However, performing decisive null hypothesis tests presents a formidable methodological barrier in population biology (Krebs 1978; Tamarin 1978). Studies with natural populations present inherent difficulties in replicating experiments and controlling variables and thus alternative explanations for the observed results can often be forwarded (Chitty 1967b; Watson and Moss 1970; Hayne 1978). Conversely, laboratory population experiments offer greater control yet often suffer from an uncertainty in the application of their results to natural populations (Blair 1964; Mertz and McCauley 1980).

Pupfish (Cyprinodon spp.) appear to be particularly well-suited for experimentally evaluating population regulation theories. Many pupfishes exist naturally in small, relatively simple ecosystems that can be easily duplicated; for example, I have observed that desert pupfish (C. macularius) acclimate readily to small artificial water bodies, exhibiting life histories, behaviors, and population dynamics similar to those in native habitats. Unlike the vast majority of most other species of vertebrates, in pupfish it is possible to make observations and to do controlled and replicated experiments on entire populations under essentially natural conditions.

The objective of my study was to rigorously test regulatory emigration in desert pupfish. I tested emigration as a regulatory behavior by 1) comparing the dynamics of open and closed populations

and by 2) comparing emigration rates of pupfish from populations in pools having different amounts of resources. If emigration acts as a self-regulatory mechanism to adjust numbers to resources, then one would predict that 1) fence effects occur in pupfish populations when emigration is prevented, and 2) as resource carrying capacities are changed, emigration rates change, increasing with decreased resources and decreasing with increased resources.

CHAPTER 2

MATERIALS AND METHODS

Pupfish (Cyprinodon macularius) were collected from Bates Well, Organ Pipe Cactus National Monument (OPCNM) Arizona, in April 1982. Bates Well is a small refugium established in 1978 for Quitobaquito pupfish (Kynard 1979). The Quitobaquito pupfish is native to Quitobaquito Springs (OPCNM), one of the few habitats where C. macularius still exist (Miller 1981; McMahon and Miller in press). For one month prior to experiments, pupfish were held in a large outdoor pool at the Arizona Cooperative Fishery Research Unit research facility in Tucson, Arizona and fed to excess daily with a dry flake food.

Population Dynamics of Pupfish in Open and Closed Pools

Pupfish populations regulated to resources by emigration of individuals that are in excess of resources implies that closed populations will overpopulate and overutilize resources. I tested the null hypothesis of no difference between pupfish populations in open than in closed systems by comparing pupfish populations in four open pools to those in four closed pools from May 1982 to March 1984. Experimental pools were 1.8 m in diameter and 1 m deep and made from metal shells lined with blue, form-fitting 10 mil polyvinyl sheeting. Water depths were maintained at 23 cm by adding water on a weekly basis or as needed. Pools were placed side-by-side in an unshaded

area. A 2.5 cm layer of coarse sand was added for substrate. The pools provided environmental conditions similar to those encountered by pupfish in nature. The substrate surface area of 2.55 m² was similar to the substrate area of 3.25 m² in Mexican Springs, Ash Meadows, Nevada (Soltz 1974), a small spring that contained a self-sustaining population of 40-60 Cyprinodon nevadensis (Soltz and Naiman 1978).

To control the variable effect of predation, pools were covered by a 2 cm mesh bird netting and predacious aquatic insects were removed by hand-net. Experimental pools were identical except that a fiberglass coated 30.5 cm wide by 70 cm long wood channel was attached to each of the four pools open to emigration (Figure 1). An endpiece at the poolside entrance to each channel maintained water levels equal to those in closed pools. Two 3.8 cm high notched plexiglass panels glued 15 cm apart on a 30 x 15 cm shelf on top of the channel end-piece (Figure 2) served as a one-way outlet for emigrating pupfish. The inside of the channel was painted blue to match pool liners.

To open the one-way outlet, small submersible pumps (.03 hp) in the channels pumped water via a 1.3 cm diameter tube into a net in the channels (Figure 2). Water flow from each pump was adjusted to provide a 1.0 cm deep overflow on the shelf and a volume of 1.0 l/min. The overflow velocity was sufficiently slow (.25 cm/sec) so that pupfish of all sizes had the choice, once they had swum onto the shallow shelf, of either emigrating or returning to the main pool. To leave the main pools, a fish had to swim through a small (2 cm) notch in the first panel, onto the shallow shelf, and over a small V-notch in the second panel into the trap.

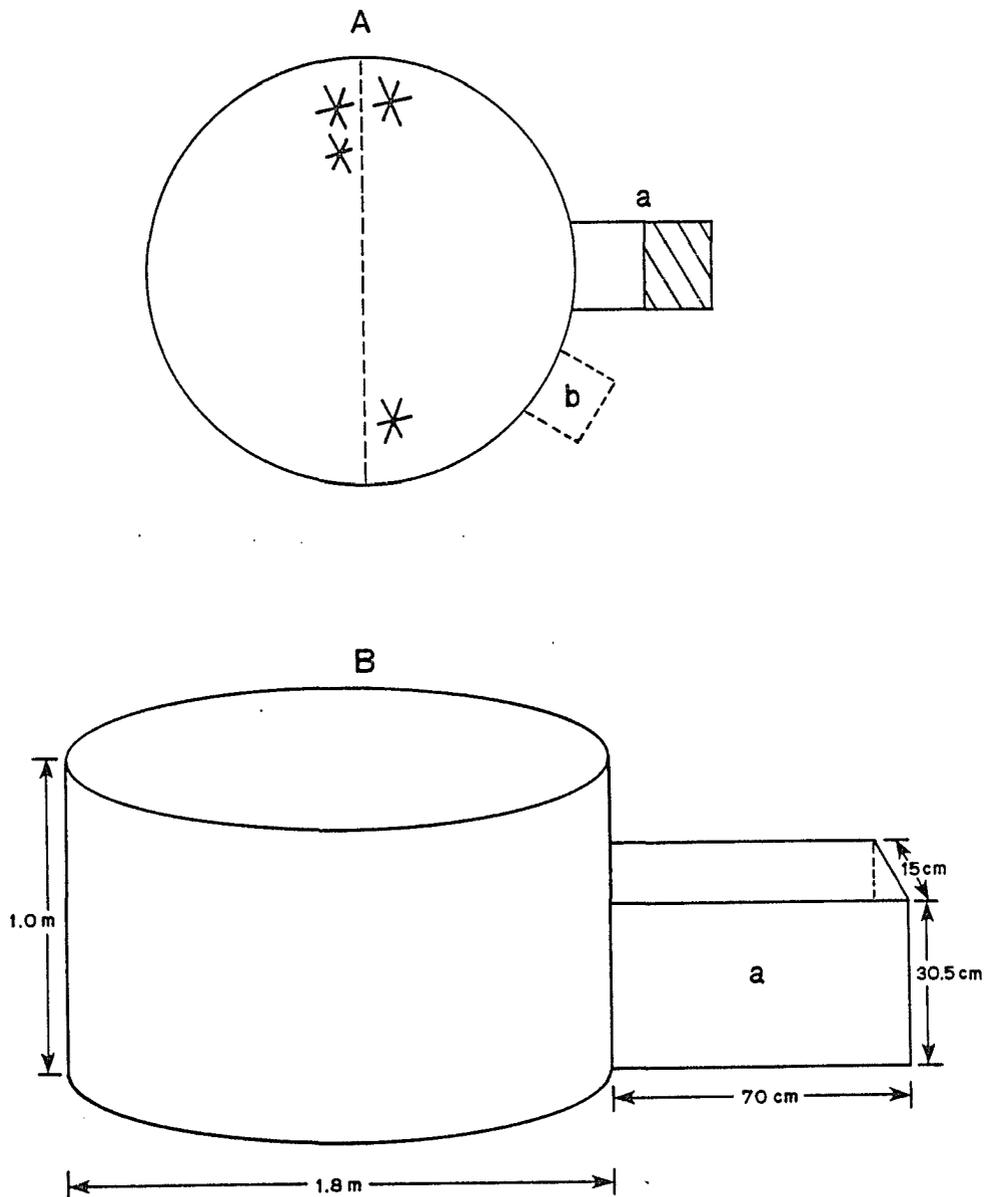


Figure 1. Top (A) and side (B) views of main pool and outlet channel (a). Closed pools were identical except that they did not have an outlet channel. A screened compartment attached to one pool containing a continuous-recording thermograph is indicated by "b". Dashed line (-----) in top view of pool indicates location of barrier used in the resource manipulation experiment. Large asterisks (*) indicate location of plastic plants.

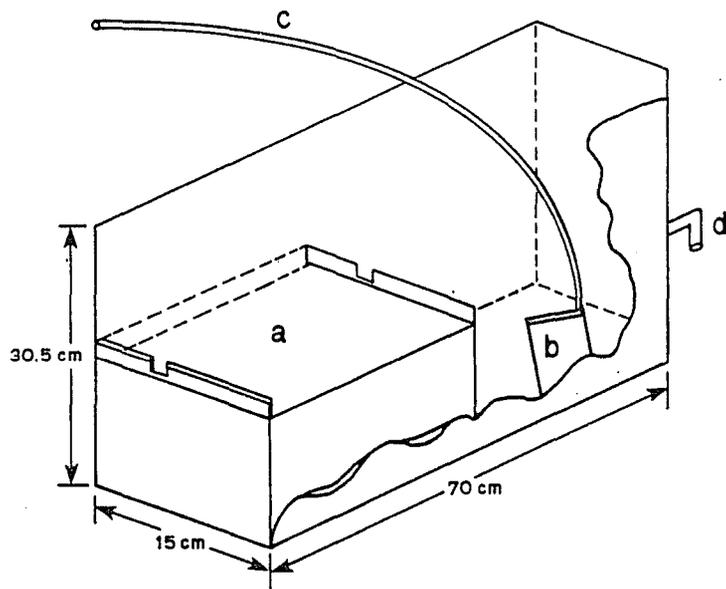


Figure 2. Side view of outlet channel showing shelf area (a), pump (b), tube (c) carrying water to pool, and overflow drain (d).

Pools were opened to emigration by activating pumps for 3 days every 2-3 weeks. To ensure acclimation of resident fish to disturbance and water flow, the second panel of the outlet shelf was screened the first 24 hours of pump operation. At 0800 hours on the second day, screens were removed and fish allowed to emigrate for 48 hours. Emigrants ≥ 20 mm standard length (SL) were counted, sexed, measured to the nearest .5 mm SL, and weighed to the nearest .001 g on a Mettler balance by adding fish (blotted dry) to a tared water sample. Fish > 20 mm SL were counted and measured but not weighed. Two days was deemed sufficient for most emigration to occur since in preliminary laboratory experiments (five male and five female adult pupfish 25-30 mm SL were added to two 360 liter tanks, each with 2.5 grams of flake food/day and four concrete blocks), most emigrants (seven in one pool and eight in the other) left within the first 48 hours over the ten day period the tanks were opened. Open pools provided pupfish conditions similar to those they counter in isolated pools of intermittent desert streams when water flow increases during periods of rainfall (Deacon and Minckley 1974; Constantz 1981). To mimic the effects of water circulation in open pools, pumps circulated water in closed pools for three days after pumping in open pools; the outlet tube was placed 10 cm above the water surface to obtain the effect of water flow over a shelf.

Populations of pupfish were started on 27 May 1982 by adding two males (27-37 mm SL) and three females (25-35 mm SL) to each pool. Fish reproduced for approximately two months before any pools were

opened to emigration. Fish were not fed over the course of the study; a natural food base was established in each pool by filling pools with water inoculated with 9.5 liters of green pond water and allowing pools to stand six weeks prior to introducing fish. Available food consisted of algae, insects, and detritus that fell or developed in the pools. Four artificial plants weighing 30 grams (excluding lead weight on bottom), each made of 1.25 x 16 cm clear plastic strips, served as cover (Figure 1). Additional plant cover was provided by Chara which colonized all pools. By the time fish were introduced, the water in every pool had taken on a slight greenish cast; there was a brownish layer of periphyton on the plastic plants, and large numbers of chironomid larvae were present.

Every pool was seined (3 mm mesh net) in July, September, October 1982, March, May, July, September-October 1983, and March 1984 until visual checks revealed all fish had been removed. Sampling variation was estimated at 3% based on repeat sampling of a pool within one week in March 1984. All sampling was done between 1200-1500 hours. Fish \geq 20 mm SL were counted, measured, sexed, and weighed to nearest .001 g. Fish $<$ 20 mm were counted, measured, and sexed (if possible) but were not weighed (to minimize handling stress in fish of such small size). Males were identified by the presence of an elongated, black-tipped anal fin, metallic blue coloration, and a black-tipped dorsal fin (Barlow 1961). Fish as small as 18 mm exhibited male coloration. Size at maturity in females was probably near 20 mm (an egg was extruded from a 21 mm female) (see also Soltz 1974). Handling

mortality was minimal; only on rare occasions were 1 or 2 dead fish found the day after sampling. Fish were observed feeding and males observed defending territories within 20 minutes after return to pools. Sampling of all pools was completed within a 2 to 3 week period. Whole samples were not taken during winter months (temperatures $< 15^{\circ}$ C) when fish were buried under plants and detrital floc. Small samples (15-20 fish measured and returned) were taken from each pool on 13 December 1983 and on 26 January 1984 for length and weight measurements.

