

APPLIED ASPECTS OF THE THERMAL BIOLOGY, ECOLOGY, AND LIFE HISTORY
OF THE BLUE TILAPIA, TILAPIA AUREA (PISCES: CICHLIDAE)

BY

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TABLE OF CONTENTS

	PAGE
ACKNOWLEDGMENTS	ii
ABSTRACT	vi
 CHAPTER	
I. INTRODUCTION	1
Background	1
Objectives	3
Nomenclature	10
II. COLD TOLERANCE OF BLUE TILAPIA: EFFECTS OF SALINITY, CHRONIC EXPOSURE TO ACUTELY-SUBLETHAL TEMPERATURES, AND RATE OF TEMPERATURE DECLINATION	12
Introduction	12
Methods	14
Effect of Salinity on Low Temperature Tolerance	15
Effect of Chronic Exposure to Acutely-Sublethal Temperatures	15
Effect of Temperature Declination Rate	16
Statistical Considerations	16
Results	17
Effect of Salinity on Low Temperature Tolerance	17
Effect of Chronic Exposure to Acutely-Sublethal Temperatures	23
Effect of Temperature Declination Rate	23
Discussion	27
III. PERIODICITY OF HABITATION OF A STENOTHERMAL SPRING RUN IN NORTH-CENTRAL FLORIDA BY BLUE TILAPIA	35
Introduction	35
Study Area	36
Methods	42
Results	42
Discussion	45

IV.	A LABORATORY COMPARISON OF GROWTH, SURVIVAL, AND FORAGING ABILITIES OF EARLY LIFE HISTORY STAGES OF BLUE TILAPIA AND LARGEMOUTH BASS	51
	Introduction	51
	Methods	53
	Survival and Growth Trials	54
	Relative Foraging Ability Trials	56
	Results	58
	Survival and Growth Trials	58
	Relative Foraging Ability Trials	72
	Discussion	91
	Advantages of Large Initial Size	95
	Feeding Strategies	98
	Evolutionary Considerations	98
	Potential Impacts	101
V.	THE TROPHIC ECOLOGY OF EARLY LIFE HISTORY STAGES OF BLUE TILAPIA IN LAKE GEORGE, FLORIDA: OVERLAP WITH SYMPATRIC SPECIES	103
	Introduction	103
	Methods	103
	Results	104
	Discussion	110
VI.	RELATIVE PREFERENCE OF LARGEMOUTH BASS FOR BLUE TILAPIA AND BLUEGILL AS FORAGE	113
	Introduction	113
	Methods	114
	Results	115
	Discussion	117
VII.	NEST-SITE SELECTION BY BLUE TILAPIA AND LARGEMOUTH BASS IN SILVER GLEN SPRINGS RUN: CIRCUMSTANTIAL EVIDENCE OF COMPETITIVE EXCLUSION	122
	Introduction	122
	Methods	124
	Results	125
	Discussion	135
VIII.	REPRODUCTIVE BIOLOGY OF BLUE TILAPIA IN SILVER GLEN SPRINGS RUN / LAKE GEORGE, FLORIDA	142
	Introduction	142
	Methods	142
	Results	143
	Discussion	165

IX.	AGE, GROWTH, AND MORPHOMETRIC RELATIONSHIPS OF BLUE TILAPIA IN SILVER GLEN SPRINGS RUN / LAKE GEORGE, FLORIDA	179
	Introduction	179
	Methods	179
	Results and Discussion	180
	Morphometric Relationships	180
	Validation of Aging Technique	182
	Age and Growth	187
X.	OVERVIEW AND CONCLUSIONS	198
	Objectives	198
	Results and Implications	199
	Recommendations for Further Research	203
	Thermal Biology	204
	Early Life History	207
	Predator-Prey Relationships	207
	Suppression of Largemouth Bass Spawning	208
	Reproductive Biology and Age-Growth Relationships	208
	Additional Comments and Recommendations	209
	Summary	212
	LITERATURE CITED	214
	BIOGRAPHICAL SKETCH	238

Abstract of Dissertation Presented to the Graduate School
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APPLIED ASPECTS OF THE THERMAL BIOLOGY, ECOLOGY, AND LIFE HISTORY
OF THE BLUE TILAPIA, TILAPIA AUREA (PISCES: CICHLIDAE)

By

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Laboratory and field research was conducted on issues relevant to the effective management of the blue tilapia, Tilapia aurea, an exotic cichlid established in U.S. waters.

