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EXPERIMENTAL ANALYSIS OF THE ROLE OF EMIGRATION IN POPULATION REGULATION OF DESERT PUPFISH[1]

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Abstract. Pupfishes (genus *Cyprinodon*) have existed for long periods in small desert springs and streams that often lack competitors, major predators, and large environmental changes. How their populations are regulated in these systems is poorly known. We experimentally examined the role of emigration in regulating populations of pupfish by (1) comparing the dynamics of populations held in four pools open to emigration with those of populations held in four pools closed to emigration over a 22-mo period and (2) comparing the rates of emigration from open pools having different densities of pupfish in relation to resources.

When pupfish populations were prevented from emigrating, they exhibited symptoms of overpopulation similar to those well documented for fenced populations of small mammals. Their numbers increased more than populations in open pools, mortality was high, and body condition and recruitment were low. Again, as in small-mammal populations, these responses were absent in pupfish populations in open pools, where 84% of the total numbers of fish produced emigrated. The timing and magnitude of pupfish emigration was similar in all four open pools and was related to seasonal temperature changes. More males emigrated than females, and emigrants had significantly lower condition factors than residents.

When densities of pupfish in relation to resources were doubled in two open pools, the percentages of pupfish that emigrated (41.8 and 42.2%) were almost equal to the 50% drop in resources. In contrast, only 15.5 and 16.0% emigrated from two control pools, where pupfish densities in relation to resources were left unchanged. Our results, demonstrating that emigration is a potentially significant mechanism for regulating populations of desert pupfish, are consistent with data from a variety of other animals (small mammals, hydra, roe deer), suggesting that population regulation via a behavioral spacing mechanism may be common among mobile animals.

Key words: Cyprinodon macularius; *emigration; fence effects; fish behavior; population dynamics; population regulation; stunting.*

INTRODUCTION

Population regulation has long been a controversial issue in ecology. Important questions have centered on the extent to which populations are limited by extrinsic and intrinsic mechanisms and how the factors involved in regulating numbers operate (Krebs 1978, 1985, Fowler 1986). One of the main impediments to answering these questions has been the difficulty in replicating experiments and isolating potential causal agents of population regulation from cooccurring phenomena (Hayne 1978, Tamarin 1978*a*, Sinclair 1986). Population studies of pupfish (genus *Cyprinodon*) offer a unique opportunity to overcome some of the methodological difficulties in testing population regulation theories.

Pupfishes are among the last survivors of the once diverse fish fauna that existed in the Chihuahuan, Mohave, and Sonoran deserts of North America during the last pluvial (cool, wet) period that ended ≈10 000 yr ago (Miller 1981, M. Smith 1981). As waters receded, remnant populations of these little (<50 mm) oviparous fishes were isolated in the few remaining small desert springs and streams (Brown 1971, Soltz and Naiman 1978). Unlike the complex habitats of most vertebrates, the small and relatively simple natural habitats of pupfish can easily be duplicated in small artificial pools, where the fish exhibit life histories, behaviors, and population dynamics indistinguishable from those observed in nature (Kodric-Brown 1981; T. E. McMahon, *personal observation*). With pupfish, therefore, it is feasible to perform controlled and replicated experiments with entire populations under nearly natural conditions.

Observations of pupfish in nature have shown that their numbers change little in environmentally stable springs and as much as 100-fold in highly variable desert streams (Brown 1971, Soltz 1974, Soltz and Naiman 1978, Deacon and Deacon 1979). These changes in natural population numbers relative to environmental changes suggest that pupfish numbers are linked

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to habitat size and available resources (Deacon and Deacon 1979), but the mechanism or mechanisms involved are not known (Chernoff 1985). Pupfish are often found in habitats that lack major predators, interspecific competitors, and large environmental changes (i.e., small, constant-temperature springs) (Miller 1948, 1981, Brown 1971, Soltz and Naiman 1978), implying that the major extrinsic factors commonly forwarded as limiting animal populations (climate: Andrewartha and Birch 1954; predation: Holling 1959, Erlinge et al. 1984; and interspecific competition: Park 1948, Larkin 1956; see also review by Tamarin 1978*a*) cannot be absolutely necessary to regulate pupfish populations in general. Intrinsic mechanisms suggested as limiting pupfish numbers include (1) decreased fecundity (resulting when algal productivity is low and pupfish population density high) (Minckley and Deacon 1973, Kennedy 1977), (2) egg cannibalism (Loiselle 1980), and (3) emigration (Young 1980).

Our study focused on emigration as a mechanism of population regulation. The need for greater understanding of the role of emigration in the population dynamics of animals has become increasingly recognized by ecologists (Lidicker 1975, Taylor and Taylor 1977, Lomnicki 1978). Evidence for its importance in population regulation has come from a number of studies that show (1) population numbers closely tracking changes in resource availability through changes in emigration rates (e.g., Dethier and MacArthur 1964, Lomnicki and Slobodkin 1966, Slaney and Northcote 1974, Mason 1976, Walton et al. 1977) and (2) overpopulation rapidly resulting when emigration is prevented (Krebs et al. 1969, 1973, Boonstra and Krebs 1977). For pupfish, however, the importance of emigration for population regulation is uncertain, since some of the small aquatic islands they inhabit seem to be closed to emigration (Deacon and Deacon 1979), and, therefore, selection against emigratory behavior might be expected (Van Valen 1971, Tamarin 1978*b*).

Our study examined how emigration affects the demographics of pupfish populations, especially whether emigratory losses might result in regulation of numbers. We experimentally examined the role of emigration in regulating population numbers of a desert pupfish, *Cyprinodon macularius,* by comparing (1) the dynamics of pupfish populations in pools open to emigration with those closed to emigration over a 22-mo period and (2) the variation in emigration rates of pupfish from open pools having different population density : resource (food and cover) ratios. If emigration acts to regulate pupfish numbers, we predicted that (1) overpopulation would occur in closed pools and (2) changes in density : resource ratios in open pools would be accompanied by changes in emigration rates that would adjust pupfish numbers to the amounts of resources available (Lomnicki 1978, 1980). Alternatively, we predicted that other mechanisms for regulating pupfish numbers would be involved if overpopulation was absent from pupfish populations in closed pools and if emigration from open pools was independent of changes in density : resource ratios (Lidicker 1975).

MATERIALS AND METHODS

Fish

Cyprinodon macularius were collected in April 1982 from Bates Well, Organ Pipe Cactus National Monument (OPCNM), Arizona. Bates Well was established in 1978 as a refugium for pupfish from Quitobaquito Springs, OPCNM (Kynard 1979), one of the few remaining natural habitats where *C. macularius* still exist (Miller 1981, McMahon and Miller 1985). Descriptions of the ecology and behavior of *C. macularius* can be found in Barlow (1961) and Minckley (1973). Prior to experiments, pupfish were held for 30 d in a large outdoor pool and fed daily with a dry flake food.

Experimental pools

Population dynamics were compared between pupfish held in four closed pools and those held in four pools periodically opened to emigration from May 1982 to March 1984. Pools consisted of circular metal sheets lined with blue, form-fitting polyvinyl sheeting (Fig. 1). Pools were small enough (2.6 m^2 and 600 L) to allow capture of nearly all fish for accurate determination of population parameters yet large enough to approximate the size of natural pupfish habitats. For example, Mexican Springs, Nevada, the smallest natural spring known to contain pupfish (*C. nevadensis*), had a surface area of only 3.25 m^2 and a volume of only 330 L (Brown 1971, Soltz 1974).

Pools had a water depth of 23 cm, a 2.5-cm layer of coarse sand as substrate, and were covered with 2-cm-mesh netting to prevent predation by birds. All pools were placed together in an unshaded area at an outdoor research facility in Tucson, Arizona. Open pools differed from closed pools only in having a wooden channel attached to the side to allow emigration (Fig. 1). A shelf placed in each wooden channel served as a one-way outlet for emigrants; two notched panels were installed in each shelf, one at the point where water from the main pool flowed onto the shelf and the other at the point where water from the shelf flowed into the emigration channel. Emigration was made possible by the addition of enough fresh water to the main pools to bring water levels above the notch in the first shelf panel. Flow over shelves and into emigration outlets was controlled by pumping (via small submersible pumps) water from the emigration channel back into the main pool (Fig. 1). Pump-flow was adjusted to provide a 1.0-cm water depth on a shelf and a discharge rate from the pool of ~1.0 L/min. To leave a pool, a fish had to swim through the notch in the first panel, onto the shelf and through the notch in the second panel, from which it then dropped into a net. The water velocity over the shelves was low enough (25 mm/s) for a pupfish of any size to choose, once it had swum onto the shelf, either to emigrate or to return to the main pool. Accurate identification and enumeration of emigrants is normally a major problem when studying emigration (Lidicker 1975), but the design of our outlet channels increased the probability that pupfish leaving the main pool were true emigrants (see also Butler 1980).