At each sampling period, measurements of length, weight and sex were taken from all fish in every pool for comparing the number of fish, size-class distributions, sex ratios, biomasses, and recruitment within and between pool types. Similar measurements were made of emigrant pupfish for comparing size-class distributions and sex ratios with residents. Linear length-weight relationships were derived for all closed or all open pool fish (sexes combined) ≥ 20 mm at each sampling period by regressing log fish weight on log length ($\log W = a + b \log L$) by the method of least squares (Ricker 1975). A one-way analysis of covariance (Zar 1974) was used to test for differences in log length-log weight regressions of pupfish in open versus those in closed pools by testing the null hypothesis of no difference in slopes or elevations between pool types. A condition factor ($K_{SL} = 100 W/L^3$, where W = weight in grams and L = standard length in cm; Bagenal and Tesch 1978) was calculated for each fish ≥ 20 mm to show differences in length-weight between size groups or pool populations. Use of this formula assumes a slope of 3 in the length

weight regression equation and provided an index for comparing the gross nutritional state of fish (Weatherley 1972). Both methods were applied in this study since analysis of covariance techniques permit rigorous statistical comparisons of the length-weight relationship of fish in each pool type while condition factors depict length-weight differences in a more qualitative fashion (LeCren 1951).

Mortality was estimated by determining the difference in population numbers in the same pools between two consecutive sampling times (in open pools the number of emigrants were subtracted). Estimates of mortality by size-class in closed pools were obtained by comparing length-frequencies between samples; in open pools, by comparing length-frequencies between samples after adding length-frequencies of emigrants. Changes in population numbers in open and closed pools over time were measured by:

$$G_{t \rightarrow t+1} = \frac{N_{t+1} + E_{t \rightarrow t+1}}{N_t}, \text{ where } G = \text{percent change in population}$$

size from time t to time $t+1$ for each pool type, N = population size at t and $t+1$, and E = total number of emigrants between samples. Total production of fish in open and closed pools over the course of the study was determined by the formula:

$$\sum_{1}^8 P = N_{t+1} - N_t + E_{t \rightarrow t+1}, \text{ where } \sum_{1}^8 P = \text{sum of the number of}$$

fish lost or gained between each of 8 sampling periods, N = population size at t and $t+1$, and E = number of emigrants between samples.

Environmental conditions in pools were maintained as closely as possible to meet the objective of the presence or absence of an outlet for emigration as the sole variable acting differentially on open and closed populations. However, due to the near-natural conditions under which experiments were run, small variations in resources and some of the other environmental conditions were likely to occur between pools. Variations in food, cover, and water quality were monitored where possible and taken into consideration in interpreting comparisons between pools.

Food production was monitored by measuring detritus depth, on the assumption that depth of floc overlying sand substrate is an indicator of food production. Detritus depths were measured in each pool on 17 June and 9-11 November 1983 and on 26 January-1 February 1984. Depths were measured to the nearest 1 mm every 10 cm along each of two transect lines across each pool, yielding 30 depth measurements per pool. When plant cover was too thick to make measurements, depths were measured in the closest plant-free areas adjacent to the transects. Initial transect locations were chosen randomly; all subsequent transect measurements were made along these same locations. Detritus depths were analyzed by using a nested analysis of variance (ANOVA) (Snedecor 1956) to test the null hypothesis of no difference in detritus depths among open pools or among closed pools and between open versus closed pools.

Plant cover (Chara plus plastic plants) was measured on 19 June and 2 November 1983 and on 26 January 1984 as the percent of

total substrate area covered. Differences in plant cover between open and closed pools were analyzed by t-test.

Temperature was monitored with a continuous-recording thermograph (Figure 1). Dissolved oxygen, pH, and conductivity were measured periodically.

General Observations

Observations were made of spawning behavior, length of breeding season, and behavior of pupfish in relation to temperature and to use of cover. Newly hatched fry were determined by waving a hand over the bottom and scoring their abundance as absent, present (<10), or abundant (≥ 10).

Resource Manipulation Experiment

To test the prediction that pupfish self-regulate by emigration, I measured residency-emigratory response of pupfish to changes in resources. The assumption was made that if regulation occurs, then carrying capacity should change with changes in resources, increasing with resource increases and decreasing when resources decrease. Thus, changes in carrying capacity should be accompanied by changes in emigration rates such that pupfish numbers adjust to the amount of resources present within a habitat (Lomnicki 1978). I tested the null hypothesis that "emigration of pupfish is independent of resource carrying capacity," by comparing the emigration rates of fish from two undisturbed populations to those in two populations wherein resources were suddenly reduced by 50%.

I ran this experiment with pupfish populations that had been established over a 22 month period in the four open pools (described in the previous section). Two weeks after pool populations had been sampled, a barrier (1.6 mm mesh fiberglass screen) was stretched and anchored across the center of two of the four pools. All fish in these two pools with reduced resources were restricted to the section having an outlet (Figure 1). The two remaining pools were left undisturbed so as to serve as controls.

After a one week acclimation period, pumps in all pools were activated to allow emigration. Twenty-four hours after activation of pumps, outlet screens were removed. Traps were checked at 0800 and 1800 hours each day for 9 days (11-19 April 1984) for emigrants. All emigrants were sexed, measured, and those ≥ 20 mm SL were weighed. After termination of the experiment, the percent of the total population that emigrated from pools with reduced resources was compared to the percent that emigrated from control pools. Percentages were used rather than absolute numbers because initial numbers varied between pools (147 and 79 in pools with reduced resources and 112 and 50 in control pools).

CHAPTER 3

RESULTS

Temperature followed a seasonal pattern similar to Quitobaquito Springs (Kynard and Garrett 1979) (Figure 3). Temperatures were identical in all pools except for a $\pm 2^{\circ}$ C difference when water was trickled into open pools during periods of emigration. Temperatures ranged from 4° C to 34° C (upper lethal levels for C. macularius are $41-44^{\circ}$ C (Lowe and Heath 1969) and the lower lethal level for C. nevadensis is $< 3^{\circ}$ C (Hirshfield et al. 1980).

Dissolved oxygen (DO) and pH levels were similar in open and closed pools (Appendix Tables 1 and 2). D.O. ranges were 3.2 to 20.0 mg/l in open pools, and 3.2 to 17.5 mg/l in closed pools (\bar{x} = 5.0 to 8.0 mg/l in all pools). Levels were well within the tolerance range of pupfish (Lowe et al 1967). The pH ranged from 6.0-8.9 in all pools.

Conductivity ranged from 575-1200 umhos in open pools and 585-2200 umhos in closed pools (Appendix Table 3). Values were lower in open pools due to the addition of well water (550 umhos) when outlet channels were flooded to allow fish to emigrate. When conductivity of closed pools was more than double that of open pools, pool water was removed and well water added until conductivities were equal. Differences in conductivity between open and closed pools were never

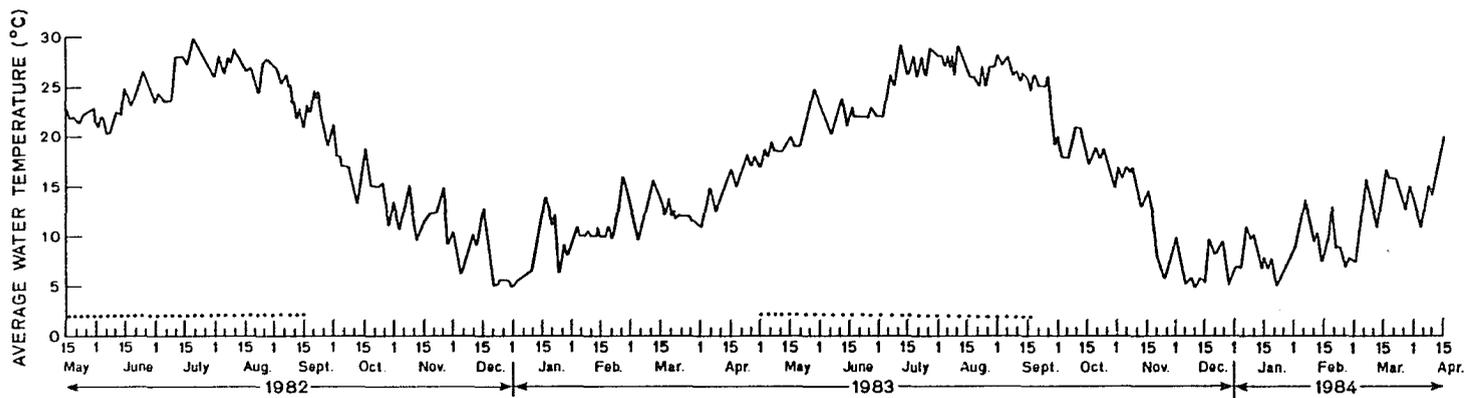


Figure 3. Average daily water temperature of pupfish pools. Dotted line indicates breeding season.

Detritus depths and plant cover were measured in June and November 1983 and in January 1984. The first year I made only visual comparisons and estimated that there were no major differences between open and closed pools in amounts of detritus or plant cover. Detritus accumulated in every pool, increased during summers, and showed little or no change during winter (Table 1). Detritus in open and closed pools was about equal in June 1983. Open pools had approximately 20% more than closed pools during November 1983 and January 1984 (ANOVA, $.10 < p < .05$, Table 4). Plant cover varied widely in both open and closed pools, but differences between the means for each pool type were not statistically significant for any period (Table 2). In all pools except closed pool C4, Chara declined as the season progressed; by January 1984, cover in these pools was almost entirely plastic plants.

Development of Populations

The small number of pupfish introduced into each of eight pools in May 1982 reproduced rapidly, reaching mean peak numbers by September 1982 (Figure 4; Appendix Table 4). Within four days after the start of the study, one or more male pupfish in each pool had developed blue coloration and started defending territories, excluding all intruders except responsive females and fry < 15 mm in length. During the first summer, males used two breeding systems of those described for pupfish by Kodric-Brown (1981). If nearly equal in size, males divided pools into two equal-sized territories. Where size differences exceeded 4 mm, one large male defended most of the pool and confined smaller males to a pool periphery.

Table 1. Mean detritus depth in each open and closed pool and a nested analysis of variance of the amount of detritus among open or closed pools and between pool types (open vs. closed) for each sampling date.

OPEN					CLOSED					
<u>.01</u>	<u>.02</u>	<u>.03</u>	<u>.04</u>	<u>\bar{x}</u>	<u>Dates</u>	<u>C1</u>	<u>C2</u>	<u>C3</u>	<u>C4</u>	<u>\bar{x}</u>
6.1	6.9	8.1	7.6	7.2	June '83	9.6	7.9	8.7	6.6	8.2
15.1	16.2	14.2	19.0	16.1	Nov. '83	13.9	14.8	12.4	12.8	13.5
17.0	17.1	17.0	16.8	16.9	Jan. '83	12.1	14.0	12.7	13.9	13.2

<u>JUNE '83</u>	<u>SOURCE</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>
	Pool types	1	62.016	62.016	1.74
	Pools	6	213.834	35.639	1.203
	Detritus	232	6868.133	29.604	
	Total	239	7143.983		

<u>NOV. '83</u>	<u>SOURCE</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>
	Pool types	1	429.336	429.336	5.326*
	Pools	6	483.69	80.615	1.53
	Detritus	121	12204.77	52.607	
	Total	129	13117.80		

<u>JAN. '83</u>	<u>SOURCE</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>
	Pool types	1	765.15	756.15	5.07*
	Pools	6	894.6	149.1	3.425**
	Detritus	232	10098.4	43.52	
	Total	239	11758.15		

* = significant at .10 level

** = significant at .05 level

Table 2. Percent substrate area covered by plants (plastic plants and Chara) in each open and closed pool. The t-test values test for significant differences in the mean (\bar{x}) percent plant cover in open and closed pools at each sampling date.

<u>OPEN</u>					<u>CLOSED</u>					
<u>01</u>	<u>02</u>	<u>03</u>	<u>04</u>	<u>\bar{x}</u>	<u>Dates</u>	<u>C1</u>	<u>C2</u>	<u>C3</u>	<u>C4</u>	<u>\bar{x}</u>
24.0	22.6	14.8	24.1	21.4	19 June '83	11.5	15.8	16.7	19.5	15.9
44.3	13.2	16.4	3.7	19.4	2 Nov. '83	4.6	9.4	20.0	31.1	16.3
14.8	11.5	8.5	3.7	9.6	26 Jan. '84	4.6	7.9	8.7	34.4	13.9

t-test

June $t_6 = 1.98, .10 < p < .05$

Nov. $t_6 = .29, p > .20$

Jan. $t_6 = .59, p > .20$

During the first summer, there was high reproduction and recruitment in all pools (Figures 4 and 5). Fry were observed in every pool from 15 June until early September. Recruitment in closed pools was 1045 (211-303 per pool). Recruitment in open pools was 760 (171-224 per pool); 185 (27-56 per pool) fry emigrated. Total production during this period was similar in open and closed pools (945:1045).