Cold tolerance of blue tilapia was enhanced at isosmotic salinities. Time and temperature interacted to elicit cold death; a model was developed to quantify this interaction. Considerable heterogeneity in thermal tolerance among individual fish was observed.

Blue tilapia moved in and out of a stenothermal spring run in direct response to seasonal changes in surface-water temperatures.

Survival, growth, and relative foraging abilities of early life history stages of blue tilapia exceeded those of larvae of a representative native centrarchid in laboratory experiments. The

success of the blue tilapia in colonizing systems and rapidly achieving high abundances may be a result of this high relative proficiency in exploiting available trophic resources. In Lake George, young tilapia fed primarily on microcrustaceans and exhibited a high degree of trophic overlap with larval shad.

In laboratory electivity experiments, largemouth bass offered juvenile blue tilapia and bluegill of equal size exhibited a preference for tilapia as forage.

Nest-site selection by blue tilapia was characterized in a stenothermal spring run and compared to historical data on largemouth bass nesting in the run prior to the presence of tilapia. Blue tilapia preferentially selected nest sites in vegetated, shallow-water areas; microhabitat characteristics corresponded to those formerly used by largemouth bass. Because nesting by largemouth bass is behaviorally suppressed under crowded conditions, the presence of nesting tilapia may have been responsible for an observed decline in number of bass nests in the run.

Blue tilapia in the Silver Glen Springs Run / Lake George system spawned from March through June although nesting in the stenothermal run was initiated in late December. Gonadal recrudescence was correlated with increasing photoperiod. Fecundity estimates ranged as high as 8599.

Maximum estimated age of blue tilapia in this system was 4+ years. Growth was rapid; estimated total lengths at ages I, II, III, and IV were 280, 359, 397, and 423 mm, respectively. Scale rings of males were unreliable annuli.

CHAPTER I INTRODUCTION

Background

Introduction of a new species has long been one of the fishery biologist's most potent management techniques. Addition of an exotic game fish can generate renewed public interest in a fishery, enhance visibility of the responsible agency, and may even, on occasion, improve the quality of fishing. Exotics have also been introduced to control nuisance vegetation, insects, or fishes or to provide an improved forage base for native species. Others have become established accidentally, escaping from aquacultural facilities. Unfortunately, successful, popular, and ecologically 'benign' introductions are infrequent. Rather, the expected benefits typically fail to materialize, negative consequences arise, and reclamation proves to be impossible (Elton 1958; McDowall 1968).

Florida is particularly susceptible to the introduction of exotic fishes because of its subtropical climate, extensive environmental perturbation, and abundance of ornamental aquarium fish farms (Courtenay et al. 1974). Currently, 16 species of exotic fishes are believed to be established in Florida waters and an additional 6 species are listed as possibly established (Shafland et al. 1983).