Pupfish populations in pools

Pupfish populations were started on 27 May 1982 by adding two adult males (27–37 mm standard length, SL) and three females (25–35 mm SL) to each of eight pools. Fish reproduced for 2 mo before pool outlet channels were opened to emigration. Fish were not fed over the course of the study, but a natural food base was established in each pool by adding water inoculated with 9.5 L of green pond water and letting pools stand 6 wk before introducing fish. Available food consisted of algae, insects, and detritus that fell or developed in the pools. Four artificial plants (made up of bundles of 1.25 × 16 cm clear plastic strips) were added to each pool to serve as cover. *Chara* colonized all pools and provided additional cover. When fish were first introduced into pools, the pool waters had a slight greenish cast, periphyton had developed on the plastic strips, and large numbers of chironomid larvae were present.

Variations in environmental conditions in pools

Food, cover, and water quality were monitored in all pools, since variations in these environmental conditions were likely to occur under the near-natural conditions in which the study was conducted. Food was monitored by measuring the depth of detritus overlying the sand substrate on the assumption that depth of floc was an indicator of food production. Detritus depths were measured in June and November 1983 and in January 1984 to the nearest 1.0 mm every 10 cm along two transect lines across each pool, yielding 30 depth measurements per pool. When plant cover obscured the bottom, detritus depths were measured in the closest plant-free area. Initial transect locations were chosen randomly; all subsequent measurements were made at those same locations. Plant cover (*Chara* plus plastic plants) was mapped in each pool in June and November 1983 and in January 1984; the percent of total substrate area covered was determined from these measurements. Differences in detritus depths and plant cover between open and closed pools were analyzed by *t* tests.

Temperature was recorded continuously with a thermograph placed in a screened compartment attached to one pool. Dissolved oxygen, pH, and conductivity were measured periodically in all pools. Water in closed pools was removed, and fresh water was added when conductivities became more than twice the level of that in open pools. Conductivities tended to be higher in closed pools because of evaporation and lower in open pools as a result of the addition of fresh water when pools were opened to allow emigration.

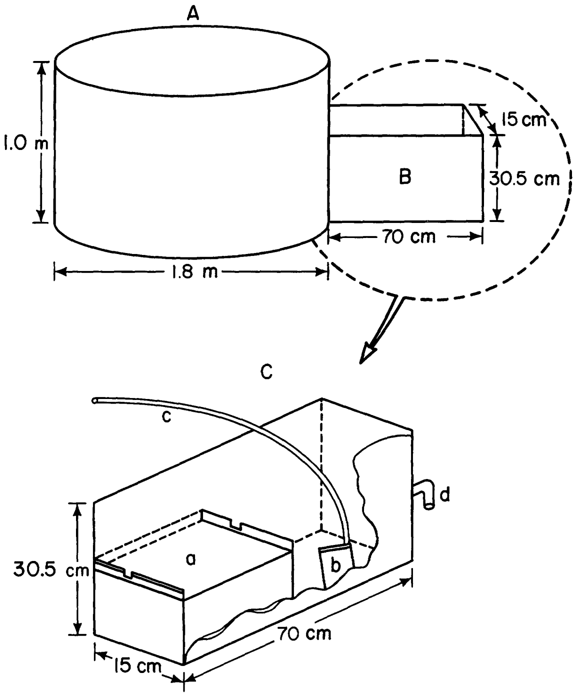

FIG. 1. Diagram of experimental pools. (A) Side view of main pool and (B) emigration channel, of pools open to emigration. Closed pools were identical except that they lacked emigration channels. (C) Enlarged view of emigration channel: a = outlet channel shelf with two notched panels, b = pump, c = tube carrying water from emigration channel to main pool, d = overflow drain. (Not shown: net positioned to capture fish exiting from main pool through the panel closest to the pump.)

Measurements of pupfish in pool populations

Censuses were made of pupfish in all pools about every 2 mo except during winter (November–February) when pupfish were inactive and buried under plants and detrital floc. Fish were collected with a 3-mm mesh seine. Pools were seined until no more fish were taken in seine hauls. About 3% of the fish were missed by this procedure as estimated by repeat seinings of the same pool within 1 wk during March 1984. Seining was done between 1200 and 1500.

At each census, fish ≥20 mm SL were counted, measured to the nearest 0.5 mm, sexed, weighed to the nearest 0.001 g (by adding fish to a tared water sample on a Mettler balance), and then returned to pools. Being handled during these measurements was apparently not too stressful for the fish as feeding and male territorial defense activities resumed within 20 min after fish were returned to pools. Fish <20 mm SL were counted, measured, and sexed, if possible, before being returned to pools; we did not weigh these small fish, to minimize handling time and reduce stress which they are less capable of sustaining than larger fish. Handling mortality from censusing was minimal; only rarely were dead fish found after measurements were made and then only one or two at any one time. Adult males were identified by the presence of an elongated, black-tipped anal fin, metallic blue coloration, and black-tipped dorsal fin (Barlow 1961). Fish as small as 18 mm SL exhibited male coloration. Females at sizes near 20 mm SL were estimated to be sexually mature since an egg was extruded from a female 21 mm SL (see also Soltz 1974).

Differences between the dynamics of the populations of pupfish in open and in closed pools were determined by comparing population sizes, condition factors, reproduction, mortality, net production, length–frequency distributions, and sex ratios. Condition factors ($K = 100\ M/L^3$, where M = mass [in grams] and L = SL [in centimetres]: Bagenal and Tesch 1978) were calculated for fish $\geq$20 mm SL to show differences in length–mass relationships. Use of this formula assumes a slope (b) of 3 in the length–mass regression equation ($\log M = a + b \log L$) and provides an index for comparing the gross nutritional statuses of fish (Weatherley 1972). Reproduction in open pools was determined as the sum of the number of fry recruited plus the total number of fry that emigrated during the intervals between censuses. In closed pools, reproduction was assumed to be the number of fry recruited only. Mortality in closed pools was determined by taking the difference in population numbers between two consecutive censuses; in open pools, mortality was calculated in the same way except that the number of emigrants between censuses was subtracted from the difference in numbers between corresponding censuses, in order to separate population losses due to emigration from those due to mortality. Net production (in numbers) of fish in each pool over the entire study period was computed as the total sum of the numbers of fish lost or gained from pool populations in the intervals between censuses. Length–frequency distributions were compared using a Kolmogorov-Smirnov test (Zar 1974).

Emigration of pupfish from open pools

The four pools with exits were opened to emigration by activating water pumps for 3 d every 2–3 wk. By providing outlets for emigration through increases in water level, pupfish were provided conditions similar to those they encounter in natural desert streams in which small pools that become isolated during dry periods are "opened" to emigration by rising water levels after rainfall (Deacon and Minckley 1974, Constantz 1981).

To allow acclimation of fish to disturbances caused by activation of the pumps (pumps were always activated around 0800), we screened notches in outlet channels for the first 24 h of the 72-h test periods that pumps were operated. At 0800 on the 2nd d, screens were removed, and fish could emigrate for the next 48 h. Emigrants $\geq$20 mm SL were counted, sexed, measured to the nearest 0.5 mm SL, weighed to the nearest 0.001 g, and removed from the outlet channels. Fish $<$20 mm SL were counted and measured but not weighed. Two days were deemed sufficient for fish to emigrate because, in preliminary experiments, all fish that emigrated from two tanks that had 2.5 g of flake food added per day and four concrete blocks for cover (7 of 10 fish introduced into one tank and 8 of 10 in the other) left within 48 h after tanks were opened to emigration; no other fish left the tanks during the remainder of a 10-d period.

Pumps were used to circulate water in closed pools to mimic the effects of water circulation in open pools when outlet channels were in operation. The end of a pump hose was placed 10 cm above the water surface to obtain the same effect that water flowing over a shelf made in open pools. Pumps were run in closed pools during the 3 d following pump operation in open pools.