Recruitment was lower and more variable in 1983. Closed pools had lower recruitment than open pools (Figures 4 and 5) and fry were rarely seen (Table 3). Fry were present in open pools but were less numerous than during the preceding year. Three hundred and ninety-eight fry (20-267 per pool) were produced in open pools from March to September 1983 and 65 (0-29 per pool) in closed pools. The reasons for the lower production and for the lower recruitment in closed pools were not obvious. I found no differences in breeding behavior between open and closed populations. Blue, territorial males were present in all pools from mid-April to mid-September and spawning occurred both in open and closed pools. Breeding behavior was also similar; the 3 or 4 largest males in each pool defended cleared areas of approximately .25 m diameter and numerous (10-15) small (20-22 mm, age I) "satellite" males (Kodric-Brown 1981) defended small patches of vegetation or substrate along the pool periphery. There was some evidence that egg production and survival was lower in closed pools. I found a positive relationship between female condition factor and egg production; open and closed pools had similar sizes and numbers of female pupfish ≥ 20 mm (Figure 6), but females in closed pools were in much poorer condition (average condition factors of 2.45 versus that of

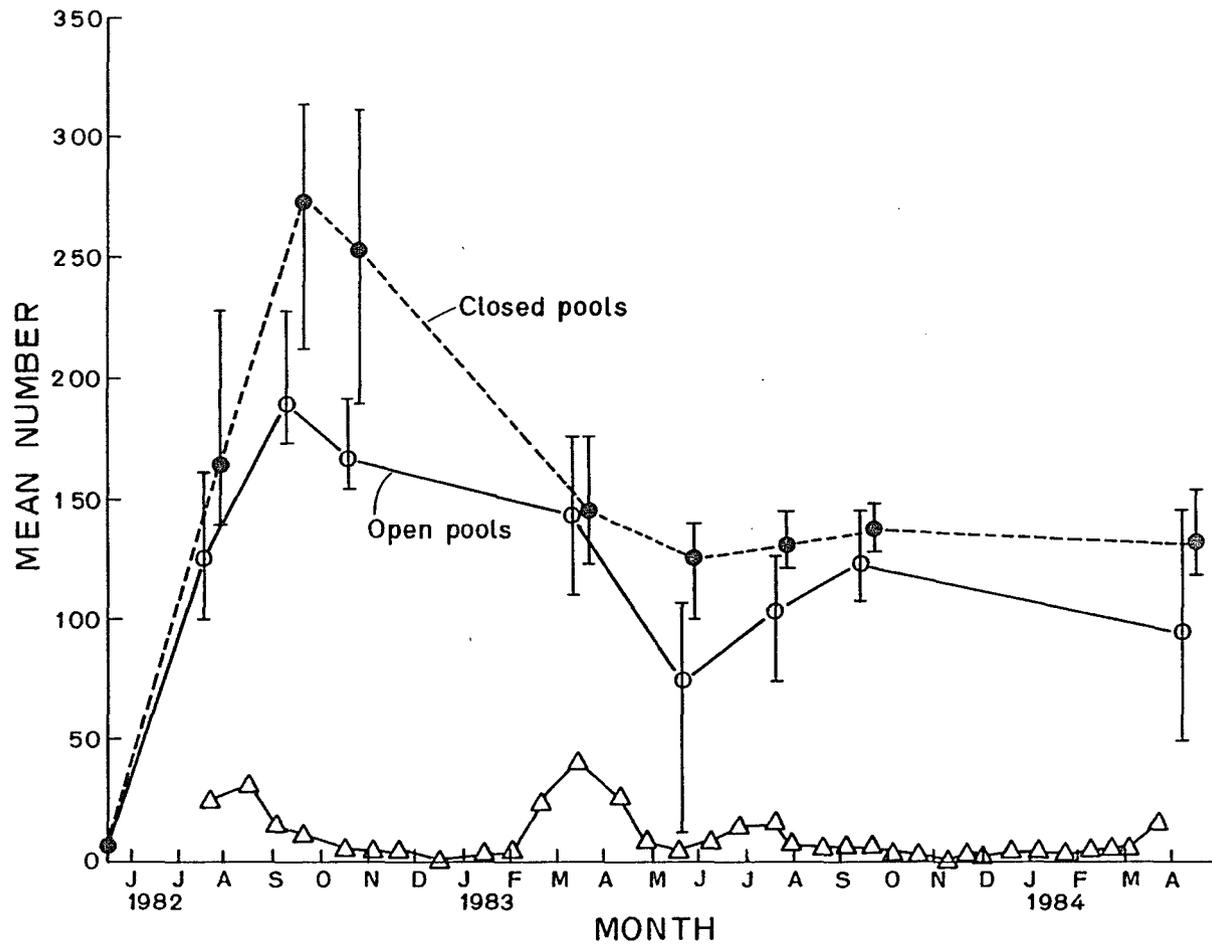


Figure 4. Mean numbers of pupfish found in the four pools open and the four pools closed to emigration. Vertical bars indicate range. Triangles (Δ) indicate the mean number of pupfish emigrating from the four open pools.

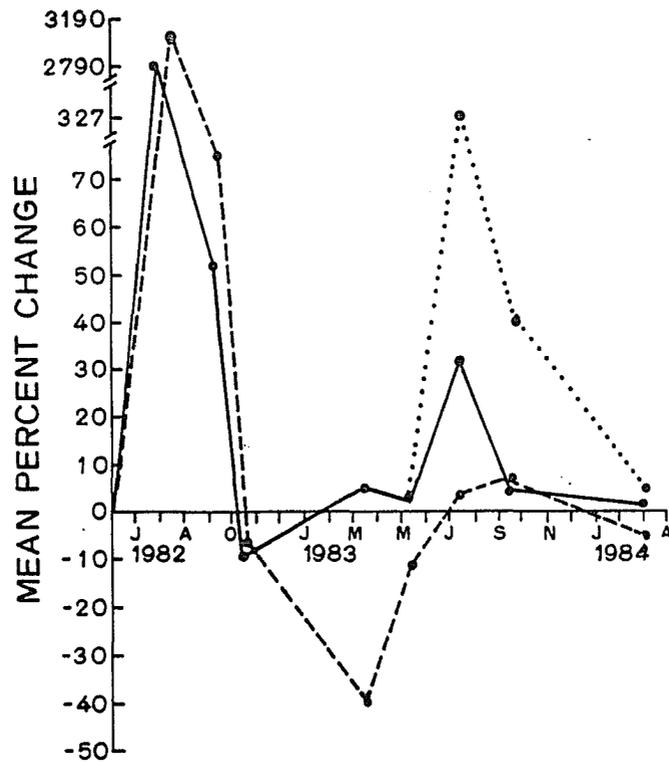


Figure 5. Mean percent change in numbers between sampling times in open (——) and closed (-----) pools. Due to a much higher growth rate than the other open pools in 1983, the percent change in numbers for pool 03 was not used in calculating the mean percent change in open pools from May 1983 to March 1984; its percent change in numbers is shown separately (.....).

Table 3. Relative abundance of fry in each open and closed pool in 1983.

<u>DATE</u>	<u>01</u>	<u>02</u>	<u>03</u>	<u>04</u>	<u>C1</u>	<u>C2</u>	<u>C3</u>	<u>C4</u>
17 May	+	o	+	o	o	o	o	o
4 June	o	o	+	+	o	o	o	o
17 June	+	o	++	+	o	o	+	o
14 August	+	o	++	o	+	o	o	+
27 August	+	+	++	o	o	o	o	o
7 Sept.	+	+	+	+	o	o	o	o

o = no fry observed

+ = 10 fry present

++ = \geq 10 fry present

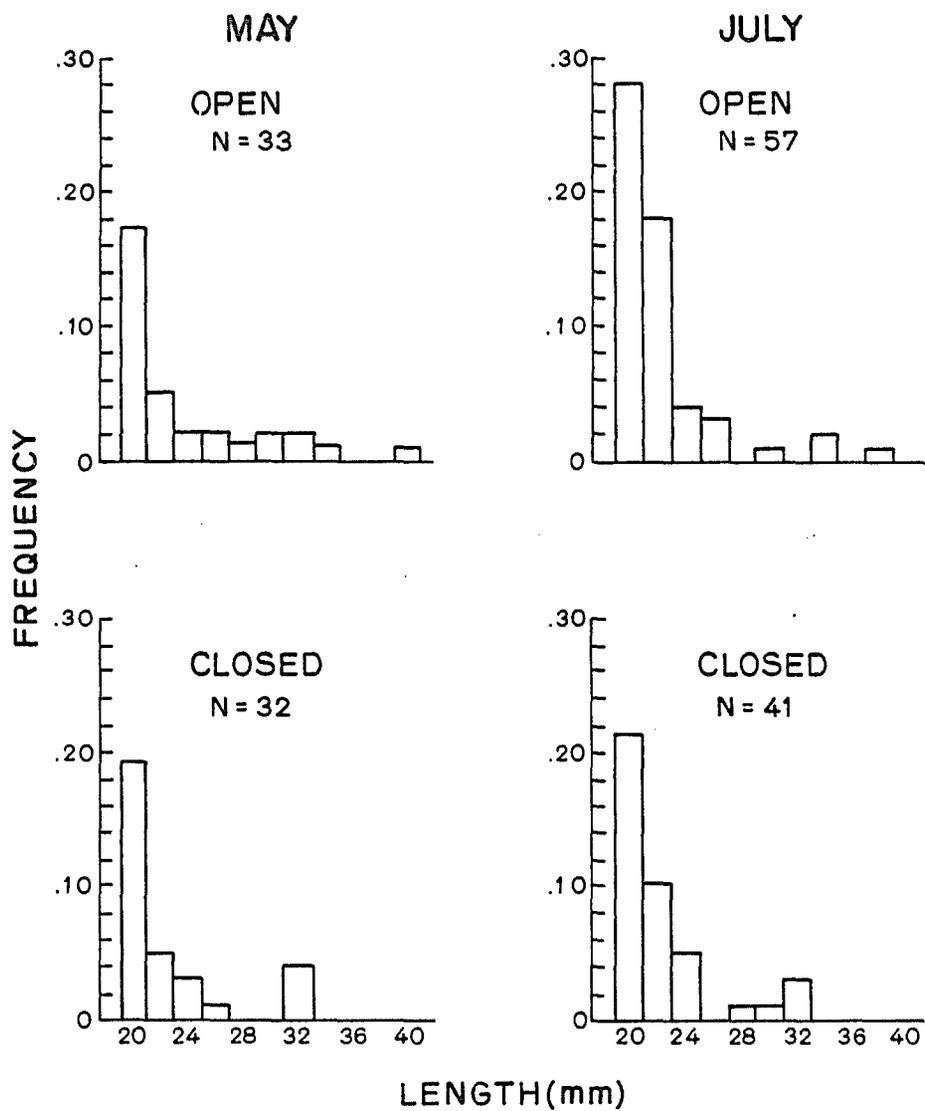


Figure 6. Length-frequency distribution of female pupfish ≥ 20 mm in length in the four open and the four closed pools in May and July 1983.

2.97 for females in open pools) at the onset of breeding in May (Table 4). Also, there was an increase in recruitment of fry in closed pools from July to September (see Figure 9 in length-frequency section) that was preceded by an increase in condition factor from 2.45 in May to 3.01 in July (Table 2). In addition, desert pupfish are known to cannibalize their eggs (Loiselle 1980) and male territories that are abandoned for even short periods are rapidly invaded by fish that feed on the bare substrate. Therefore, since closed pools had a larger number of fish \geq 18 mm, there were more potential egg cannibalizers, and they probably had higher rates of egg cannibalism.

Populations in open pools exhibited negative growth (in numbers) in only one period; closed populations had negative growth in four periods and only slight (<5%) positive growth in numbers during the 1983 breeding season (Figure 5). Even though nearly twice the number of fish were produced in open pools than in closed pools over the entire study (258-500:126-156), mean numbers remained higher in closed pools than in open pools throughout the study. There was little variation between open pools and between closed pools in the size of populations. Coefficients of variation at each sample averaged 14.8% in closed pools and 16.8% in open pools except during spring (Appendix Table 4).

Population Losses

Fish that were produced in pools that were not recruited into the standing population either died or emigrated (open pools only). During the study an estimate of 734 fish died in closed pools compared

Table 4. Mean Condition factors (K_{SL}) of female pupfish ≥ 20 mm in length from each open and closed pool.

SD = Standard Deviation and SE = Standard Error

May 1983	Open Pools			Closed Pools			
	mean K _{SL}	SD	# of ♀♀	mean K _{SL}	SD	# of ♀♀	
01	2.92	.33	13	C1	2.65	.19	6
02	3.01	.13	9	C2	2.26	.73	10
03	3.12	.36	4	C3	2.30	.14	9
04	2.83	.20	7	C4	2.60	.27	7
$\bar{x} = 2.97$ (SE = .06)			33	$\bar{x} = 2.45$ (SE = .10)			32
July 1983							
01	2.98	.20	14	C1	3.04	.22	7
02	2.84	.13	7	C2	3.17	.22	15
03	3.08	.09	6	C3	2.93	.21	7
04	2.95	.21	30	C4	2.89	.26	12
$\bar{x} = 2.96$ (SE = .05)			57	$\bar{x} = 3.01$ (SE = .06)			41

to 145 in open pools despite the much greater production in open pools (Appendix Table 4). Open pools lost almost as many fish as closed pools (667:734) but 78.3% of the total open pool loss was through emigration.