The blue tilapia, Tilapia (= Sarotherodon = Oreochromis) aurea, is an exotic cichlid of paramount concern in Florida. The species naturally inhabits lowland lakes, ponds, rivers, and streams in Africa

from Senegal east to the Chad basin, the lower Nile, and Palestine (Trewavas 1965; Philippart and Ruwet 1982). An important food fish, it is propagated in aquacultural operations worldwide and supports extensive commercial fisheries (Fryer and Iles 1972; Lowe-McConnell 1982; Philippart and Ruwet 1982; Trewavas 1982a). Blue tilapia were first imported into Florida in August 1961, when the Florida Game and Fresh Water Fish Commission acquired 3000 juvenile blue tilapia from Auburn University to investigate the potential of the species as a sport fish and as a Hydrilla control agent (Crittenden 1962). The fish were stocked into naturally fertile, reclaimed phosphate pits at the Pleasant Grove Research Station near Tampa. The species proved to be neither an effective aquatic vegetation control agent nor a sport fish (Buntz and Manooch 1968), and the experimental stock at Pleasant Grove was exterminated. However, some of the fish were surreptitiously transferred to nearby open waters by persons unknown (Buntz and Manooch 1968). The descendants of this transplant apparently comprise Florida's current blue tilapia population. Early eradication attempts failed (Ware 1973) and the species (occasionally aided by fishermen) expanded its range through Florida's extensive canal and natural waterway systems. It is now the most widely distributed exotic fish species established in the state. Courtenay et al. (1984) recorded established populations in the following 18 counties in central and south Florida: Alachua, Brevard, Dade, DeSoto, Hardee, Hernando, Hillsborough, Lake, Manatee, Marion, Orange, Osceola, Palm Beach, Pinellas, Polk, Sarasota, Seminole, and Volusia. In addition, Foote (1977) reported the species from Charlotte, Glades, Highlands, and Pasco counties. I have collected the fish in the St. Johns River in Putnam County. Established

populations occur in two private ponds in Duval County (P. B. Southall, personal communication). In light of its wide distribution and inexpugnability the blue tilapia must be considered, at least for the foreseeable future, a permanent component of Florida's ichthyofauna and must be managed accordingly.

Objectives

Development of a sound management protocol for the blue tilapia requires a thorough understanding of the life history, environmental physiology, and ecology of the species. To this end, the Florida Game and Fresh Water Fish Commission has conducted extensive research on the species. However, considerable deficiencies remain in our knowledge of the biology of the fish. My goal, in conducting the research presented here, was to augment understanding of the ecology of the blue tilapia on issues relevant to the effective management of the species in U.S. waters.

When a species is introduced outside of its native range, it may be subjected to physical conditions dissimilar to those to which it is adapted. How the species is affected by these conditions, and how it reacts to them, may have important implications in its management. Because the blue tilapia is native to tropical and sub-tropical regions, and because it is known to suffer mortality during winter in temperate climates, I examined physiological and behavioral aspects of the thermal biology of the species.

Not only is an organism affected by its physical environment, but it must also, by necessity, interact with other biotic entities. Therefore, introduction of an exotic species will alter the structure

and function of an ecosystem. The form and magnitude of these alterations will influence how the introduced species is managed. Therefore, I examined selected interactions between blue tilapia and native organisms.

Finally, knowledge of the life history of a species in an exotic environment must be obtained to effectively manage it there. Therefore, I examined the most basic life history characteristics, reproductive biology and age and growth, of the blue tilapia in north-central Florida. The following objectives identify the specific topics I investigated.

1. To determine the effects of salinity, chronic exposure to acutely-sublethal temperatures, and temperature declination rate on the low temperature tolerance of blue tilapia.

A primary consideration in the management of an exotic species concerns where the species can, and cannot, be expected to survive outside of its native range. The sensitivity of blue tilapia to low temperatures is apparently the most important, if not the only, factor delimiting the eventual distribution of this species in North America (Courtenay et al. 1980; Shafland and Pestrak 1982). However, low temperature tolerance may be influenced by a number of factors. For example, cold tolerance of euryhaline fishes may be enhanced at isosmotic salinities. Additionally, extended exposures to acutely-sublethal temperatures may ultimately result in death (Yashouv 1960; Hauser 1977), and different rates of temperature declination may effect manifold lower lethal temperatures (Fry 1947). To better characterize

the low temperature tolerance of the blue tilapia, and thereby facilitate determination of its potential range in North America, I examined the effects of salinity, cooling rate, and extended exposure to acutely-sublethal temperatures on the cold tolerance of the species.