Manipulation experiment

Long-term experiments provided information on the role of emigration in the dynamics of pupfish pool populations, but whether changes in density : resource ratios triggered emigration could only be inferred as we had only rough estimates of the amount of food and cover available. To determine more directly the importance of resource availability in triggering emigration in pupfish, we compared the relative proportions of pupfish populations that emigrated from two undisturbed open pools with the relative proportions of populations that emigrated from two pools in which resources (food and cover) were reduced by one-half (density : resource ratios doubled). If emigration in pupfish is tightly linked to the availability of resources, we predicted that $\approx$50% of the pupfish would emigrate from manipulated pools.

The manipulation experiment was run 2 wk after measurements for long-term changes in pupfish populations were completed. To double fish density in relation to resources, barriers (1.6-mm mesh screen) were placed across the center of two open pools, and all pupfish in each pool were restricted to the side having the outlet channel. The two remaining open pools were left undisturbed and served as controls. Before opening pools to allow emigration, pupfish were acclimated for 1 wk after barriers were erected, to allow time for adjustment to the manipulation. Because of the sudden doubling of density : resource ratios, pools were left open for 9 d (11–19 April 1984) during this experiment instead of the 2 d used during long-term experiments.

RESULTS

Population dynamics of pupfish in pools

Variations in environmental conditions between pools.—Environmental conditions generally differed little between open and closed pools. Temperatures were similar in all pools and followed seasonal patterns (Fig. 2) similar to those of Quitobaquito Springs (Kynard and Garrett 1979). Seasonal extremes of 4° and 34°C were well within the tolerance range of *C. macularius* (the lower tolerance for a close relative, *C. nevadensis,* is $<3°$: Hirshfield et al. 1980; the upper lethal limit for *C. macularius* is 41°–44°: Lowe and Heath 1969). Average water temperatures for both summers (25°–30°) were in the optimum range for reproduction of *C. macularius* (Kinne 1960).

Dissolved oxygen ranged from 3.2 to 20.0 mg/L in open pools and from 3.2 to 17.5 mg/L in closed pools. Dissolved oxygen was usually between 5.0 and 8.0 mg/L, with lower values occurring during the summers in early morning hours. The lowest values of dissolved oxygen were well above the minimum of 0.3 mg/L that *C. macularius* can tolerate (Lowe et al. 1967). Hydrogen ion concentrations varied little between open and closed pools, with pH ranging from 6.0 to 8.9 during the study (McMahon 1984).

Conductivities ranged from 575 to 1200 μS in open pools ($\bar{X} \pm$ SE $= 767 \pm 97$) and 585 to 2200 μS in closed pools ($\bar{X} \pm$ SE 1057 ± 218) (McMahon 1984). Differences in conductivity between open and closed pools were considered insignificant as they corresponded to salinity differences of only <1 g/kg, a small difference to *C. macularius* when considering that this species can reproduce in salinities from 0.0 g/kg to as high as 35 g/kg (Kinne and Kinne 1962).

Detritus accumulated in all pools during summer and fall and changed little during winter (Table 1). Open pools accumulated detritus at a faster rate during the summer and autumn of 1983 (average = 16–23% more). There were no significant differences in the amounts of plants that developed in each of the pool types (Table 1).

Population sizes. The small number of pupfish introduced into each experimental pool in May 1982 reproduced rapidly. By fall 1982, population numbers had increased in every pool to the highest levels that were observed during the 22-mo study (Fig. 2). Populations in closed pools, however, increased faster than those in open pools and had significantly higher numbers when all populations reached their peak ($\bar{X} \pm$ SE: closed $= 276.0 \pm 22.8$ fish, open $= 195.0 \pm 12.4$ fish; $t = 4.60$, df $= 6$, $P < .01$).

After peak numbers, pupfish populations declined in all pools over winter (November–February), but declines were much greater in closed pools than in open pools ($\bar{X} = 44.2$ vs. 25.4%, respectively). By March, population sizes in open and closed pools were nearly identical (Fig. 2). Numbers continued to decline in all pools during the spring (March–May) of 1983, with numbers in open populations declining by an average of 51.4% (due to emigration) and in closed populations by an average of 12.4% (due to mortality).

Pupfish numbers changed little in closed pools from May 1983 to March 1984, averaging 135 fish per pool. However, in open pools, average numbers of pupfish during this same period increased during the summer from a spring low of 75 to a high in the autumn of 124 and again declined during the winter to a low of 97. Pupfish numbers in open and closed pools were significantly different (t values $= 2.84$–4.44, df $= 6$, $P < .05$) at each of the four censuses performed during this period.

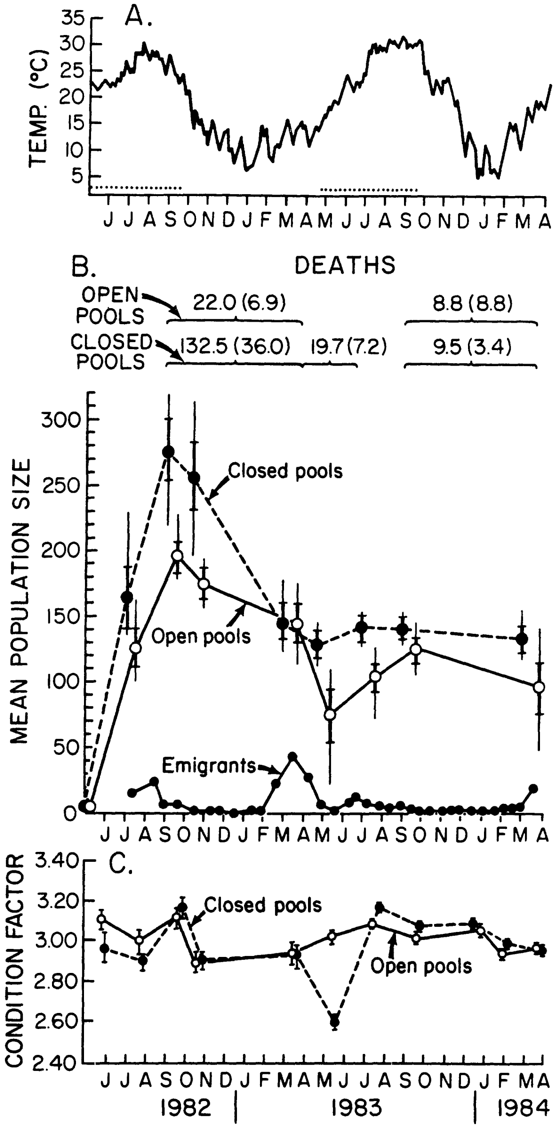

FIG. 2. Summary of temperature data and population dynamics in experimental pools open to and closed to emigration, from May 1982 to March 1984. (A) Mean daily water temperature in pool with thermograph (horizontal dotted lines show breeding seasons). (B) Mean numbers of deaths (1 ± SE), mean population sizes (vertical lines = range of values around mean, short horizontal bars show ±1 SE), and mean numbers of emigrants (from open pools). (C) Mean condition factors (±1 SE) of pupfish ≥20 mm SL in open and closed pools.

Changes in pupfish numbers were similar among

TABLE 1. Comparison of detritus depth and percent plant cover in four open (O) and four closed (C) pools measured in June and November 1983 and January 1984.

	Open pools					Closed pools					
Dates	O1	O2	O3	O4	$\bar{X}$ (SE)	C1	C2	C3	C4	$\bar{X}$ (SE)	t
					Detritus depth (mm)						
June 1983	6.1	6.9	8.1	7.6	7.2 (0.43)	9.6	7.9	8.7	6.6	8.2 (0.64)	−1.87
Nov. 1983	15.1	16.2	14.2	19.0	16.1 (1.04)	13.9	14.8	12.4	12.8	13.5 (0.54)	3.29*
Jan. 1984	17.6	17.1	17.0	16.8	17.1 (0.17)	12.1	14.0	17.7	13.9	13.2 (0.46)	12.38**
					% plant cover						
June 1983	24.1	22.6	14.8	24.1	21.4 (4.46)	11.5	15.8	16.7	19.5	15.9 (1.66)	−0.69
Nov. 1983	44.3	13.2	16.4	3.7	19.4 (8.73)	4.6	9.4	20.0	31.1	16.3 (5.90)	−0.29
Jan. 1984	14.8	11.5	8.5	3.7	9.6 (2.35)	4.6	7.9	8.7	34.4	13.9 (6.89)	0.59

* $P < .05$, ** $P < .01$; t test comparing pools that were open vs. closed to emigration. Percentages were arcsine-transformed prior to computations.

pools within each pool type. Coefficients of variation of mean population sizes determined at each census averaged 14.8 ± 3.4% SE in closed pools and 16.8 ± 2.5% SE in open pools over the 22-mo study, excluding March censuses, when numbers in open pools varied more due to differences in the magnitude and timing of the spring peak of emigration.