Mortality and/or emigration increased in four periods during the study (Figure 4). From September to October 1982, 90 fish died in closed pools and 110 fish (27 emigrated and 83 died) were lost from open pools. Most fish that died or emigrated were < 20 mm. The greatest losses occurred during October 1982 to March 1983, when 446 died in closed and 114 (89 emigrated and 25 died) were lost from open pools. Losses were again mostly fish < 20 mm. Most of the mortalities occurred from 1 November-1 March when low water temperatures caused pupfish to bury under plants and detrital floc. During this period 86 dead fish were found on the bottoms of closed pools (totals: C1=23, C2=4, C3=9, C4=50) but only 10 were found in open pools (totals: O1=2; O2=5; O3=1; O4=2). All dead fish except one were age 0 and < 22 mm. Mortalities were highest right after a rapid temperature decline ($\geq 5^{\circ}$ C in 48 hr.) to levels < 10° C. The greatest number of mortalities occurred during a 7-day cold spell in early January 1983 when water temperature dropped to 5-6 $^{\circ}$ C (Figure 7). Many dead fish had a whitish fungus on the head region but it could not be determined if this was the cause of death or a post-mortem invasion. Populations continued declining from March to May 1983, with 79 mortalities in closed pools and none in open pools (283 were lost from open pools but all through emigration). Mortalities of pupfish during

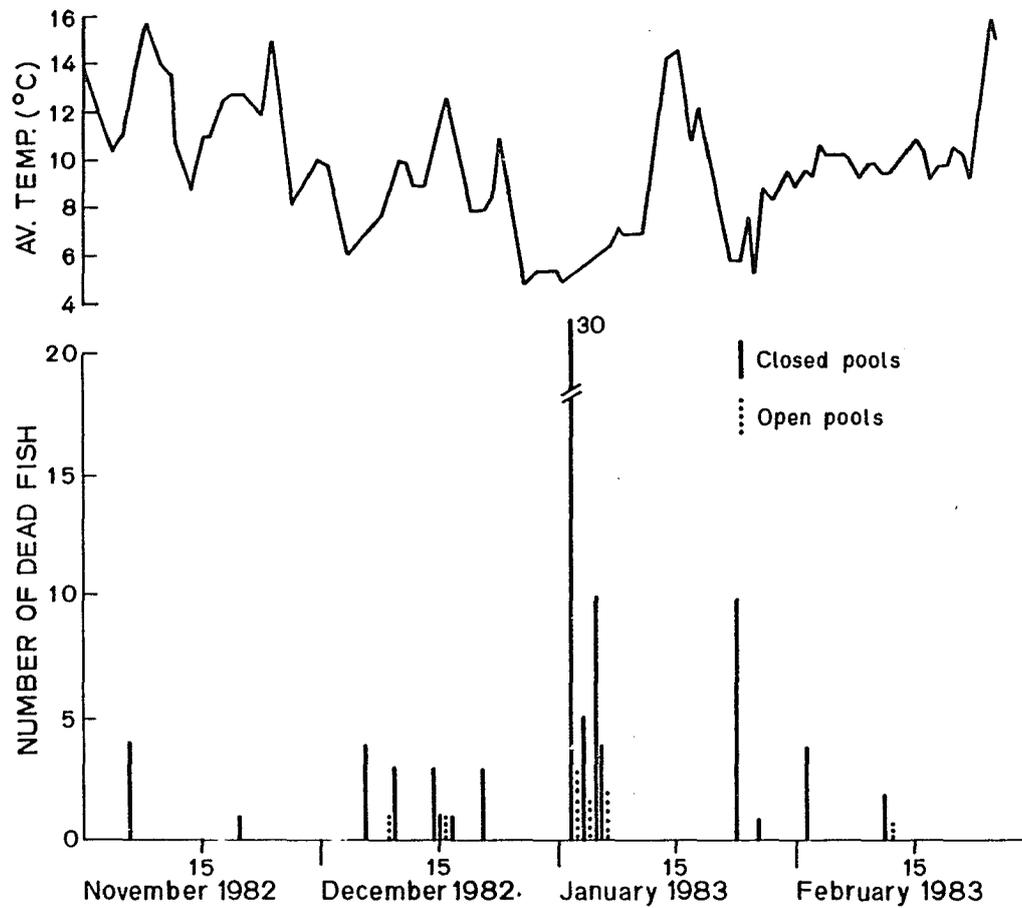


Figure 7. Total number of dead pupfish found in open and closed pools and average daily water temperature from 1 November 1982 - 15 February 1983.

September, 1982 to May 1983 showed positive relationships to the initial population size in september (closed $r=.994$, $n=4$, $p <.01$ and open, $r=.885$, $n=4$, $p <.01$). During this period, mortality in closed pools was 5.6 times greater than in open pools (609:108).

Overwinter mortality in both open and closed pools was much less severe in 1983-84. Open pools lost 136 fish from September 1983 to March 1984 (101 emigrated and 35 died). Closed pools had 38 mortalities over this same period (0-15 per pool, all < 20 mm). Four dead fish were found in closed pools and none in open pools from 1 November 1983 to 1 March 1984.

Length-weight Relationships

There were significant differences in length-weight between pupfish in open and closed pools in 1983 (Table 5). These differences were most pronounced in May when fish from closed pools showed signs of starvation. From March to May 1983, mean condition factors of fish in closed pools declined markedly from 2.93 to 2.60 (Figure 8). During this same period, condition factors of fish in open pools increased from 2.93 to 3.02. Closed pools that had the largest drop in condition factor ($C2=2.71 \rightarrow 2.50$; $C3=2.88 \rightarrow 2.48$) also had the highest mortalities ($C2=28$ and $C3=35$ fish lost). Fish in closed pools weighed an average of 18.6% less than those in open pools (ratio of adjusted means, Snedecor 1956:395). Based on length-weight regressions calculated for May 1983, 25 mm SL fish from closed pools averaged 0.420 g. The same size fish from open pools averaged 0.478 g. In addition,

Table 5. Length-weight regression of pupfish ≥ 20 mm in length (sexes combined) from open and closed pools at each sampling period.
 r = correlation coefficient
 n = sample size
 W = weight in grams
 L = standard length in mm
 F values give results of a one-way analysis of covariance for differences in slopes and elevations of length-weight regression for pupfish in open versus those in closed pools.

May 1982	Open: $\log W = -4.282 + 2.85 \log L$, $r = .969$, $n = 20$
	Closed: $\log W = -4.136 + 2.71 \log L$, $r = .941$, $n = 20$
	Differences in slopes $F_{1,36} = .144$ Differences in elevations $F_{1,37} = 2.60$
July 1982	Open: $\log W = -5.301 + 3.51 \log L$, $r = .968$, $n = 18$
	Closed: $\log W = -4.737 + 3.13 \log L$, $r = .995$, $n = 22$
	Differences in slopes, $F_{1,36} = 2.91$ Differences in elevations, $F_{1,37} = .889$
September 1982	Open: $\log W = -4.679 + 3.12 \log L$, $r = .994$, $n = 23$
	Closed: $\log W = -4.434 + 2.95 \log L$, $r = .988$, $n = 32$
	Differences in slopes, $F_{1,51} = 2.04$ Differences in elevations, $F_{1,52} = .390$
October 1982	Open: $\log W = -4.762 + 3.16 \log L$, $r = .992$, $n = 28$
	Closed: $\log W = -4.839 + 3.22 \log L$, $r = .992$, $n = 37$
	Differences in slopes, $F_{1,61} = .313$ Differences in elevations, $F_{1,62} = .411$
March 1983	Open: $\log W = -4.826 + 3.21 \log L$, $r = .988$, $n = 31$
	Closed: $\log W = -4.953 + 3.29 \log L$, $r = .986$, $n = 38$
	Differences in slopes, $F_{1,65} = .365$ Differences in elevations, $F_{1,66} = 1.52$
May 1983	Open: $\log W = -4.766 + 3.18 \log L$, $r = .990$, $n = 65$
	Closed: $\log W = -5.282 + 3.51 \log L$, $r = .996$, $n = 75$
	Differences in slopes, $F_{1,136} = 13.60^{**}$ Differences in elevations, $F_{1,137} = 91.81^{**}$
July 1983	Open: $\log W = -4.615 + 3.07 \log L$, $r = .987$, $n = 123$
	Closed: $\log W = -4.608 + 3.08 \log L$, $r = .985$, $n = 121$
	Differences in slopes, $F_{1,240} = .002$ Differences in elevations, $F_{1,241} = 9.12^*$
September 1983	Open: $\log W = -4.42 + 2.92 \log L$, $r = .974$, $n = 161$
	Closed: $\log W = -4.55 + 3.03 \log L$, $r = .959$, $n = 230$
	Differences in slopes, $F_{1,387} = 1.65$ Differences in elevations, $F_{1,388} = 4.41^*$

Table 5. (Continued)

December 1983	Open: $\log W = -4.587 + 3.05 \log L$, $r = .979$, $n = 67$
	Closed: $\log W = -4.40 + 2.92 \log L$, $r = .974$, $n = 70$

Differences in slopes, $F_{1,133} = 1.36$	
Differences in elevations, $F_{1,134} = 1.05$	
January 1984	Open: $\log W = -4.498 + 2.97 \log L$, $r = .977$, $n = 58$
	Closed: $\log W = -4.483 + 2.97 \log L$, $r = .983$, $n = 67$

Differences in slopes, $F_{1,121} = .005$	
Differences in elevations, $F_{1,122} = 1.66$	
March 1984	Open: $\log W = 4.677 + 3.11 \log L$, $r = .976$, $n = 192$
	Closed: $\log W = -4.816 + 3.21 \log L$, $r = .974$, $n = 421$

Differences in slopes, $F_{1,609} = 2.76$	
Differences in elevations, $F_{1,610} = 1.40$	

* = p .05

** = p .01

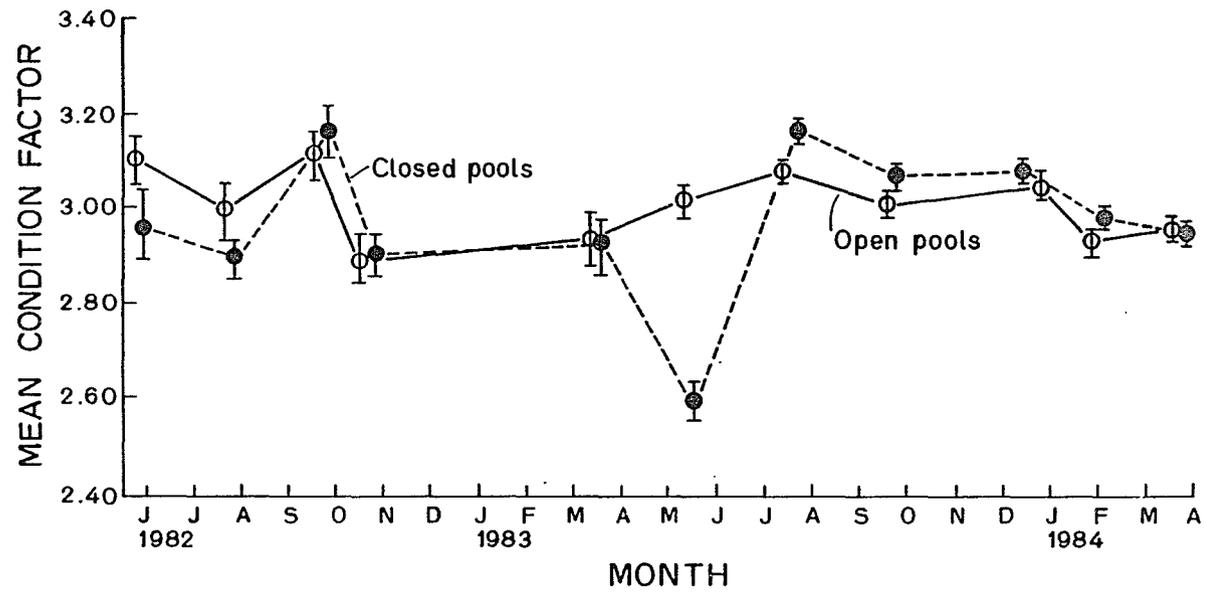


FIGURE 8. Mean condition factor of pupfish ≥ 20 mm in length from open and closed pools. Vertical bars indicate ± 1 standard error.

the higher slope and lower y-intercept of the regression line showed that smaller fish from the closed pools were in poorer condition relative to open pool fish than were larger ones.

Fish in both open and closed pools showed increased condition factors (3.12 and 3.07) in July 1983. Covariance analysis showed a significantly higher regression line for closed pool fish, but the difference was slight; closed pool fish weighing 3.2% more than open pool fish. All fish showed a slight drop in condition as summer progressed, (3.07 in closed and 3.02 in open pools by September). At this time, closed pool fish weighed an average of 5.3% greater than those in open pools. Through the winter of 1983-84, condition factors of fish in both open and closed pools declined from 3.05 to 2.95. During this time, no differences were found in the length-weight regressions.

Length-Frequency Distributions

I did not measure lengths of fish < 20 mm until July 1983. Prior to July 1983, populations consisted primarily of fry < 20 mm and fish ≥ 20 mm showed no differences in length-frequencies.

Length frequencies were significantly different between fish in open and closed pools from July 1983 to March 1984 (Figure 9; 2 x 14 contingency table, G-test, $p < .05$; Zar 1974). In 1983, fish in closed pools showed signs of stunting as they consisted mostly of a single year-class within a narrow size range (Figure 9). Fish in open pools had a broader, flatter distribution of lengths and the 1983 year class was of similar strength to that of 1982. A wider

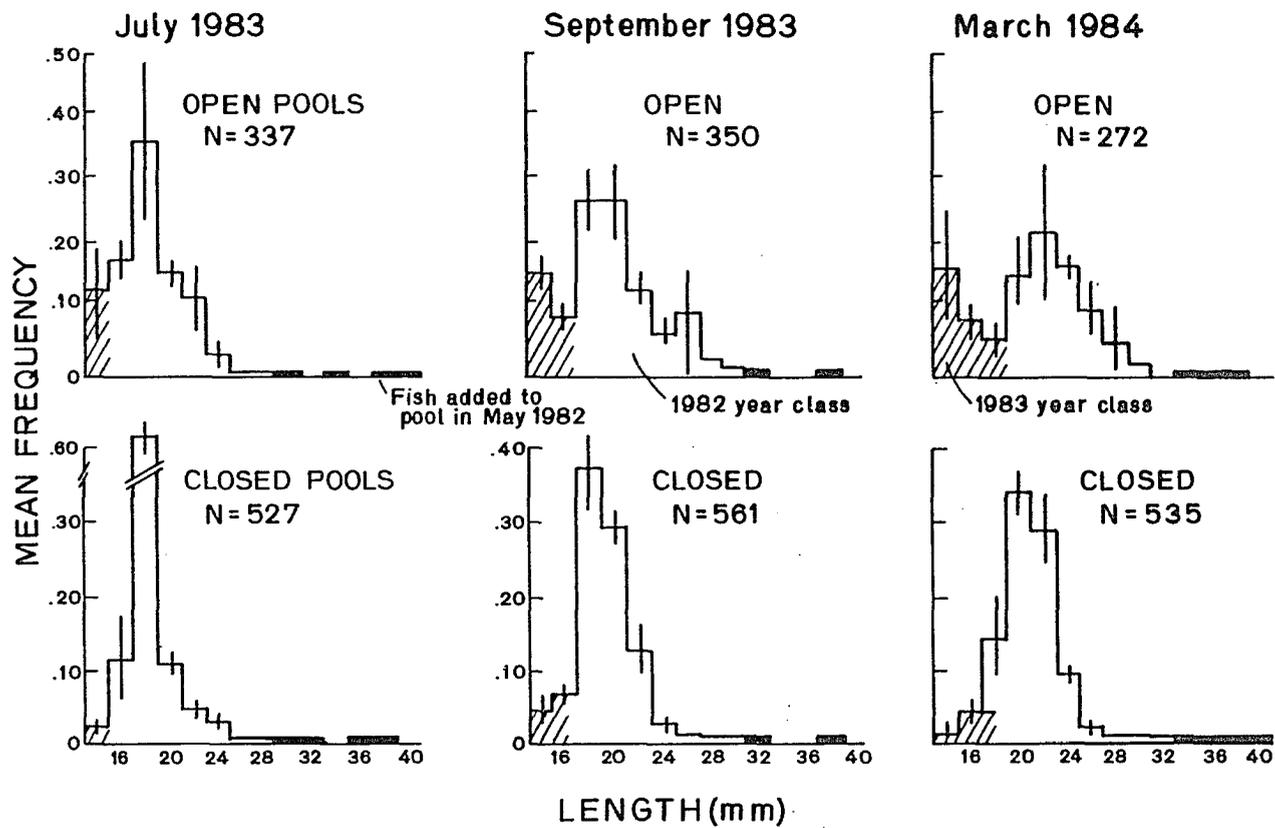


FIGURE 9. Length-frequency distributions of pupfish in open and closed pools in July and September 1983 and March 1984. Vertical bars indicate ± 1 standard error.

size range suggests open pool fish grew faster than fish in closed pools.