2. To determine the periodicity of habitation of a stenothermal spring run by blue tilapia.

Blue tilapia have been observed congregating in heated effluents (Buntz and Manooch 1968; Noble et al. 1975) and in stenothermal spring runs (Shafland and Pestrak 1982) during periods when surface-water temperatures are low. However, the phenomenon has never been systematically documented. Preliminary speculations indicated that these refugia may be critical to the survival of the species in north-central Florida (J. A. McCann, personal communication). If, during winter, blue tilapia actively select habitats where water temperatures are elevated, then locations of these thermal refugia would have to be considered when assessing habitat suitability on thermal criteria. To elucidate this phenomenon, I documented the periodicity of habitation of a stenothermal spring run by blue tilapia, testing whether abundances of blue tilapia in the run were inversely correlated with surface-water temperatures.

3. To compare the relative growth, survival, and foraging abilities of early life history stages of blue tilapia and largemouth bass (Micropterus salmoides) at equivalent food concentrations.

The range of the blue tilapia in Florida has expanded rapidly since introduction of the species in 1961; it is now the most extensively distributed exotic fish established in the state. Concurrently, populations of blue tilapia have demonstrated an ability to attain high densities and dominate fish assemblages, often within a few years of colonizing systems (Ware 1973; Germany and Noble 1977). Phytoplanktivory by adults permits such densities to persist, but the rapidity with which these abundances are achieved, often from very small founder populations, and by a species with relatively low fecundity, suggests that early life history survivorship in this species can be relatively high. Because acquisition of sufficient food is a major determinant of early life history survivorship in fishes, I hypothesized that the success of the blue tilapia in colonizing systems and rapidly achieving high abundances is a result of enhanced survivorship and growth during early life history stages conferred by a high relative proficiency in exploiting available trophic resources. I therefore compared the growth, survival, and foraging abilities of early life history stages of blue tilapia and a representative native centrarchid, the largemouth bass (Micropterus salmoides), over a range of food abundances in laboratory experiments. I predicted that if tilapia were more proficient at exploiting available forage, then at equivalent forage abundances survival and growth of tilapia would

exceed those of bass and that these differences could be traced to interspecific differences in foraging performance.

4. To characterize and compare food selection of early life history stages of blue tilapia and sympatric native species under natural conditions.

A potential impact of the blue tilapia, heretofore not considered, concerns exploitative competition between early life history stages of blue tilapia and native species for trophic resources. If, as hypothesized above, young blue tilapia are highly effective zooplanktivores, then their presence may increase demand upon the zooplanktonic resource of a system and thereby directly affect survival of larvae of native fishes. However, evaluation of this possibility has been hindered by the lack of information on food habits of young blue tilapia in natural systems. I therefore examined the food habits of young blue tilapia and sympatric species in Lake George, Florida, to a) characterize the trophic ecology of young blue tilapia under natural conditions, and b) determine the extent of interspecific overlap for food between young blue tilapia and native fishes.

5. To determine the relative preference of largemouth bass for blue tilapia and bluegill (Lepomis macrochirus) as forage.

Because blue tilapia have become a dominant component of fish assemblages in many systems and may be displacing native forage fishes, concern has developed regarding the effects of the species on predator-

prey interactions. The largemouth bass, a popular and economically valuable sport fish in Florida, is a top predator and could potentially be affected by changes in forage fish assemblages. Largemouth bass are known to consume blue tilapia (Swingle 1960; Lewis and Helms 1964; Chew 1974; Ludbrook 1974; Noble et al. 1975; Shafiland and Pestrak 1981; V. P. Williams, personal communication) but the relative suitability of blue tilapia as forage for bass has not been evaluated. I therefore conducted laboratory electivity experiments to determine the relative preference of largemouth bass for juvenile blue tilapia and bluegill, a native centrarchid often prominent in the diet of largemouth bass.