Condition factors.—Condition factors of pupfish in open and closed pools fluctuated seasonally between 2.8 and 3.2, except during the spring of 1983 when there was a marked drop in condition factors of closed-pool fish (Fig. 2). During this period, closed-pool fish showed pronounced symptoms of starvation. Their mean condition factor declined from 2.93 in March to 2.57 in May, whereas the mean condition factor of open-pool fish increased from 2.93 to 3.02. The length–mass regressions of pupfish during this period were significantly different (closed: $\log M = -5.282 + 3.51 \log L$, $r^2 = 0.98$, $N = 75$; open: $\log M = -4.77 + 3.18 \log L$, $r^2 = 0.98$, $N = 65$; ANCOVA, slopes: $F = 13.6$, df = 1136, $P < .01$; and elevation: $F = 91.8$, df = 1137, $P < .01$), with pupfish in closed pools weighing an average of 18.6% less than those in open pools (ratio of adjusted means: Snedecor 1956). The higher slope and lower intercept of the length–mass regression for closed-pool fish indicated that mass differences between pool types were highest between smaller fish.

Reproduction.—During the first summer (June–September), production of fry was similar in open and closed pools (Table 2, $t = 1.01$, df = 6, $P > .25$). However, pupfish numbers in closed pools grew at faster rates than in open pools because many of the fry produced in open pools emigrated ($\bar{X} \pm$ SE = 48.25 ± 6.5 fish per pool). This circumstance accounts for the significantly higher number of pupfish in closed pools when populations reached their peak in fall 1982.

During the 1983 breeding season, recruitment in closed pools was very low (≈10% of 1982 levels). Male territories and spawning were observed in both open and closed pools from May to September, but fry were rarely seen in closed pools (McMahon 1984), and an average of only 18.5 ± 6.5 fry were recruited per closed pool compared with an average of 116.5 ± 60.7 fry per open pool (Table 2). Low egg production appeared to be a primary cause for low recruitment in closed pools. Despite open and closed pools having similar numbers and sizes of mature females when spawning began in the spring (Table 2), mean condition factors of females in closed pools in May were significantly lower than those for open-pool females (2.45 ± 0.10 vs. 2.97 ± 0.06, respectively; $t = 8.92$, df = 6, $P < .01$). Although fry production in open pools in 1983 was far greater than in closed pools, the numbers produced were about half the number produced in 1982.

TABLE 2. Summary of mortality, reproduction, and emigration of pupfish in pools that were open or closed to emigration. Data in rows A3 and D–G are for 1982 and 1983 combined.

	Open pools		Closed pools	
	$\bar{X}$	(SE)	$\bar{X}$	(SE)
A) Average fry production per pool				
1) 1982	283.2	(6.7)	268.5	(23.4)
2) 1983	116.5	(60.7)	18.5	(6.5)
3) Combined years	350.0	(56.3)	287.2	(29.8)
B) Avg. no. mature females > 20 mm per pool in 1983	17.5	(3.6)	19.2	(2.6)
C) Fry production per female in 1983 (B/A2)	6.7		0.96	
D) Avg. mortality per pool	36.2	(11.8)	164.0	(29.3)
E) Proportion of fry produced that were lost to mortality (D/A3)	0.10		0.57	
F) Avg. no. emigrants per pool	293.7	(55.3)	···	
G) Proportion of fry produced that emigrated (F/A3)	0.84		···	

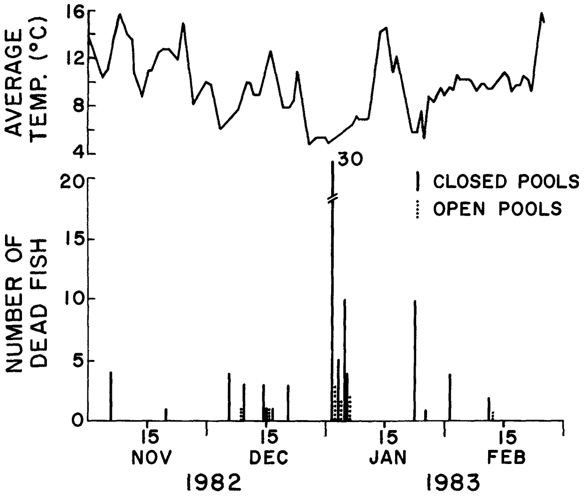

FIG. 3. Total numbers of dead fish found on the bottoms of pools open to and closed to emigration and average daily water temperature in pool with thermograph from 1 November to 15 February 1983.

This difference appeared to be due to the emigration of some of the large (and more fecund) females from open pools during 1983 (McMahon 1984).

Mortality.—In all pools, highest mortality occurred during winter, especially the first winter following peak numbers (Fig. 2). During this period, an average (±SE) of 132.5 ± 36.0 fish died in closed pools, and an average of 22.0 ± 6.9 fish died in open pools (difference significant, $t = 2.57$, df = 6, $P < .05$). Nearly all dead fish were fry <20 mm SL. Most mortality occurred when water temperatures were <12° (November–February) and pupfish were buried beneath plants and detrital floc. Pupfish in closed pools appeared more susceptible to cold temperatures. A total of 86 dead fish was observed in closed pools ($\bar{X}$ ± SE = 21.5 ± 8.3 dead fish per pool), with most deaths occurring after rapid temperature declines of >5° in 48 h; during the same period, a total of only 10 dead fish was found in open pools ($\bar{X}$ ± SE = 2.5 ± 0.4 dead fish per pool)

TABLE 3. Mean condition factors (K) and number of dead pupfish in closed pools (C) during March–May 1983. Standard errors around means shown in parentheses.

	K	No. dead fish
C1	2.70 (0.12)	13
C2	2.50 (0.16)	28
C3	2.48 (0.17)	35
C4	2.63 (0.12)	3
$\bar{X}$ =	2.57 (0.03)	19.75 (7.23)

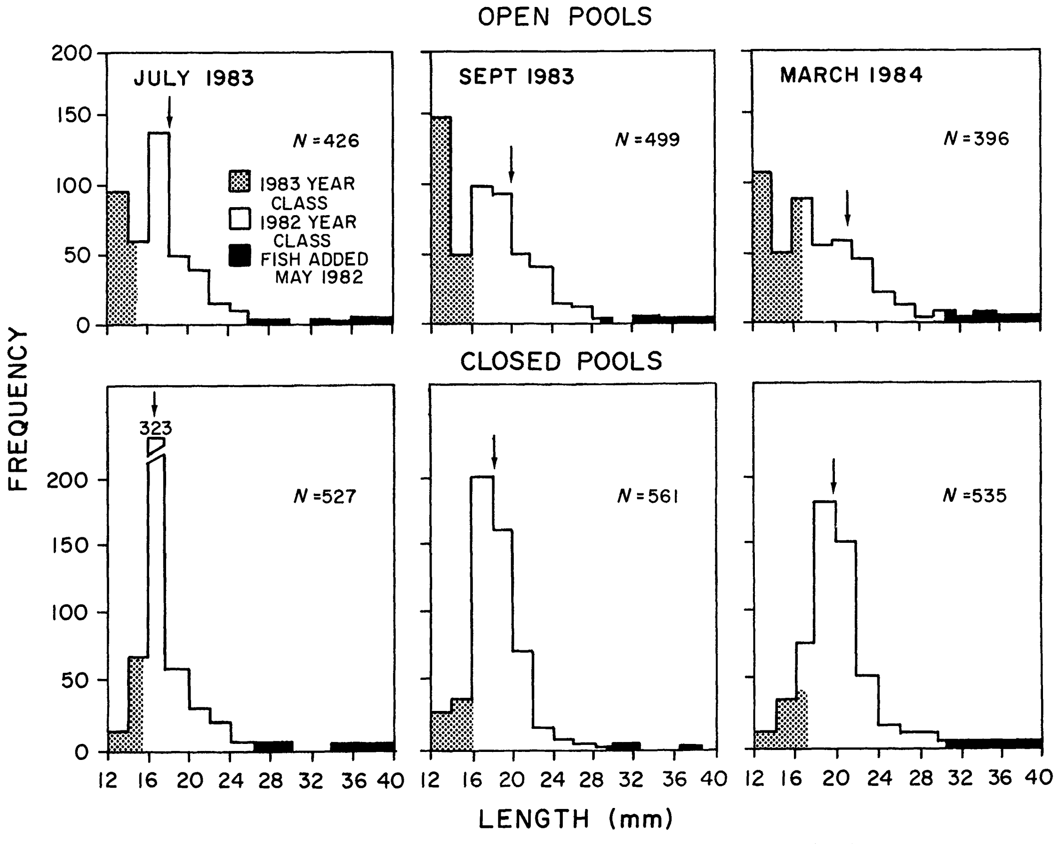

FIG. 4. Length–frequency distributions of pupfish in pools open to and closed to emigration in July and September 1983 and March 1984. Year classes indicated on graphs. Vertical arrows indicate mean length of fish from 1982 year class.