Sex Ratios

Average sex ratios varied between open and closed pools (Table 6). On four occasions, there was a greater proportion of males in closed than in open pools. Sex ratios of the total numbers of fish in closed pools was significantly higher than a 1:1 (M:F) ratio ($\chi^2=10.74$, $p < .005$) whereas the total number of fish in open pools had equal numbers of males and females ($\chi^2=.40$, $p < .25$).

Biomass

Biomass comparisons of open and closed populations were restricted to fish ≥ 20 mm. Differences between open and closed pools were usually negligible (Figure 10). Biomass increased exponentially in all pools in the spring of 1983 as fish hatched the previous summer grew to ≥ 20 mm SL. By spring 1984, biomass of open pools started stabilizing (due to excess numbers emigrating). In closed pools, biomass continued to increase as the much larger number of age I fish grew into the ≥ 20 mm size range. Biomass-size distributions were similar between open and closed pools through July 1983. By September 1983-March 1984 biomass of adult pupfish in closed pools was primarily fish 20-24 mm SL; biomass in open pools was more evenly distributed among size classes (Figure 11).

Table 6. Sex ratios (M/F) in open and closed pools each sampling date. Sample size is in parentheses. Differences in mean (\bar{x}) sex ratios between pupfish populations in open and closed pools were tested using a t-test. An asterisk(*) indicates a significant difference at the .05 level of probability. SD indicates standard deviation.

	<u>OPEN POOLS</u>				\bar{x}	(SD)
	<u>01</u>	<u>02</u>	<u>03</u>	<u>04</u>		
May '82	.67 (5)	.67 (5)	.67 (5)	.67 (5)	.67 (-)	
*July	.67 (5)	.67 (5)	.67 (5)	.33 (4)	.58 (.17)	
September	.80 (9)	.67 (5)	2.00 (6)	1.00 (4)	1.12 (.60)	
October	1.5 (10)	.60 (8)	2.00 (6)	.33 (4)	1.11 (.82)	
March '83	1.2 (11)	2.00 (12)	1.33 (7)	3.00 (4)	1.88 (.82)	
May	1.15 (28)	.89 (17)	1.60 (13)	.20 (12)	.96 (.59)	
*July	1.36 (33)	1.43 (17)	1.50 (15)	1.11 (59)	1.34 (.17)	
*September	.67 (50)	1.70 (65)	1.10 (21)	.90 (70)	1.09 (.44)	
*March '84	.71 (77)	.94 (64)	.60 (16)	.60 (40)	.71 (.16)	

Totals

Males = 353

Females = 369

N = 722

	<u>CLOSED POOLS</u>				\bar{x}	(SD)
	<u>C1</u>	<u>C2</u>	<u>C3</u>	<u>C4</u>		
May '82	.67 (5)	.67 (5)	.67 (5)	.67 (5)	.67 (-)	
*July	.67 (5)	.67 (5)	1.00 (4)	.67 (5)	.75 (.165)	
September	1.00 (6)	4.5 (11)	2.0 (6)	.50 (6)	2.00 (1.78)	
October	2.5 (7)	.60 (16)	.40 (7)	.15 (8)	.91 (1.07)	
March '83	3.5 (9)	1.80 (14)	1.20 (11)	3.5 (9)	2.50 (1.18)	
May	2.5 (21)	1.18 (24)	1.00 (18)	.86 (14)	1.38 (.75)	
*July	3.28 (30)	1.80 (42)	2.57 (25)	1.00 (24)	2.16 (.98)	
*September	1.63 (100)	1.67 (72)	1.30 (53)	1.20 (53)	1.45 (.235)	
*March '84	1.43 (107)	1.03 (116)	.95 (120)	.61 (79)	1.00 (.34)	

Totals

Males = 576

Females = 470

N = 1,046

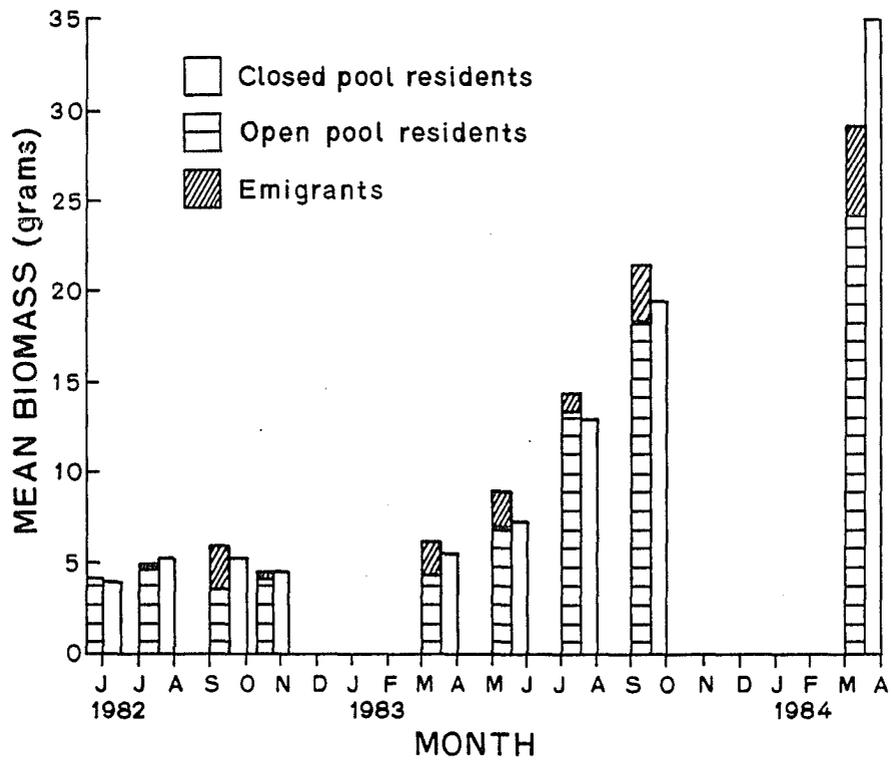


FIGURE 10. Mean biomass, in grams net weight, of residents and emigrants ≥ 20 mm in length from the four open pools and residents from the four closed pools.

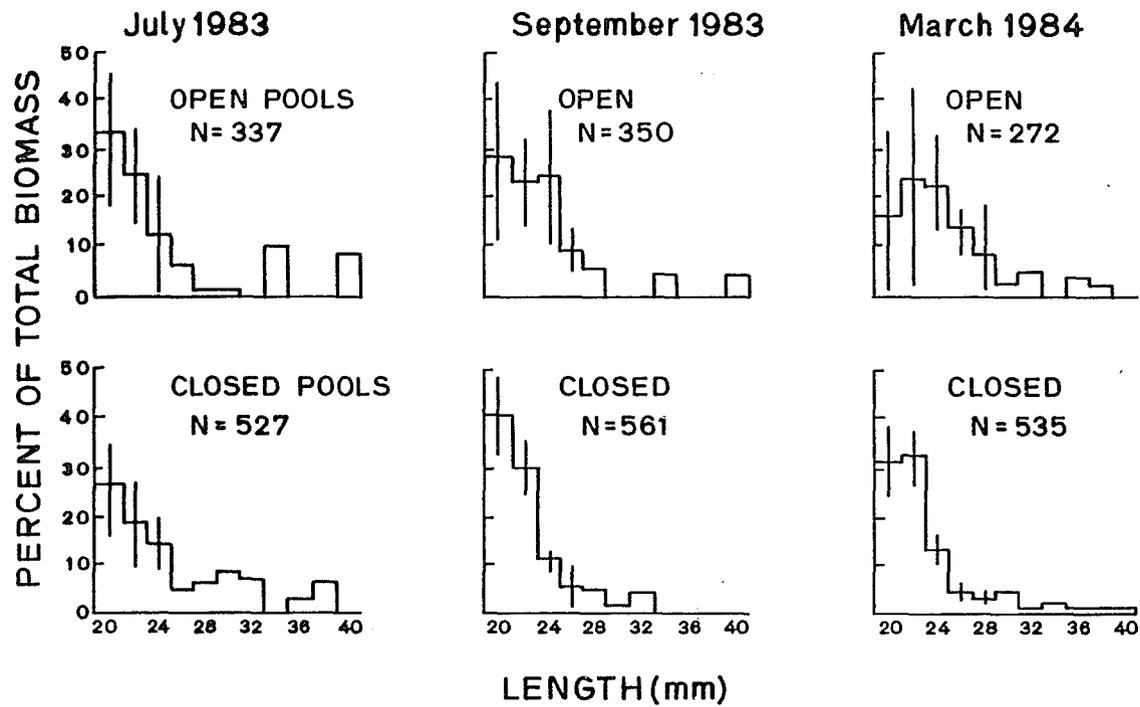


FIGURE 11. Mean percent of total biomass found in each size class of pupfish from the four open and four closed pools in July and September 1983 and March 1984. Vertical bars indicate ± 1 standard deviation.

Emigration

Patterns of Emigration

Emigration patterns were similar in each pool (Figure 12). Emigration was highest in spring and summer. Pupfish emigrated at high levels during summer 1982 as populations were increasing rapidly. Emigration declined in early September and remained low during the winter of 1982-3, but increased dramatically to its highest levels during a six-week period in early spring. Emigration declined after this spring peak but increased again in summer 1983 after breeding resumed and populations were increasing. Emigration again declined to low levels from September to February and again showed a marked increase in early spring 1984.

Pupfish consistently showed a rapid emigratory response when outlet channels were first opened. Of the total number of fish that left open pools (959), nearly one-half (49.8%) emigrated within the first six hours and 69% left within the first 24 hours of the 48 hours that outlets were opened.

Emigration Triggers

In an attempt to determine the factors that triggered emigration, I correlated the timing of emigration to standing numbers, rates of increase in numbers, and temperature. My measurements of resources were too infrequent and too rough for use in correlating emigration with amounts of detritus (Table 1) or plants (Table 2).