6. To characterize nest-site selection of blue tilapia and largemouth bass in a stenothermal spring run.

The possibility of competition between blue tilapia and native centrarchids for spawning areas has commanded a great deal of public attention (Harris 1978) and scientific speculation. Buntz and Manooch (1968) collected spawning blue tilapia, bluegill, and redear sunfish (Lepomis microlophus) sympatrically along the shoreline of Lake Parker, Florida, and therefore inferred that competition for spawning grounds occurred between these species. Noble et al. (1975) observed that year classes of largemouth bass apparently failed to recruit in Trinidad Lake, Texas, in the presence of high densities of blue tilapia, and postulated that tilapia suppressed reproduction by bass. Subsequent pond experiments (Noble et al. 1975; Shafiland and Pestrak 1983) established that high densities of blue tilapia can inhibit or suppress spawning by largemouth bass. Competition with centrarchids for

nesting habitat has therefore often been invoked as a major ecological impact of blue tilapia in U.S. waters (e.g. Ware 1973; Courtenay et al. 1974; Taylor et al. 1984). However, no studies have been conducted to investigate this interaction under field conditions. Aided by a pre-tilapia study of largemouth bass nesting (Horel 1951), I examined nest-site selection by blue tilapia and bass in a stenothermal spring run in north-central Florida. Spawning by largemouth bass is behaviorally suppressed in crowded environments (Chew 1972) in response to high rates of interspecific encounter (Barwick and Holcomb 1976; Smith 1976; Smith and Crumpton 1976). If microhabitat preferences of blue tilapia for nest sites correspond to those of bass in allopatry, then behavioral suppression of nesting by bass could be inferred.

7. To characterize the reproductive biology of blue tilapia in Silver Glen Springs / Lake George, Florida.
8. To determine age, growth, and morphometric relationships of blue tilapia in Silver Glen Springs / Lake George, Florida.

Knowledge of the life history characteristics of a species is essential for its effective management. Because the life history of the blue tilapia in open waters in the U.S. is poorly known, I described the reproductive biology and age and growth relationships of the Silver Glen Springs Run / Lake George blue tilapia population.

Each objective is addressed in a separate chapter. A final chapter integrates the various sections and suggests promising avenues for further research.

Nomenclature

Two taxonomic issues concerning the blue tilapia require commentary. The original stock imported to the United States by Auburn University was initially misidentified as T. nilotica, a closely related species. The error was perpetuated in the early North American literature concerning the species. Smith-Vaniz (1968) correctly identified the fish, but many subsequent publications continued to misidentify the species. Auburn University later acquired the real T. nilotica, adding to the confusion. Caution should be exercised when reading accounts regarding these species, especially those generated by the early studies. The second issue concerns the generic nomenclature within the tribe Tilapiini. Trewavas (1973) divided this complex into two genera defined by structural and behavioral features. The genus Tilapia (sensu stricto) was differentiated from Sarotherodon (including T. aurea (sensu lato)) structurally by the configuration of gill rakers and pharyngeal and mesethmoid bones. Behaviorally, Sarotherodon included the mouthbrooders, whereas substrate spawners were assigned to Tilapia. Any reference to Sarotherodon aureus in the literature should therefore be considered synonymous with T. aurea. Subsequently, Trewavas (1982b, 1983) further divided the mouthbrooders. In Sarotherodon brooding is paternal or biparental, in Oreochromis maternal. Blue tilapia fall into the latter category. Reference to

Oreochromis is already common in the current literature (e.g. Edwards et al. 1983; Gaigher and Krause 1983).