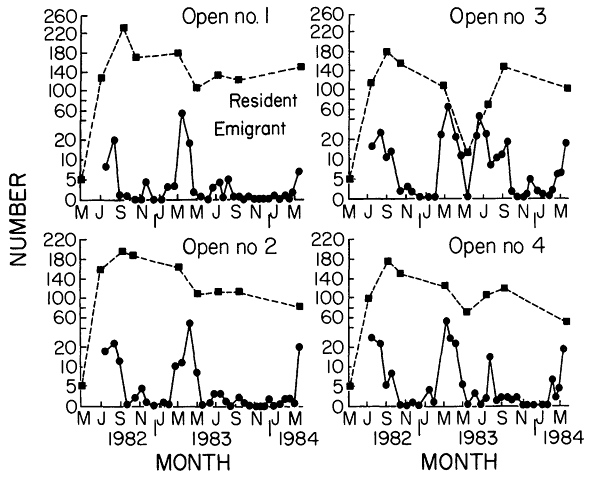

FIG. 5. Number of resident and emigrant pupfish from the four pools open to emigration.

(Fig. 3). The highest number of dead fish was found during a 7-d cold spell in early January 1983.

Although most pupfish mortality occurred during winter, an additional 19.7 ± 7.2 pupfish died in closed pools during spring (March to May) of 1983. No pupfish died in open pools during this period. The higher mortality of closed-pool fish was probably a result of low condition factors. Their condition factors were much lower than those of fish in open pools (Fig. 2) and the highest mortality of closed-pool fish tended to occur in populations having the lowest condition factors (Table 3). Again, as was the case after the winter of 1982–1983, most dead fish were young-of-the-year. However, six (1–2 per pool) of the dead fish were large ($>$30 mm SL) fish introduced at the start of the study.

Pupfish mortality was negligible in all pools over the summer (May–September) of 1983 but increased again during the winter (November–March), when a mean of 9.5 ± 3.4 fish died in closed pools, and 8.8 ± 8.8 deaths occurred in open pools. All mortality was again small fish ($\leq$21 mm SL). By the end of the study, 4.5 times as many fish died in closed as in open pools (Table 2).

Net production.—The net number of pupfish produced in open pools (sum of census counts, numbers that died, and numbers that emigrated) averaged (±SE) 331.75 ± 56.7 fish per pool. This value was $>$2.5 times the net production in closed pools (sum of census counts and numbers that died = 127.0 ± 3.56 fish per pool) despite open pools averaging fewer fish per pool throughout most of the study (Fig. 2).

Length–frequency distributions.—Concurrent with differences between pool types in recruitment, mortality, and condition factors, length–frequency distributions also were significantly different between pool types during the 2nd yr of the study (Fig. 4; D values = 0.38, 0.36, and 0.38 for July 1983, September 1983, and March 1984, respectively; all $P < .001$; Kolmogorov-Smirnov test). Pupfish in closed pools were primarily fish from the 1982 year class bounded within a narrow size range, whereas fish in open pools were more evenly distributed between the fish of the 1982 and 1983 year classes. Growth rates of pupfish in closed pools seemed to be slower, as the mean lengths of fish from the 1982 year class were significantly less than those of open-pool fish (t values = 3.1, 4.1, and 4.3 for July 1983, September 1983, and March 1984, respectively; all df = 6; all $P < .005$; Fig. 4).

Sex ratios.—The average (±SE) male : female ratio of pupfish in closed pools (1.2 ± 0.18, $N = 1046$) was significantly higher than 1:1 $\chi^2 = 10.74$, $P < .005$), whereas there were about equal numbers of males and females (sex ratio = 0.99 ± 0.09, $N = 722$) in open pools ($\chi^2 = 0.4$, $P > .25$).

Emigration.—Of the total numbers of fish produced in open pools ($\bar{X} = 350$ per pool, $N = 946$; Table 2), 84% emigrated. Of those that emigrated, 662 (70%) left within the first 24 h of the 48-h periods that outlet channels were opened.

Emigration was high during each summer as populations increased through reproduction, declined in the autumn and remained low during winter, and increased again dramatically each spring (Fig. 5). This annual emigration pattern was strikingly similar in all four open pools.

Temperature appeared to influence emigration strongly. Spring peaks in emigration (Fig. 5) occurred at about the same time that water temperatures exceeded 15° and declined during autumn when temperatures declined below this same level (Fig. 2). Very few fish emigrated after temperatures dropped to below 12°. A plot of the proportion of pupfish emigrating from pool populations when fish were active (15 February–15 October) vs. population size revealed no apparent relationship between emigration and population density (Fig. 6).

Most pupfish that emigrated during 1982 were young-of-the-year ($<$20 mm SL). During 1983–1984, as populations matured, an increasing number of fish between 20–24 mm SL emigrated (McMahon 1984). Nearly twice as many males as females emigrated (81:43, $\chi^2 = 11.65$, $P < .01$); this difference was particularly evident during July 1983–March 1984 when 73% of the 77 emigrants $>$18 mm in length were males.

The condition factor of each emigrant $\geq$20 mm SL was paired with the mean condition factor of residents from the same pool and a corresponding size class (i.e., 20–24, 25–29, etc. mm SL). Overall, the condition factors of emigrants were significantly less than those of residents (Wilcoxon paired-sample test, $Z = 3.7$, $N = 100$, $P < .001$).

Manipulation Experiment

Almost half (41.8 and 42.2%) of the pupfish emigrated from two manipulated pools in which densities had been doubled in relation to resources; during the same period, only 15.5 and 16.0% of the populations

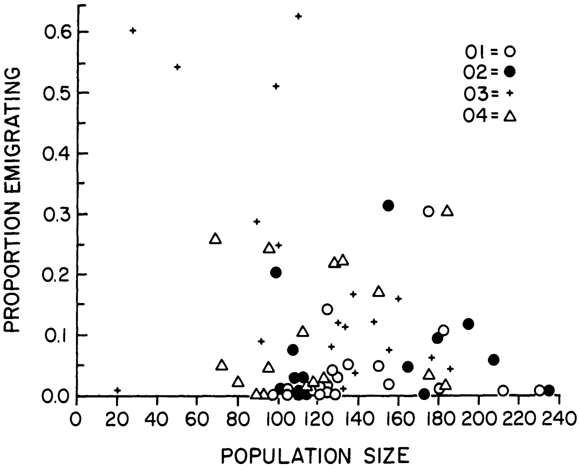

FIG. 6. Proportion of pupfish populations that emigrated from open pools vs. population size. Data shown for the periods 15 February–15 October 1982–1984.

emigrated from two pools in which density : resource ratios had not been manipulated (Fig. 7). The difference in mean emigration between manipulated and unmanipulated pools was highly significant (arcsine transformation, $t = 73.75$, df = 2, $P < .001$). Most of the emigration occurred within 72 h after pool outlet channels were opened.

DISCUSSION

Models for population regulation by emigration (Taylor and Taylor 1977, Lomnicki 1978, 1980) theorize that behavioral spacing of animals in relation to available resources leads to a division of resources among individuals in a population and emigration of those individuals lacking access to resources. Regulation of a population results from the accumulation of these individual residency–emigratory responses. Our experimental results support such a mechanism operating to regulate population numbers in pupfish.

In our long-term experiment, pupfish populations in closed pools showed symptoms of overpopulation (high numbers followed by declines in reproduction, increased mortality, and starvation) nearly identical to those observed in enclosed populations of small mammals (Krebs et al. 1969, 1973, Boonstra and Krebs 1977). During this same period, overpopulation responses were not observed in pupfish from open pools.

Evidence that pupfish in closed pools exceeded the carrying capacity of resources is provided by the differences observed in population dynamics between pupfish in closed and in open pools. During the 1st yr of the study, pupfish in closed pools entered the winter at high densities and low condition factors, leading to a much higher overwinter mortality. Fish rely heavily on stored energy reserves during winter (Newsome and Leduc 1975, Mason 1976, Oliver et al. 1979), thus closed-pool fish were more susceptible to starvation and other environmental stresses (e.g., rapid declines in water temperature). Overwinter mortality was further augmented by the small size of the pupfish in this 1st yr. Small fish are more susceptible to starvation than larger fish because of their lower energy reserves and higher energy demands per unit mass (Mason 1976, Oliver et al. 1979).