Standing numbers of a resident population (t and $t+1$) was estimated by adding the number of emigrants (for a particular emigration

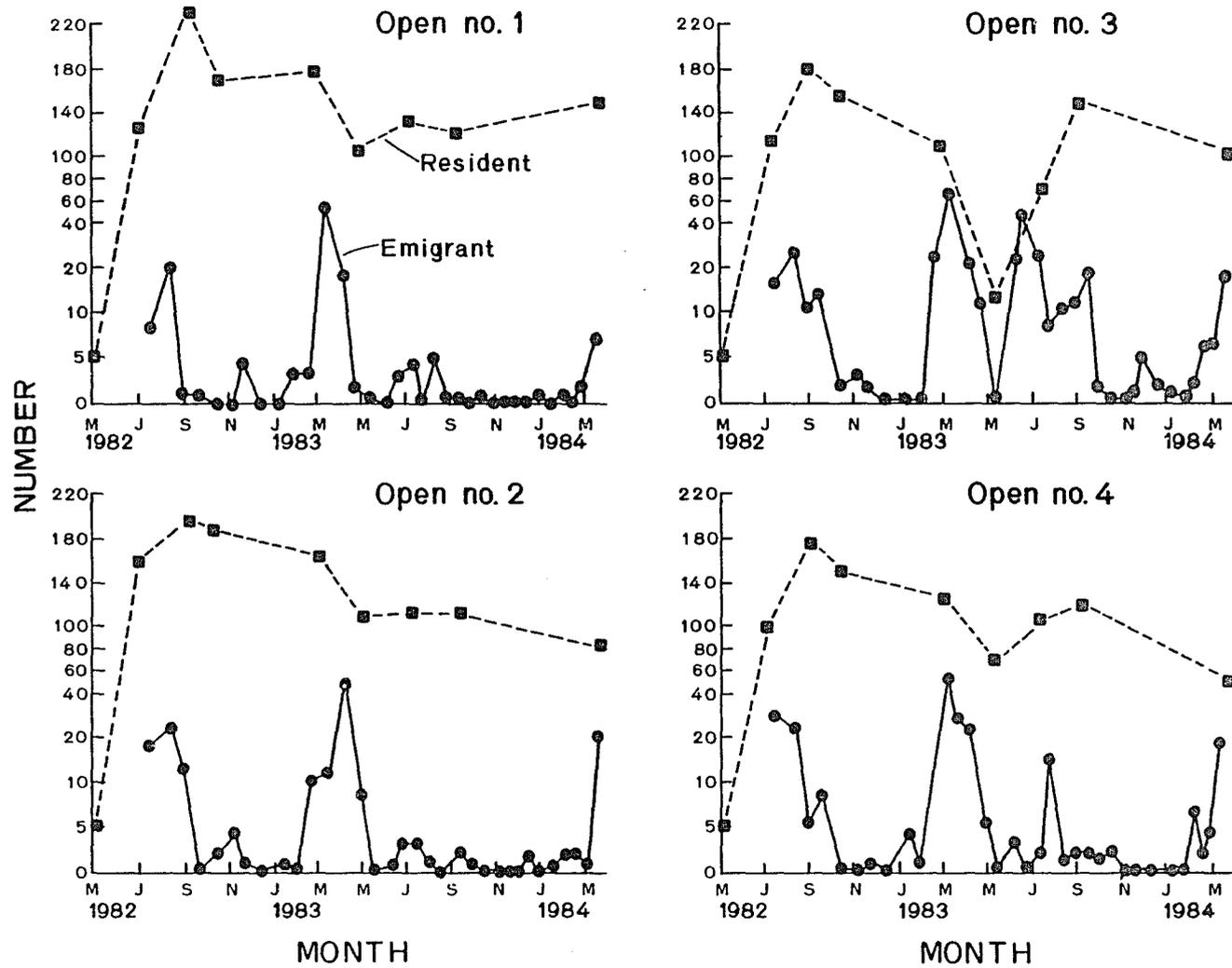


FIGURE 12. Number of resident and emigrant pupfish from each of four pools open to emigration.

period) to the numbers counted at time $t+1$. Correlations of emigration and standing numbers for the period of 15 February-1 October were significantly positive when data for all four populations were pooled ($r=.222$, $n=76$, $p < .05$). When each pool was analyzed separately, correlations for pools 01 and 04 were significant (01, $r=.468$, $n=19$, $p < .025$; 04, $r=.420$, $n=19$, $p < .05$) but pools 02 and 03 were not (02, $r=.285$, $n=17$, $.10 < p < .25$; 03, $r=.091$, $n=19$, $p < .25$). These correlations indicate that emigration may be a partial function of density.

Emigration during the breeding season showed a slight positive relationship to the rate of population increase. In the summer 1983, pools 03 and 04 had higher rates of increase than 01 and 02 and also higher numbers of emigrants, and pool 03 had a higher rate of increase and number of emigrants than pool 04 (Figure 12).

Some temperature changes appeared to trigger emigration. Spring peaks in emigration in 1983 and 1984 were accompanied or immediately preceded by rapid rises in temperature above 20° C (Figure 3). Autumn declines in emigration coincided with declining water temperature. The lowest rates of emigration occurred from October to February when water temperature was $\leq 12^{\circ}$ C.

Characteristics of Emigrants

Nearly twice as many males as females (pooled $X^2=11.65$, 1 d.f., $p < .01$) emigrated from open pool resident populations which had about equal numbers of males and females (Tables 6 and 7). Only during the first year of the study did more females than males emigrate. The higher proportion of emigrant males was statistically significant during July-September 1983 and September-March 1984 (Table 7).

Table 7. Sex ratios (M/F) of resident and emigrant pupfish. The chi-square values test for homogeneity in the proportion of males and females of resident vs. emigrant fish. Total number of fish in each sample shown in parentheses.

	<u>SEX RATIO</u>		<u>Chi-square</u>
	<u>Residents</u>	<u>Emigrants</u>	
July-September 1982	.79 (21.5)	.25 (10)	1.54
September-October	1.00 (26)	.5 (1)	-
October-March 1983	1.41 (32.5)	1.5 (10)	.01
March-May	1.08 (52)	1.83 (17)	.85
May-July	1.11 (97)	2.00 (9)	.66
July-September	1.12 (165)	6.00 (21)	8.26*
September-March 1984	.88 (201.5)	2.11 (56)	7.71*
<hr/>			
TOTAL	.956 (722)	1.88 (124)	11.44*

* = $p < .01$

There were proportionately more small (< 20 mm) than larger fish among emigrants during the early stages in the development of populations (Table 8). During this period, residents were also proportionately small. As the populations matured, proportionately more residents were >20 mm and higher frequencies of fish >20 mm emigrated. Emigrants consistently showed a higher frequency of fish 20-24 mm and a lower frequency of fish < 20 mm in length than did resident populations, but this difference was significant only during the July-September 1983 period (Table 8).

Emigrant pupfish > 20 mm in length usually had poorer condition factors than residents. In six of the nine periods used for comparisons, most emigrants were in poorer condition than residents from the same pool and size class (Table 9); 40 of the 67 fish in poorer condition than residents had condition factors beyond one standard deviation from the mean. During the 1983 breeding season (March-September) emigrating fish were heavier on average than residents. Of heavier emigrants, more were males than females ($\chi^2=14.08$, 1 d.f., $p < .01$); among lighter emigrants, males and females were in equal numbers ($\chi^2=1.61$, 1 d.f., $p > .10$).

Resource Manipulation Experiment

Nearly one-half (42.2 and 41.8%) of the pupfish emigrated from open pools when resources were reduced by 50% (Figure 13). In two open pools in which resources were not changed, many fewer fish emigrated (15.2 and 16.0%). Most emigration occurred \leq 60 hr after

Table 8. Percent of the total number (N) of residents (R) and emigrants (E) from open pools (sexes combined) in each size class. G-test values test for significant differences in length-frequency distributions of residents and emigrants for each period between samples.

Dates	Standard Length (mm)					N	G-test
	< 20	20-24	25-29	30-34	35+		
July-September 1982	R: 96.7	1.03	.16	1.27	.83	643.5	6.18
	E: 93.3	2.05	1.02	2.05	1.50	195	
September-October	R: 96.35	2.27	.25	.70	.43	724.5	.95
	E: 96.20	3.70	0	0	0	27	
October-March 1983	R: 95.10	2.93	.74	.72	.56	626	7.66
	E: 89.70	6.80	1.70	0	.86	116	
March-May	^a R: 89.0	8.20	1.19	1.06	.40	378	4.91
	^a E: 91.5	6.25	1.75	0	.50	200	
May-July	^a R: 72.30	22.07	3.08	1.42	1.10	316	7.93
	^a E: 61.11	22.22	5.55	5.55	5.55	18	
July-September	^a R: 57.29	34.33	6.92	.44	1.17	343	11.25*
	^a E: 26.92	48.08	25.00	0	0	26	
September-March 1984	^a R: 41.60	42.24	13.60	1.44	.48	312.5	5.56
	^a E: 35.71	51.19	13.09	0	0	84	

^a = pool 03 excluded from analysis

* = $p < .05$

Table 9. Number of emigrants with condition factors less than, equal to, or greater than the mean for residents from the same pool and the same size class (20-24, 25-29, 30-34, 35-39, 40+ mm). The number of emigrating fish in each sex is shown in parentheses. "?" connotes fish of unknown sex.

Dates	"Less than" (M,F,?)	"Equal to" (M,F,?)	"Greater than" (M,F,?)	N
July-September 1982	6 (0,4,2)	1 (1,0,0)	4 (2,2,0)	11
Sept.-October	1 (0,1,0)	0	0	1
October-March 1982	13 (6,4,3)	1 (1,0,0)	3 (2,1,0)	17
March-May	4 (1,3,0)	0	10 (8,2,0)	14
May-July	4 (1,3,0)	0	5 (5,0,0)	9
July-September	10 (8,2,0)	2 (2,0,0)	16 (14,2,0)	28
Sept.-December	1 (1,0,0)	0	0	1
Dec.-January 1984	8 (6,2,0)	0	4 (2,2,0)	12
January-March	20 (13,7,0)	2 (1,1,0)	6 (4,2,0)	28
TOTALS	67 (36,26,5)	6 (5,1,0)	48 (37,11,0)	121

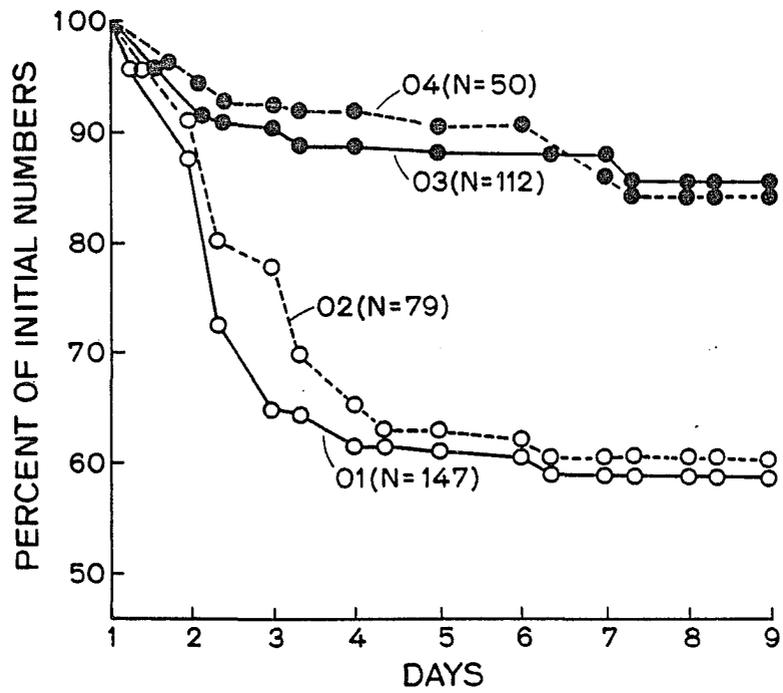


FIGURE 13. Percent of pupfish population emigrating from pools wherein resources were reduced by 50% (open circles) and from pools left undisturbed (closed circles). Initial population size (N) in each pool shown in parentheses.

pools were opened and populations remained relatively stable for the remainder of the nine-day experiment.

Emigrants from pools with reduced resources were 22-26 mm in length with few fish < 20 mm (Figure 14; 2 x 16 contingency test, $G=48.75$, $p < .05$). Emigrants from pools with unchanged resources were mostly < 20 mm ($G=14.96$, $p < .05$). There was no statistically significant difference in sex ratios (chi-square test for independence, $p > .10$) or condition factors (t-test, Table 10) between residents and emigrants in any pool.

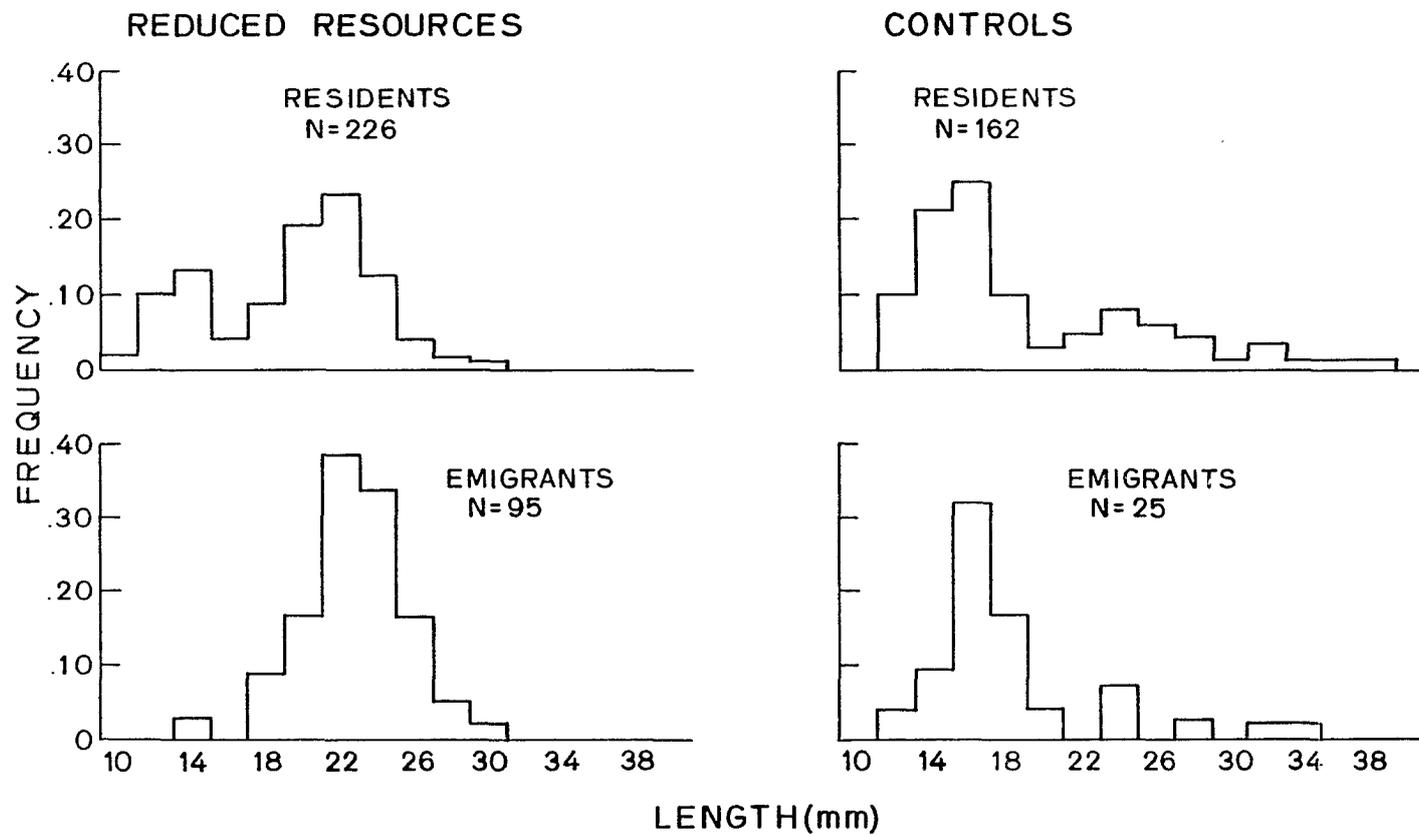


FIGURE 14. Length-frequency distributions (pools combined) of residents and emigrants from the "reduced resources" and "control" (undisturbed) pools used in the resource manipulation experiment.