CHAPTER II
COLD TOLERANCE OF BLUE TILAPIA:
EFFECTS OF SALINITY, CHRONIC EXPOSURE TO ACUTELY-SUBLETHAL
TEMPERATURES, AND RATE OF TEMPERATURE DECLINATION

Introduction

The sensitivity of blue tilapia to low temperature is apparently the primary, and possibly only, factor delimiting the eventual distribution of this species in North America (Courtenay et al. 1980; Shafland and Pestrak 1982). While the blue tilapia seems to be the most cold-resistant of the mouthbrooding tilapias (Chervinski 1982), considerable variation exists among reports of cold tolerance for the species (Table 1). The lower lethal temperature (6-7°C) reported by Shafland and Pestrak (1982) is probably the most relevant of the cited temperatures pertaining to the blue tilapia in the southeastern United States. In a controlled laboratory study using fish captured in Florida, they decreased water temperatures by 1°C/day until death. Cold tolerances of fishes may be altered by a number of factors, however, including acclimation temperature, cooling rate, water quality, duration of exposure, and experimental animal size. For example, Chervinski and Lahav (1976) noted that blue tilapia maintained at 11°C suffered less mortality in dilute sea water (5 ppt NaCl) than in fresh water, and Allanson et al. (1971) observed that T. mossambica in fresh water succumbed to secondary chill coma at 11°C, whereas fish exposed to the same temperature in dilute sea water were unaffected. These findings suggest that euryhaline thermophilic fishes may be more

Table 1. Summary of reported effects of low temperature on blue tilapia.

Temperature (C)	Effect	Conditions and source
13-14	Growth terminated	Ponds, laboratory (Yashouy 1960)
10	Ceased movement	"
8	Entered cold stupor	"
<8	Sluggish gill ventilation	"
6-7	Loss of equilibrium	"
5	Death	"
8.9	Death	Ponds, fish <152 mm TL (McBay 1961)
5.0-8.9	No mortality	Ponds, fish >152 mm TL, exposure of less than 3 days (McBay 1961)
< 12.8	Death	Ponds, fish 229-279 mm TL, exposure of 32 days (McBay 1961)
11.7	No mortality	Florida phosphate pits (Crittenden 1965)
8.0-8.5	Death	Laboratory (Sarig 1969)
9	Began to die	Laboratory, acclimated to 18 C (Chervinski and Lahav 1976)
11	Began to die	Laboratory, acclimated to 28 C (Chervinski and Lahav 1976)
< 10	Some mortality	Trinidad Lake, TX; short exposures (Germany and Noble 1977)
6-9	Death	Trinidad Lake, TX; total mortality of population after exposure of about one month (Germany and Noble 1977)
5.6	Median lower lethal temperature	Laboratory, 0.8 C/hour decrease (Lee 1979)
6	No mortality	Ponds, exposed for only a few hours daily (Chervinski and Stickney 1981)
13-16	Decrease in feeding rate	Laboratory, 1 C/day decrease (Shafland and Pestrak 1982)
10-12	Cessation of feeding	"
7-8	Loss of equilibrium	"
6-7	Death	"

tolerant of low temperatures at isosmotic salinities than in hyper- or hyposmotic media. Additionally, extended exposures to acutely-sublethal temperatures may ultimately result in death (Yashouv 1960; Hauser 1977), and different rates of temperature declination may effect manifold lower lethal temperatures (Fry 1947). These factors are probably responsible for at least some of the variability in lower lethal temperatures reported for blue tilapia. To better characterize the low temperature tolerance of the blue tilapia, and thereby facilitate determination of its potential range, I examined the effects of salinity, cooling rate, and extended exposure to acutely-sublethal temperatures on the cold tolerance of the species.

Methods

Experiments were conducted in a 500-liter fiberglass tank equipped with a thermostatically-controlled chilling unit and viewing window. The chilling unit maintained water temperatures within 0.5 C of target but temperatures within the plexiglass compartments fluctuated only ± 0.2 C. Dechlorinated tap water (pH 8.0-8.2) was used.