The high rate of mortality that continued among pupfish in closed pools during the spring of 1983 probably was due to increasing energy demands caused by increases in temperature. Food requirements and metabolism of pupfish increase rapidly at temperatures >17°C (Gerking and Lee 1983). Therefore, temperatures above this level during the spring of 1983 probably triggered a further decline in the condition of pupfish, which resulted in additional mortality. In contrast, pupfish in open pools had high emigration rates, good condition factors, and suffered no mortality (Fig. 2).

Continued high densities led to slow growth and low recruitment in closed-pool fish the 2nd yr of the study. Pupfish at high densities and low food availability produce smaller and fewer eggs (Minckley and Deacon 1973, Kennedy 1977), and the relationship we found between low female condition factor and low fry production in closed pools was consistent with this pattern. High cannibalism of eggs and fry probably contributed to the low recruitment. Closed pools had more potential cannibals (pupfish >18 mm) than open pools (Fig. 4), and in closed pools male territories that were vacated for even short periods were rapidly invaded by fish that began feeding on the substrate. Increases in cannibalism in conjunction with increases in population density or decreases in food availability have been documented in other fishes (Meffe 1984*a*, Dionne 1985).

The pattern of slowed growth or stunting observed in closed-pool fish provides additional evidence that these populations exceeded carrying capacity. Long

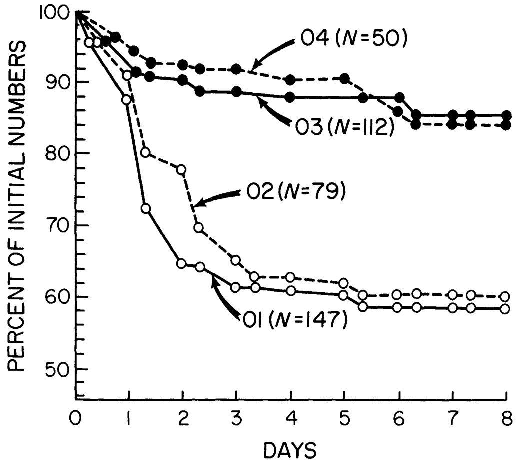

FIG. 7. Manipulation experiment results. Percent of pupfish populations that remained in the two manipulated open pools (resources reduced by 50% in relation to density) shown as open circles and in two open pools left undisturbed shown as closed circles. N = initial population size.

considered evidence for overpopulation, stunting in fish is characterized by narrow length-frequency distributions and is commonly observed in populations confined to areas closed to emigration. In these areas, the high densities that rapidly develop increase competition for limited food enough to slow individual growth and reduce recruitment (Swingle and Smith 1940, Anderson 1973, Hackney 1979, Persson 1983).

In sharp contrast to pupfish in closed pools, pupfish in open pools had lower population densities, lower mortality rates, higher growth rates, higher net production, higher fry recruitment (during 1983), and apparently higher food availability (=detritus depth) than pupfish from closed pools. Their length–frequency distributions, length–mass relationships, and reproductive cycles closely resembled those observed in natural populations of *Cyprinodon macularius* and other pupfishes (Soltz 1974, Naiman 1976, Kennedy 1977, Kynard and Garrett 1979). Our results parallel previous studies showing a similar lack of symptoms of overpopulation in animals living in areas open to emigration but distinct symptoms of overpopulation occurring when emigration is prevented. These include studies of small mammals (Krebs et al. 1969, 1973, Boonstra and Krebs 1977, Gaines et al. 1979, Beacham 1981), hydra (*Hydra littoralis*) (Lomnicki and Slobodkin 1966, Lomnicki 1980), and roe deer (*Capreolus capreolus*) (Andersen 1961, Strandgaard 1972). The similarity of overpopulation responses to confinement among such a diverse assortment of animals suggests that population regulation via a behavioral spacing mechanism (Chitty 1960) may be pervasive in many species of mobile animals.

Results from our manipulation experiment suggest that overpopulation in open pools was prevented by emigration of pupfish when density was high relative to available resources. The small variation within treatments and the consistent patterns of emigration over the course of this experiment (emigration occurring mostly within the first 72 h with little change thereafter), plus the similarity of seasonal patterns of emigration among open pools during the long-term experiment, limit the possibility that pupfish left pools by accident, through simple wandering, or in response to social disruption caused by artificially doubling density : resource ratios. Further support for our findings that emigration in pupfish is closely linked to available resources is provided by Jennings (1985) who observed emigration rates of *C. macularius* changing in direct proportion to changes in amounts of food and cover. The triggering of emigration in response to changes in resources also has been demonstrated for a number of other fishes (e.g., Slaney and Northcote 1974, Bianchi 1984, Wilzbach 1985).

The lack of a positive relationship between population density and emigration has been interpreted as evidence against emigration operating as a mechanism to regulate populations (Gaines and McClenaghan 1980). We also found no positive relationship between density and emigration of pupfish in our long-term experiment. However, our manipulation experiment results demonstrated that emigration was not a simple function of population size. Within each treatment, pupfish emigrated in almost identical proportions despite a considerable difference in population sizes between pools, suggesting that emigration should be viewed as neither independent nor dependent on population size per se, but rather as a function of density in combination with resources.

Temperature appeared to play a major role in causing the seasonal patterns of emigration that we observed. As noted earlier, spring peaks in emigration occurred at a time of increasing energy requirements yet relatively low food availability and the decline in emigration in the fall and winter corresponded to times when low temperatures decrease food requirements and activity levels of pupfish (Gerking and Lee 1983).

Studies of emigration in small mammals have shown that males and females have different critical resource needs and hence different spacing behavior and emigratory patterns (Fairbairn 1978, Krebs 1985). Emigration in pupfish also varied according to sex. In this study, about two-thirds of emigrants were males. Unlike females, sexually mature male pupfish generally require individual territories for successful breeding, with larger males excluding smaller ones from optimal breeding sites (Barlow 1961, Soltz 1974, Kodric-Brown 1981). Thus it seems likely that the preponderance of small males among emigrants was due to their inability to obtain suitable breeding sites.

At first glance, emigration would seem unable to function as a mechanism for regulating populations of pupfish in many of their natural habitats. Pupfish often occur in small aquatic islands surrounded by desert. Yet even in small springs, pupfish maintain relatively stable numbers despite their capacity for rapid increase (Young 1980), and lack evidence of overpopulation (such as poor condition factors and narrow length–frequency distributions) (Soltz 1974) that would be expected if these habitats were actually closed to emigration. Moreover, most small desert springs have overflows through which emigration can occur (Soltz 1974). Young (1980) found such movements to occur commonly from a springlike refugium. Even cave systems (e.g., Devil's Hole, Nevada), which lack surface overflows and are presumed to be closed to emigration (Deacon and Deacon 1979, Chernoff 1985), may have underground avenues through which fish can emigrate (McMahon 1984, see also Woods and Inger 1957).

In desert streams, the role of emigration in the population dynamics of pupfish is difficult to discern. Pupfish are often confined at high densities in isolated pools for many months during periods of drought (Miller 1943, Deacon and Minckley 1974, Constantz 1981). Most emigratory movements probably occur right after rainfall when the large and sometimes rapid changes in streamflow would mask fish movements (e.g., Meffe 1984*b*). As the results of our manipulation experiment demonstrated, however, high numbers of pupfish trapped in isolated pools could decrease almost immediately through emigration after outlets become opened. Constantz (1981) observed just such a drop in numbers in another desert stream fish, the Sonoran topminnow (*Poeciliopsis occidentalis*), after increased streamflow "opened" isolated pools to emigration.

Our results suggest that pupfish readily emigrate from a known habitat into unknown areas when density: resource ratios exceed some critical level. Yet, if emigrants have a low probability of surviving (Soltz 1974, Constantz 1981) then it is difficult to see how such a lethal trait could have evolved (Taylor and Taylor 1977, Lomnicki 1978). This question has always been the major obstacle to the acceptance of emigration as a regulatory mechanism.