Table 10. Mean condition factors (sexes combined) for resident and emigrant pupfish ≥ 20 mm in length from each reduced resource or control pool used in the resource manipulation experiment. Standard deviation of the mean is given in parentheses.

<u>"Reduced Resources" Pools</u>	<u>Mean Condition Factor</u>	
	<u>Residents</u>	<u>Emigrants</u>
01	2.76 (.21) n = 74	2.74 (.26) n = 51
02	3.19 (.23) n = 62	3.03 (.24) n = 31
<u>"Control" Pools</u>		
03	3.03 (.20) n = 16	2.96 (.29) n = 4
04	2.96 (.22) n = 40	2.83 (.13) n = 6

CHAPTER 4

DISCUSSION

C. macularius is one of 30 species of pupfishes inhabiting Sonoran, Chihuahuan, and Mohave deserts of North America (Miller 1981). Pupfishes are among the last survivors of once diverse fish faunas that inhabited the extensive and interconnected freshwater and estuarine systems that existed in these regions during the last pluvial (cool, high precipitation) period ending 10,000-12,000 years ago (Miller 1981). Their broad physiological, ecological, and behavioral tolerances have enabled them to persist in a wide spectrum of environments, from the extreme of the small, nearly constant environments of desert springs to the widely variable environments of desert streams (Brown 1971; Soltz and Naiman 1978).

The theory of self-regulation has not been applied to account for population regulation in desert pupfish. Given their high reproductive capacity, ability to reproduce over many months (Crear and Haydock 1970; Kennedy 1977), and omnivorous food habits (Cox 1972; Naiman 1979), however, pupfish would quickly overpopulate an area without the capability to adjust numbers to resources. In particular, the survival of pupfishes for long periods in the small, restricted habitats of desert springs would seem to point both to the existence and necessity of such a mechanism. Pupfish are known to

emigrate (Soltz 1974; Young 1980), but whether emigration can regulate pupfish numbers to resources has not been established. At first glance emigration would appear unable to function as a regulatory mechanism in some pupfish habitats since desert springs and the pools of desert streams appear as habitat islands (Brown 1971) that lack emigration outlets. Yet, desert springs usually have an overflow of water or some other avenue through which emigration could occur (Soltz 1974; R.R. Miller pers. comm.). For example, the subterranean cavern that forms the only habitat for the Devils Hole pupfish (C. diabolis) has no surface outlet but the extensive underground water system could serve as a "dispersal sink" (a place into which dispersers/emigrants move, sensu Lidicker 1975 and Tamarin 1978) for emigrating pupfish. Intermittent desert streams often confine pupfish to closed pools for many months, but here, too, a behavioral spacing mechanism could operate when streamflow increases during the next period of precipitation or reduced evaporation (Deacon and Minckley 1974; Constantz 1981). Thus, no natural populations of pupfish are known that would require regulatory mechanisms other than emigration.

The central premise of the theory of self-regulation by emigration is that animals have evolved a behavioral spacing mechanism such that regulation results when those without access to resources (i.e., those in excess of resource carrying capacity) emigrate. To test this theory using desert pupfish, I tested the predictions that 1) fence effects would occur in desert pupfish populations if emigration is prevented, and 2) as resources increase, emigration

decreases, and as resources decrease, emigration increases. In the following, I examine the tests of these predictions, and how the results provide insight into population dynamics of desert pupfishes, of fishes as a whole, and of their impact on the general theory of self-regulation.

Studies of enclosed rodent populations have shown that populations failed to adjust numbers to resources and consequently overpopulated and overutilized resources when emigration was prevented (Krebs et al. 1969, 1973; Boonstra and Krebs 1977). I found that closed pupfish populations exhibited fence effects nearly identical to those of fenced rodent populations. Despite similar environmental conditions in all eight pools, the four closed pool populations grew faster than the four open pool populations, increasing to a mean peak size 1.4 times greater than open pools within four months (Figure 4). Closed populations appeared unable to regulate numbers to resources since peak numbers were followed by high mortality, a decline in body condition, reduced recruitment, and stunting.

These fence effects most likely resulted when numbers in excess of carrying capacity were forced to remain in the system, causing a reduced per capital resource availability and therefore higher competition among closed pool fish for resources, especially food. Newsome and Leduc (1975) found that a lack of food for yellow perch (Perca flavescens) prevented sufficient build-up of fat reserves and led to higher overwinter mortality and lower reproductive output the following spring; such a mechanism could account for similar

effects in closed pools. Fish rely heavily on fat reserves during the winter when feeding ceases (Mason 1976), and the much higher overwinter mortality in closed pool fish suggests that due to increased competition for food, they had much lower fat reserves and therefore were more susceptible to starvation and environmental stressors (e.g., rapid declines in water temperature) than open pool fish. The positive correlation between autumn population size and overwinter mortality in closed pool fish supports this contention. Small pupfish were more susceptible to overwinter mortality as nearly all mortalities for both winters were < 20 mm SL. In other species, smaller fish had lower fat reserves, utilized reserves faster, (Latta 1969; Phillips 1969; Mason 1976), and had higher overwinter mortality than larger fish (Mason 1976; Oliver et al. 1979). The lower overwinter mortality of closed pool fish in the second winter could be attributed to a lower proportion of small fish in the populations due to a lack of recruitment the previous breeding season.

In fenced rodent populations, overpopulation resulted in habitat destruction from overgrazing causing symptoms of starvation and leading to a sharp decline in numbers (Krebs et al. 1969, 1973; Boonstra and Krebs 1977). Although I found no similar evidence of habitat destruction in closed pools, I did observe pronounced symptoms of starvation in closed pool fish in the spring 1983, just six months after peak numbers. Food requirements of pupfish have been shown to increase rapidly at temperatures $>17^{\circ}$ C (Gerking and Lee 1983). I found that closed pool fish had a rapid decline in

condition to its lowest level (Figure 8) and accompanied by 79 mortalities (Appendix Table 4) in response to temperatures increasing above this level during a two month period in the spring. In contrast, open pool fish had high emigration (Figure 12), an increase in condition factor and no mortalities. Since closed pools having the largest decline in mean condition factor also had the highest mortality, further suggests that pupfish in closed pools were starving due to their inability to adjust numbers commensurate with food resources at a time of higher food requirements but low food availability.

Production of eggs and young in pupfish, although normally at its peak in late spring and early summer (Minckley and Deacon 1973; Soltz 1974; Kennedy 1977) was greatly reduced in C. macularius in closed pools. Reduced rations are known to cause a reduction in fecundity in several species of fishes (references in Noakes 1978: 365), and this relationship could also explain the reduced recruitment in closed pools. The positive relationship I found between fry production and female condition factor is consistent with the pattern of egg production observed for C. diabolis (Minckley and Deacon 1973) and C. bovinus (Kennedy 1977) wherein many smaller and fewer eggs were produced when productivity was low and population density high. The increase in detritus and plants as the summer progressed (Tables 1 and 2) suggests that more food was available to closed pool fish for maintenance and gonad development, and hence could account for the increase in condition factor and recruitment observed in closed pools in late summer.

Stunting of closed pool populations provides further evidence for the overpopulation of pupfish in closed pools. Stunting is a commonly observed phenomenon in closed systems wherein high density fish populations have intense intraspecific competition which causes low recruitment and slow growth and which results in narrow length-frequency distributions (Swingle and Smith 1940; Anderson 1973; Hackney 1979; Persson 1983). This pattern was clearly shown in my closed pools in which pupfish had large numbers and biomasses of slow-growing fish within a narrow size range (Figures 9 and 11).

In contrast, I found no evidence for overpopulation and over-utilization of resources in open pools. Pupfish in open pools had lower numbers, higher recruitment, better condition and growth, and higher total production than pupfish in closed pools. Unlike closed pool fish, the length-frequencies (Soltz 1974; Kennedy 1977; Kynard and Garrett 1979), length-weight relationships (Naiman 1976), and reproductive cycles (Kennedy 1977; Kynard and Garrett 1979) of pupfish in open pools were similar to those found in natural populations of C. macularius and other species of pupfish. This entire pattern suggests that resources were more abundant and accessible to pupfish in open pools and supports the hypothesis that emigration of excess numbers regulates pupfish populations to resources. The distinct differences in open and closed pupfish populations are in agreement with those observed in experiments that compared open and closed populations of rodents (Krebs et al. 1969, 1973; Boonstra and Krebs 1977), Hydra littoralis, (Lomnicki and Slobodkin 1966; Lomnicki

1980), and roe deer (Capreolus capreolus, Andersen 1961 cited in Watson and Moss 1970). For example, unconfined populations of hydra had higher reproductive rates, lower population densities, higher food availability, and were in better condition than those in confined systems (Lomnicki and Slobodkin 1966; Lomnicki 1980).

The rapid and uniform increase in emigration of pupfish in response to a sudden decrease in resources strongly supports rejection of my null hypothesis that "emigration of pupfish is independent of resources." Moreover, the data suggest that every pupfish has a stereotyped behavioral spacing mechanism wherein an individual either becomes a resident or emigrates in response to resource availability. The change in emigration I observed in pupfish in response to changes in resources corroborates previous work with salmonids (Mason and Chapman 1965; Symons 1971; Slaney and Northcote 1974; Mason 1976; Mesick 1984), bluegill (Bianchi pers. comm.), crayfish (Menke 1983), and aquatic insects (Walton et al. 1977). The data also support the assumption of regulatory emigration theory that emigration acts to maintain numbers at resource carrying capacity (Taylor and Taylor 197; Lomnicki 1978). Despite considerable differences in population sizes, there was little variation in the percent of pupfish emigrating from each of the two pools having reduced resources or from each of the two pools left undisturbed. Since all pools were open for 22 months prior to the experiment, this lack of variation indicates that the differences in initial numbers reflect prior adjustments via emigration to differing resource carrying capacities in each pool. By definition, emigration from either the reduced

resources or undisturbed pools was density-independent since both had an equal proportion emigrating despite differences in population size (McClenaghan and Gains 1976; Walton et al. 1977). A similar lack of density-dependent emigration in many small mammal field studies led Gains and McClenaghan (1980:189) to infer that emigration may not operate as a mechanism of population regulation. But, closer analysis of my results reveals that emigration of pupfish was neither independent nor dependent of population size per se, but rather a function of numbers in relation to resource carrying capacity; emigration occurred from pupfish pools when numbers exceeded carrying capacity regardless of population size.

Some field observations of pupfish populations lend further support for the existence of a behavioral spacing mechanism in pupfish. Young (1980) found many small pupfish downstream from a dam constructed to create a refugium for C. radiosus and speculated that the emigration of these fish over the dam could account for the stability he observed in the size of the refugium population. Deacon and Deacon (1979) demonstrated that the population size of Devils Hole pupfish adjusted rapidly to changes in resource availability. For example, they found a significant positive correlation between algal productivity and population size one month later; they also found that the addition of lights in the cavern in autumn to increase productivity resulted in a substantial population increase followed by a decline within one month after the lights were removed. The speed and precision of these changes in numbers with changes in resources suggests that

a behavioral spacing mechanism may be involved. Pupfish (numbering 200-400 fish) are concentrated above a small, shallow shelf near the water surface, but "...it regularly occurs down to 26 m (Deacon and Deacon 1979:12)." It is not known why individuals occur at such depths, but it is tempting to speculate that they may be emigrants which, because of behavioral spacing, left the shelf area in response to lack of access to resources.

In my comparisons of open and closed pools, I found that open populations are capable of regulating their own numbers in the absence of predators or competitors. In accordance with Chitty's (1960) theory of self-regulation, my results indicate that pupfish are capable (by means of behavioral spacing) of limiting their own numbers without either destroying their food resources or depending on enemies or climatic accidents to prevent them from doing so. But, it could be suggested that, since pupfishes often occur in habitats lacking major predators or interspecific competitors and where large "climatic" changes are usually absent, perhaps an ability to self-regulate is a unique adaptation. Several data argue against this hypothesis. Recent evidence suggests that unique physiological and behavioral tolerances exhibited by pupfishes, formerly thought to be specific adaptations to desert conditions, are instead tolerances accumulated during their evolution in estuarine environments; frequent interruptions of arid conditions by pluvial periods have prevented the evolution of specialized desert adaptations (M. Smith 1981), and presumably this also holds true for the evolution of a specialized adaptation for self-regulation. Also, some present-day pupfish

habitats contain both competitors and predators (Deacon and Minckley 1974; Miller 1981), both of which were probably common when pupfish were part of more complex fish communities during recent pluvial periods (M. Smith 1981). Based on studies with guppies (Lebistes reticulatus) in closed aquaria by a number of investigators (Breder and Coates 1932; Rose 1959; Silliman and Gutsell 1958; Warren 1973), cannibalism (in combination with reduced fecundity) also has been suggested as regulating fish populations, or at least helping limit the upper population size by limiting recruitment. I found some evidence that in closed pupfish pools cannibalism and reduced fecundity were factors in limiting recruitment, but my data refute their suggested regulatory function. Instead, I found that in closed pools these factors did not serve to regulate numbers to resources, but were actually the consequences of overpopulation. I found these phenomena only in closed pupfish pools; they were not sufficient to limit populations in open pools. Based on my findings from open pupfish pools, it seems probable that, if held in an open system, emigration would also regulate numbers to resources in guppy populations.