Emigration, however, is not synonymous with mortality. Studies with other animals have documented that at least some emigrants find and become residents in suitable habitats (e.g., Woods and Inger 1957, Johnson and Gaines 1987). Lomnicki (1978) has further argued that emigration could be of selective advantage to individuals having low or no access to resources if, by emigrating, such individuals find needed resources in another area. Our study provides some support for Lomnicki's theory in that pupfish that emigrated were in poorer condition than residents, implying that emigrants had had low access to resources. Moreover, the high mortality and low reproduction of fish in closed pools (Table 2) illustrates that the chances of survival and reproduction would have been very low had they remained in an area where their access to resources was limited. Finally, it seems likely that for pupfish and other desert fishes, since their habitats are often ephemeral (G. Smith 1981, see also Taylor and Taylor 1977), that their survival has depended greatly upon emigrating individuals finding suitable areas.

We were unable to identify exactly what specific cues were involved in determining residency and emigratory responses in pupfish. Our general findings are consistent, however, with results from previous habitat-selection studies with other animals, which demonstrated that both environmental and behavioral cues are involved in triggering emigration (Wecker 1964, Sale 1969, Malcolm and Hanks 1973). These studies indicated that a combination of environmental and behavioral cues signals the presence or absence of resources and regulates "internal" physiological drives. These drives, in turn, govern the intensity of exploratory behavior. Thus, in environments where needed resources are unavailable or inaccessible due to the action of conspecifics, animals continue to explore until they eventually emigrate from an area in search of suitable habitat elsewhere. Further research on the relationship between habitat preferences, resource availability, and social behavior (e.g., Whitham 1980) is needed to better define the specific factors or combination of factors that trigger emigration and residency in pupfish and other animals.

Previous studies have established that emigration in fishes changes in response to changes in availability of resources (Slaney and Northcote 1974, Bianchi 1984, Wilzbach 1985), but our results provide the first experimental evidence that emigratory behavior alone is sufficient to regulate entire fish populations. The magnitude of emigration and the qualitative differences we observed between residents and emigrant pupfish in our study suggest that knowledge of when and how much emigration occurs and what triggers it may be crucial for understanding population dynamics of animals in general. Our work with pupfish shows them to be ideal animals for experimental population studies, and additional research with these fish may help bridge the gap in our understanding of how the behavior of individuals affects the behavior of populations.

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LITERATURE CITED

Andersen, J. 1961. Biology and management of roe deer in Denmark. Terre et la Vie **108**:41–53.

Anderson, R. O. 1973. Application of theory and research to the management of warmwater fish populations. Transactions of the American Fisheries Society **102**:164–171.

Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, Illinois, USA.

Bagenal, T. B., and F. W. Tesch. 1978. Age and growth. Pages 101–136 *in* T. Bagenal, editor. Methods for assessment of fish production in freshwaters. IBP (International Biological Programme) Handbook 3.

Barlow, G. W. 1961. Social behavior of the desert pupfish, *Cyprinodon macularius,* in the field and in the aquarium. American Midland Naturalist **65**:339–359.

Beacham, T. D. 1981. Some demographic aspects of dispersers in fluctuating populations of the vole *Microtus townsendii.* Oikos **36**:272–280.

Bianchi, E. 1984. Population regulation in bluegills (*Lepomis machrochirus*). Dissertation. University of Arizona, Tucson, Arizona, USA.

Boonstra, R., and C. J. Krebs. 1977. A fencing experiment on a high-density population of *Microtus townsendii.* Canadian Journal of Zoology **55**:1166–1175.

Brown, J. H. 1971. The desert pupfish. Scientific American **225**:104–110.

Butler, R. G. 1980. Population size, social behavior, and dispersal in house mice: a quantitative investigation. Animal Behaviour **28**:78–85.

Chernoff, B. 1985. Population dynamics of the Devil's Hole pupfish. Environmental Biology of Fishes **13**:139–147.

Chitty, D. 1960. Population processes in the vole and their relevance to general theory. Canadian Journal of Zoology **38**:99–113.

Constantz, G. D. 1981. Life history patterns of desert fishes. Pages 237–290 *in* R. J. Naiman and D. L. Soltz, editors. Fishes in North American deserts. Wiley-Interscience, New York, New York, USA.

Deacon, J. E., and M. S. Deacon. 1979. Research on endangered fishes in the national parks with special emphasis on the Devil's Hole pupfish. Pages 9–19 *in* R. M. Linn, editor. Proceedings of the First Conference on Scientific Research in National Parks. United Stated Department of the Interior, National Park Service, Transactions and Proceedings Series Number 5. Washington, D.C., USA.

Deacon, J. E., and W. L. Minckley. 1974. Desert fishes. Pages 385–488 *in* G. W. Brown, Jr., editor. Desert biology. Volume III. Academic Press, New York, New York, USA.

Dethier, V. G., and R. H. MacArthur. 1964. A field's capacity to support a butterfly population. Nature **201**:728–729.

Dionne, M. 1985. Cannibalism, food availability, and reproduction in the mosquito fish (*Gambusia affinis*): a laboratory experiment. American Naturalist **126**:16–23.

Erlinge, S., et al. 1984. Can vertebrate predators regulate their prey? American Naturalist **123**:125–133.

Fairbairn, D. J. 1978. Dispersal of deer mice, *Peromyscus maniculatus*: proximal causes and effects on fitness. Oecologia (Berlin) **32**:171–193.

Fowler, N. L. 1986. Density-dependent population regulation in a Texas grassland. Ecology **67**:545–554.

Gaines, M. S., and L. R. McClenaghan, Jr. 1980. Dispersal in small mammals. Annual Review of Ecology and Systematics **11**:163–196.

Gaines, M. S., A. M. Vivas, and C. L. Baker. 1979. An experimental analysis of dispersal in fluctuating vole populations: demographic parameters. Ecology **60**:814–828.

Gerking, S. D., and R. M. Lee. 1983. Thermal limits for growth and reproduction in the desert pupfish *Cyprinodon n. nevadensis.* Physiological Zoology **56**:1–9.

Hackney, P. A. 1979. Influence of piscivorous fish on fish community structure of ponds. Pages 111–121 *in* H. Clepper, editor. Predator-prey systems in fisheries management. Sport Fishing Institute, Washington, D.C., USA.

Hayne, D. W. 1978. Experimental designs and statistical analyses in small mammal population studies. Pages 3–10 *in* D. P. Snyder, editor. Populations of small mammals under natural conditions. University of Pittsburgh, Pittsburgh, Pennsylvania, USA.

Hirshfield, M. F., C. R. Feldmeth, and D. L. Soltz. 1980. Genetic differences in physiological tolerances of Amargosa pupfish (*Cyprinodon nevadensis*) populations. Science **207**: 999–1001.

Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Canadian Entomologist **91**:292–320.

Jennings, M. R. 1985. Behavioral interactions between desert pupfish (*Cyprinodon macularius*) and mosquitofish (*Gambusia affinis*) in systems open to egress. Dissertation. University of Arizona, Tucson, Arizona, USA.

Johnson, M. L., and M. S. Gaines. 1987. Selective basis for dispersal of the prairie vole, *Microtus ochrogaster.* Ecology **68**:684–694.

Kennedy, S. E. 1977. Life history of the Leon Springs pupfish, *Cyprinodon bovinus.* Copeia **1977**:93–103.

Kinne, O. 1960. Growth, food intake, and food conversion in a euryplastic fish exposed to different temperatures and salinities. Physiological Zoology **33**:288–317.

Kinne, O., and E. M. Kinne. 1962. Rates of development in embryos of a cyprinodont fish exposed to different temperature-salinity-oxygen combinations. Canadian Journal of Zoology **40**:231–253.

Kodric-Brown, A. 1981. Variable breeding systems in pupfishes (genus *Cyprinodon*): adaptations to changing environments. Pages 205–235 *in* R. J. Naiman and D. L. Soltz, editors. Fishes in North American deserts. Wiley-Interscience, New York, New York, USA.

Krebs, C. J. 1978. A review of the Chitty hypotheses of population regulation. Canadian Journal Zoology **56**:2463–2480.

———. 1985. Do changes in spacing behaviors drive population cycles in small mammals? Pages 295–312 *in* R. M. Sibley and R. H. Smith, editors. Behavioural ecology. Blackwell Scientific, Oxford, London, England.

Krebs, C. J., M. L. Gaines, B. L. Keller, J. H. Myers, and R. H. Tamarin. 1973. Population cycles in small rodents. Science **179**:35–41.

Krebs, C. J., B. L. Keller, and R. H. Tamarin. 1969. *Microtus* population biology: demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana. Ecology **50**:587–607.