. In my resource manipulation experiment, I found that pupfish readily left a known habitat in response to a decrease in resources. Yet, if pupfish that emigrate naturally from desert springs or the permanent pools of intermittent streams have a low probability of survival (Soltz 1974; Constantz 1981), then a major question that arises is, "Of what selective advantage is emigration to an individual

pupfish?" Indeed, a major obstacle to the acceptance of emigration as a mechanism of population regulation in pupfish and other animals is that emigration usually results in death of emigrants, and it has therefore been difficult for biologists to see how such a lethal character could have been selected (Taylor and Taylor 1977; Lomnicki 1978). Lomnicki (1978, 1980) hypothesized that emigration could be selected for if some individuals had greater access to resources than others; on this thesis, individuals that stay in an area without access to resources have no probability of surviving to reproduction and, therefore, emigration even at a low probability of finding suitable resources, has selective advantage. Comparisons of open and closed pools supported this hypothesis in that 1) the generally lower condition factors of emigrants versus residents in open pools indicates that there are individual differences in access to resources and that residents had greater access to resources and 2) there was less or no probability of surviving or reproducing in closed pools where those individuals without access to resources (that normally would have emigrated) were forced to stay. G. Smith (1981) further emphasized that the probability of survival of an emigrant pupfish (or other desert fish) is not insignificant since their habitats are often ephemeral and the suitability of a given habitat can change rapidly, for example, after a flood (see also Taylor and Taylor 1977). Similar advantages could accrue to pupfish that emigrate into the depths of Devils Hole. Although they would experience high mortality, such movements could result in colonization of new habitats over

time, as documented for cave fishes inhabiting limestone caverns (Woods and Inger 1957). As Lomnicki (1978, 1980) theorized, emigrants may have a low probability of finding suitable habitat, but this probability is greater than if they remained in a habitat where they have even less chance of surviving and reproducing. Lidicker (1975) and Tamarin (1980) discuss the evolutionary costs and benefits that accrue to an emigrating animal in more detail.

Two alternatives have been suggested to account for whether an animal becomes a resident or emigrates (Krebs 1978): 1) the "polymorphic behavior hypothesis" (Howard 1960; Chitty 1967a; Gadgil 1971; Krebs 1978) which postulates that emigrants differ genetically from residents in that they are more docile and better adapted for colonizing new habitats than residents which are more aggressive and better adapted at securing resources, and 2) the "behavior hypothesis" (Wynne-Edwards 1962) which postulates that each individual has the same genetic ability for becoming a resident or emigrant dependent solely upon access to resources. Constantz (1981) suggested similar alternatives to account for what determines which individuals in populations of fishes inhabiting intermittent desert streams leave permanent pools and invade temporary waters. Although I did not explicitly test either hypothesis, it seems unlikely that the low variation in the number of emigrants I observed from each resource level in my resource manipulation experiment and in preliminary tests (described in the Materials and Methods section) would occur if pupfish were polymorphic in their propensity to emigrate. In particular, my data

showing about 42% of resident pupfish quickly emigrating in response to a sudden reduction in resources by 50% are more consistent with the behavior hypothesis. More definitive support of the behavior hypothesis was found in reversal experiments with bluegills (Lepomis machrochirus, Bianchi pers. comm.) and Arizona trout (Salmo apache, Mesick 1984) wherein fish that had been residents became emigrants when placed into environments with resources at carrying capacity and previous emigrants became residents when placed into environments with resources below carrying capacity.

A mechanism of habitat selection developed by Sale (1969) can help explain the underlying behaviors that lead an individual pupfish to stay or leave a habitat. Sale proposed that environmental cues (e.g., food, cover) act to regulate the intensity of exploratory behavior; in an environment where resources are unavailable or inaccessible there would be increased exploratory behavior leading the animal out of the area. Evidence in support of such a mechanism is provided by Sale (1969), Wecker (1964), and Malcolm and Hanks (1973). I found that small, relatively simple habitats provided by my experimental pools (detritus, plants and substrate) were sufficient for pupfish to develop and maintain a sizeable resident population, but I was unable to identify what resources or habitat features were critical in initiating residency or emigratory responses. G. Smith (1981) suggested that for pupfish and other desert fishes that occupy the fluctuating environments of intermittent streams, residency responses will be directed toward habitat features that

indicate the permanence of the habitat (e.g., the presence of aquatic plants). By manipulating types and levels of resources and measuring emigration rates from open systems, investigators have been able to identify what resources are important in initiating residency responses in fish and other animals (Mason 1976; Butler 1980; Menke 1983; Mesick 1984). Similar experiments with pupfish would prove valuable in identifying features that constitute suitable habitat and in determining the carrying capacities of various combinations of habitat features. Results from such experiments would aid management efforts aimed at identifying the suitability of a habitat for reintroduction of C. macularius and other endangered fishes.

Artificial refugia are an important component in the effort to conserve endangered desert fishes (Soltz and Naiman 1978; Pister 1981) and some current refugia consist of small, closed systems (e.g., Williams 1977; Kynard 1979). My evidence of fence effects in pupfish pools not having an outlet for emigration suggests that populations maintained in closed refugia may be less viable than those maintained in open systems. Since numbers will build up in closed systems, they will very quickly have much larger numbers than open systems, from which excess individuals emigrate. These large numbers over-exploit the resources, and after this initial boom, there are too many fish for too little food. At this point, a decline in condition and reproduction and an increase in mortality would ensue. Closed refugia populations of pupfish would probably undergo boom-and-bust cycles every 2-3 years as old members of the population die. Presumably, the poorer condition of these fish in closed systems would

make them very susceptible to disease and other stressors that could decimate the population. Mykytowycz (1961) reported just such a case in confined populations of rabbits (Oryctolagus cuniculus). In contrast, I found that open populations of pupfish were more productive and in better condition than those in closed populations. It therefore suggests that refugia should be maintained as open systems, either by having an outlet for emigration or by periodically removing portions of the population, in order to maintain healthy, viable populations. This contention can be tested by comparing length-frequencies and condition factors of fish populations in closed refugia to those in open habitats.

In summary, my results provided two strong lines of evidence that argue for the existence of a behavioral spacing mechanism that regulates desert pupfish populations. Pupfish populations confined to systems without emigration outlets appeared to rapidly overshoot the carrying capacity of resources in their environments and show fence effects absent from open pools. The similarity of responses to confinement among closed populations of pupfish, hydra (Lomnicki and Slobodkin 1966) and roe deer (Andersen 1961 in Watson and Moss 1970) suggests that fence effects are not limited to rodents but rather are a consistent pattern exhibited by mobile animals when emigration is prevented and overpopulation and overutilization of resources ensues. The observation of fence effects in such a diverse group of animals suggests that the capability of self-regulation via a behavioral spacing mechanism is as pervasive as Chitty theorized.

Second, the rapid and uniform increase in emigration when resources were suddenly reduced, indicates that the residency-emigratory behavior of pupfish can reliably and precisely effect changes in numbers to be in consonance with resources. Taylor and Taylor (1977) referred to residency-emigratory behavior as "controlled mobility" and discussed that such an intrinsic capability could allow animals to regulate numbers to resources under conditions where resource availability is changing rapidly due to changes in quality or quantity of resources, density of competitors, or seasonally changing requirements of the animals themselves. My data support emigration as sufficient to regulate pupfish numbers to resources in open systems without the need for other factors or mechanisms.

APPENDIX A

TABLES

Table 1. Dissolved oxygen measurements (mg/l) in open and closed pupfish pools.

Date	Time (hours)	Temp (C _e)	Closed Pool #				Open pool #			
			C1	C2	C3	C4	O1	O2	O3	O4
9/24/82	1800	28	10.1	10.0	9.8	10.6	13.5	11.2	10.8	11.1
9/27/82	0715	18	6.6	6.0	5.6	6.4	7.0	7.0	-	7.1
2/04/83	1400	13	13.1	12.5	14.0	14.5	11.0	12.0	12.5	12.0
4/06/83	0900	9.5	10.2	9.4	9.8	9.8	12.0	8.1	9.8	-
6/28/83	0740	17	5.3	5.1	4.7	5.0	8.1	9.6	8.4	7.3
6/30/83	1600	28.5	18.2	17.3	17.5	18.0	20+	20+	20+	20+
7/01/83	0700	20	7.3	8.0	6.1	8.1	7.1	8.3	7.7	6.0
9/28/83	0850	-	3.2	-	-	4.8	3.2	-	-	3.2
10/10/83	1630	24	-	-	-	-	12.0	-	-	11.-
11/09/83	0715	12	9.0	8.8	8.9	8.8	9.1	8.2	8.3	8.3
11/09/83	1500	17	9.7	13.0	12.0	11.6	16.0	16.2	16.4	14.5
12/07/83	140	-	11.2	16.0	12.0	13.5	11.2	14.5	13.5	14.0
3/27/84	1300	-	12.8	13.1	13.5	15.6	13.0	13.5	13.0	14.0

Table 2. The pH of open and closed pupfish pools.

<u>Date</u>	<u>Time</u> (hours)	<u>Temp.</u> (° C.)	<u>Closed pool #</u>				<u>Open pool #</u>			
			<u>C1</u>	<u>C2</u>	<u>C3</u>	<u>C4</u>	<u>O1</u>	<u>O2</u>	<u>O3</u>	<u>O4</u>
9/24/82	1800	-	8.7	8.7	8.8	8.7	8.7	8.7	-	8.1
2/04/83	1400	13	7.3	6.5	6.8	7.1	7.3	7.4	7.4	7.2
4/06/83	0900	9.5	8.7	8.65	8.85	8.98	8.89	7.98	8.5	8.3
6/30/83	1600	28.5	8.01	-	-	-	8.35	-	-	-
7/01/83	0700	20	7.5	-	-	-	7.5	-	-	-
9/28/83	0850	-	6.9	-	-	6.6	-	6.6	7.2	-
11/09/83	0715	12	6.6	6.7	7.1	7.4	7.2	7.2	7.5	7.8
11/09/83	1500	17	6.9	7.0	7.1	7.4	6.3	6.5	6.6	6.7
11/07/83	1500	-	6.5	-	-	-	-	-	-	-
3/27/84	1300	-	6.94	8.09	8.18	8.2	8.45	8.75	8.4	8.3

Table 3. Conductivity measurements (in umhos) in open and closed pools.

<u>Date</u>	<u>Closed pool #</u>				<u>Open pool #</u>			
	<u>C1</u>	<u>C2</u>	<u>C3</u>	<u>C4</u>	<u>O1</u>	<u>O2</u>	<u>O3</u>	<u>O4</u>
2/04/83	1200	1275	1550	1000	650	675	650	600
4/06/83	1650	2000	2200	1400	580	575	580	550
4/16/83	1200	1400	1800	1050	-	-	-	-
4/23/83	1475	1620	2200	1275	800	850	800	900
5/12/83	850	900	875	800	575	700	850	875
6/27/83	1300	1650	1600	1500	800	810	675	675
7/12/83	1000	950	975	110	1100	1100	1000	1050
8/11/83	940	880	820	880	730	720	730	725
9/23/83	810	800	850	730	700	700	710	710
11/02/83	650	650	600	600	1200	1180	1200	1200
12/07/83	625	600	590	560	580	530	575	600
1/17/83	600	585	600	600	600	500	560	600
3/27/84	700	900	900	720	900	800	800	850

Table 4. Population in each open and closed pool and total number of fish emigrating from each open pool between samples.
 R = number of residents, \bar{R} = mean number of residents, SD = standard deviation, CV = coefficient of variation,
 E = number of emigrants, \bar{E} = mean number of emigrants

Open Pool #	Sampling Periods								
	May '82	July '82	Sept. '82	Oct. '82	March '83	May '83	July '83	Sept. '83	March '84
01 R: 5	129	229	164	177	106	127	120	147	
E: -	8	21	1	10	76	7	6	13	
02 R: 5	162	198	193	167	109	112	109	79	
E: -	17	36	2	16	68	7	2	31	
03 R: 5	116	177	156	112	13	74	147	112	
E: -	16	37	16	29	104	97	31	63	
04 R: 5	101	176	157	126	71	107	121	50	
E: -	29	29	8	62	58	5	18	36	
\bar{R} (SD): 5 (0)	127.0 (25.99)	195.0 (24.83)	167.5 (17.37)	145.5 (31.4)	74.74 (44.63)	105.0 (22.35)	124.25 (16.11)	97.0 (41.9)	
CV(%) = 0	20.5	12.73	10.37	21.58	59.71	21.28	12.97	43.16	
\bar{E} (SD): -	17.5 (8.66)	30.74 (7.41)	6.5 (7.14)	29.25 (23.23)	76.5 (19.76)	29.0 (45.34)	14.25 (13.07)	35.75 (20.68)	
Closed Pool #									
C1 R: 5	140	308	312	124	111	122	138	124	
C2 R: 5	148	216	190	176	141	132	129	120	
C3 R: 5	139	265	276	165	137	145	145	156	
C4 R: 5	230	315	251	124	121	128	149	134	
\bar{R} (SD): 5	164.25 (44.02)	276.0 (45.7)	257.25 (51.35)	147.25 (27.22)	131.75 (9.74)	140.25 (8.77)	140.25 (8.77)	133.5 (16.11)	
CV(%) = 0	26.8	16.55	19.96	18.49	10.97	7.39	6.25	12.07	

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