Kynard, B. E. 1979. Study of Quitobaquito pupfish—preservation, habitat and population monitoring. Final report to United States National Park Service, Tucson, Arizona, USA.

Kynard, B. E., and R. Garrett. 1979. Reproductive ecology of the Quitobaquito pupfish from Organ Pipe Cactus National Monument. Pages 625–629 *in* R. Linn, editor. Proceedings of the First Conference on Scientific Research in National Parks, United States Department of the Interior National Park Service, Transactions and Proceedings Series Number 5, Washington, D.C., USA.

Larkin, P. A. 1956. Interspecific competition and population control in freshwater fish. Journal of the Fisheries Research Board of Canada **13**:327–334.

Lidicker, W. F. 1975. The role of dispersal in the demography of small mammals. Pages 103–128 *in* F. B. Golley, K. Petrusewicz, and L. Ryszkowski, editors. Small mammals: their productivity and dynamics of populations. Cambridge University Press, London, England.

Loiselle, P. V. 1980. Spawn recognition by male *Cyprinodon macularius californiensis.* Page 46 *in* Proceedings of the Desert Fishes Council 11. Desert Fishes Council, Bishop, California, USA.

Lomnicki, A. 1978. Individual differences between animals and the natural regulation of their numbers. Journal of Animal Ecology **47**:461–475.

———. 1980. Regulation of population density due to individual differences and patchy environment. Oikos **35**: 185–193.

Lomnicki, A., and L. B. Slobodkin. 1966. Floating in *Hydra littoralis.* Ecology **47**:881–889.

Lowe, C. H., and W. G. Heath. 1969. Behavioral and physiological responses to temperature in the desert pupfish (*Cyprinodon macularius*). Physiological Zoology **42**:53–59.

Lowe, C. H., D. S. Hinds, and E. A. Halpern. 1967. Experimental catastrophic selection and tolerances to low oxygen concentrations in native Arizona freshwater fishes. Ecology **48**:1013–1016.

Malcolm, W. M., and J. P. Hanks. 1973. Landing-site selection and searching behavior in the micro-lepidopteran *Agonopteryx pulvipennella.* Animal Behaviour **21**:45–48.

Mason, J. C. 1976. Response of underyearling coho salmon to supplemental feeding in a natural stream. Journal of Wildlife Management **40**:775–788.

McMahon, T. E. 1984. The role of emigration in the dynamics and regulation of populations of the desert pupfish (*Cyprinodon macularius*). Dissertation. University of Arizona, Tucson, Arizona, USA.

McMahon, T. E., and R. R. Miller. 1985. Status of the fishes of the Rio Sonoyta basin, Arizona and Sonora, Mexico. Pages 237–245 *in* Proceedings of the Desert Fishes Council 13–15. Desert Fishes Council, Bishop, California, USA.

Meffe, G. K. 1984*a*. Density-dependent cannibalism in the endangered Sonoran topminnow (*Poeciliopsis occidentalis*). Southwestern Naturalist **29**:500–503.

———. 1984*b*. Effects of abiotic disturbances on coexistence of predator–prey fish species. Ecology **65**:1525–1534.

Miller, R. R. 1943. *Cyprinodon salinus,* a new species of fish from Death Valley, California. Copeia **1943**:69–78.

———. 1948. The cyprinodont fishes of the Death Valley system of eastern California and southwestern Nevada. Miscellaneous Publications, Museum of Zoology, University of Michigan **68**:1–155.

———. 1981. Coevolution of deserts and pupfishes (genus *Cyprinodon*) in the American Southwest. Pages 39–94 *in* R. J. Naiman and D. L. Soltz, editors. Fishes in North American deserts. Wiley-Interscience, New York, New York, USA.

Minckley, C. O., and J. E. Deacon. 1973. Observations on the reproductive cycle of *Cyprinodon diabolis.* Copeia **1973**: 610–613.

Minckley, W. L. 1973. Fishes of Arizona. Arizona Game and Fish Department, Phoenix, Arizona, USA.

Naiman, R. J. 1976. Productivity of a herbivorous pupfish population (*Cyprinodon nevadensis*) in a warm desert stream. Journal of Fish Biology **9**:125–137.

Newsome, G. E., and G. Leduc. 1975. Seasonal changes of fat content in yellow perch (*Perca flavescens*) of two Laurentian lakes. Journal of the Fisheries Reserach Board of Canada **32**:2214–2221.

Oliver, J. D., G. F. Holeton, and K. E. Chua. 1979. Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperature. Transactions of the American Fisheries Society **108**: 130–136.

Park, T. 1948. Experimental studies in interspecific competition. I. Competition between populations of the flour beetles *Tribolium confusium* Duval and *Tribolium castaneum* Herbst. Ecological Monographs **18**:265–307.

Persson, L. 1983. Food consumption and the significance of detritus and algae to intraspecific competition in roach *Rutilus rutilus* in a shallow eutrophic lake. Oikos **41**:118–125.

Sale, P. F. 1969. A suggested mechanism for habitat selection by the juvenile manini, *Acanthurus triostegus sandvicensis* Streets. Behaviour **35**:27–44.

Sinclair, A. R. E. 1986. Testing multi-factor causes of population limitation: an illustration using snowshoe hares. Oikos **47**:360–364.

Slaney, P. A., and T. G. Northcote. 1974. Effects of prey abundance on density and territorial behavior of young rainbow trout (*Salmo gairdneri*) in laboratory stream channels. Journal of the Fisheries Reserach Board of Canada **31**:1201–1209.

Smith, G. 1981. Effects of habitat size on species richness and adult body sizes of desert fishes. Pages 125–171 *in* R. J. Naiman and D. L. Soltz, editors. Fishes of North American deserts. Wiley-Interscience, New York, New York, USA.

Smith, M. L. 1981. Late Cenozoic fishes in the warm deserts of North America: a reinterpretation of desert adaptations. Pages 11–38 *in* R. J. Naiman and D. L. Soltz, editors. Fishes of North American deserts. Wiley-Interscience, New York, New York, USA.

Snedecor, G. W. 1956. Statistical methods. Fifth edition. Iowa State University Press, Ames, Iowa, USA.

Soltz, D. L. 1974. Variation in life history and social organization of some populations of Nevada pupfish, *Cyprinodon nevadensis.* Dissertation. University of California, Los Angeles, California, USA.

Soltz, D. L., and R. J. Naiman. 1978. The natural history of native fishes in the Death Valley system. Natural History Museum of Los Angeles County, Science Series **30**:1–76.

Strandgaard, H. 1972. The roe deer (*Capreolus capreolus*) population at Kalo and the factors regulating its size. Danish Review of Game Biology **7**:1–205.

Swingle, H. S., and E. V. Smith. 1940. Experiments on the stocking of fish ponds. Transactions of the North American Wildlife Conference **5**:267–276.

Tamarin, R. H., editor. 1978*a*. Population regulation. Benchmark Papers in Ecology No. 7. Dowden, Hutchinson, and Ross, Stroudsburg, Pennsylvania, USA.

———. 1978*b*. Dispersal, population regulation, and K-selection in field mice. American Naturalist **112**:545–555.

Taylor, L. R., and R. A. J. Taylor. 1977. Aggregation, migration, and population mechanics. Nature **265**:415–421.

Van Valen, L. 1971. Group selection and the evolution of dispersal. Evolution **25**:591–598.

Walton, O. E., Jr., S. R. Reice, and R. W. Andrews. 1977. The effects of density, sediment particle size, and velocity on drift of *Acroneuria abnormis* (Plecoptera). Oikos **28**: 291–298.

Weatherley, A. H. 1972. Growth and ecology of fish populations. Academic Press, New York, New York, USA.

Wecker, S. C. 1964. Habitat selection. Scientific American **195**:3–10.

Whitham, T. G. 1980. The theory of habitat selection: examined and extended using *Pemphigus* aphids. American Naturalist **115**:449–466.

Wilzbach, M. A. 1985. Relative roles of food abundance and cover in determining the habitat distribution of stream-dwelling cutthroat trout (*Salmo clarki*). Canadian Journal of Fisheries and Aquatic Sciences **42**:1668–1672.

Woods, L. P., and P. F. Inger. 1957. The cave, spring and swamp fishes of the family *Amblyopsidae* of the central and eastern United States. American Midland Naturalist **58**: 232–256.

Young, D. K. 1980. Population dynamics of *Cyprinodon radiosus*: a preliminary report. Pages 51–54 *in* Proceedings of the Desert Fishes Council 10. Desert Fishes Council, Bishop, California, USA.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey, USA.