Experimental fish were selected from stock raised and maintained in the laboratory in fresh water at 24-29 C. Fish were fed a commercial pelleted feed once daily to satiation. Juvenile fish were used, as juvenile blue tilapia are more resistant to cold temperatures than adults (Shafland and Pestrak 1982). Fish were segregated individually in plexiglass compartments within the tank. Twelve fish were used in each trial.

Effect of Salinity on Low Temperature Tolerance

Fish from a single brood were used in this series of experiments. Fish were acclimated to 20 C for at least one week prior to the initiation of each trial. They were concurrently acclimated to experimental salinities, at the rate of 1 ppt NaCl/day, by the addition of synthetic saltwater aquarium salts. Trials were conducted at 0, 5, 11.6, 20, and 35 ppt NaCl with corresponding conductivities of 250, 9300, 19800, 32000, and 53000 $\mu\text{mhos/cm}$ at 25 C, respectively. Following acclimation, temperature in the experimental tank was decreased by 1 C/day. Temperatures associated with cessation of feeding, loss of equilibrium, and death were recorded for each fish. Because only a single tank and a limited quantity of salts were available, the trials were run serially, over a period of 5 months, starting at 0 ppt and ending at 35 ppt NaCl. An additional trial at 0 ppt was then conducted to detect any shift in the thermal tolerance of the fish over the course of the trials. A total of six trials (two at 0 ppt) was therefore performed.

Effect of Chronic Exposure to Acutely-Sublethal Temperatures

Six trials were conducted to determine survival times of blue tilapia subjected to acutely-sublethal temperatures (above 6 C) in fresh water. In each trial, fish were initially acclimated to 20 C for one week. Temperature in the experimental tank was then decreased by 1 C/day until a predetermined final temperature was reached. Temperature was then held constant until all fish died. If no mortalities occurred within 60 days, the trial was terminated. The number of days until loss of equilibrium and until death, at each of the final temperatures, were

recorded for each fish. Final temperatures for the six trials were 7, 8, 9, 10, 11, and 12 C. Fish used in these trials were randomly selected from a stock consisting of two broods of distinct parentage.

Effect of Temperature Declination Rate

In the salinity series, experimental temperatures were decreased by 1 C/day. To determine the effect of alternative temperature declination rates on the cold tolerance of blue tilapia, I conducted two additional trials. In one, experimental temperatures were decreased by 1 C every third day (1 C/3 days); in the other, temperatures were decreased by 1 C every 4 hours (6 C/day). These temperature regimens were designated the retarded and accelerated rates, respectively. Prior to initiation of temperature declination, fish were acclimated to 20 C for one week. Both trials were conducted in fresh water. Temperatures associated with loss of equilibrium and death were recorded for each fish. The two trials in fresh water (0 ppt) from the salinity series (1 C/day) were integrated into the analysis of this component.

Statistical Considerations

Presence of treatment differences was evaluated using the Kruskal-Wallis distribution-free one-way layout test (Hollander and Wolfe 1973) for the salinity and declination-rate experiments. Jonckheere's distribution-free test for ordered alternatives (Hollander and Wolfe 1973) was employed for the chronic-exposure trials. To detect which particular treatments differed from one another, a distribution-free multiple comparisons procedure based on Kruskal-Wallis rank sums was implemented (Hollander and Wolfe 1973).

Results

Effect of Salinity on Low Temperature Tolerance

The temperatures at which fish stopped feeding, lost equilibrium, and died in the initial and final trials at 0 ppt NaCl were not significantly different (Tables 2-4), inferring that confounding due to the serial nature of the experimental design was absent. However, the median temperature at loss of equilibrium shifted from 7 C in the initial trial to 6 C in the final trial, and the range of temperatures at death was greater in the latter assay. Mean weight and range of weight of fish were greater in the final than in the initial trial, but temperature at death was not correlated with weight ($P = 0.3312$, $r = 0.307$; Spearman rank correlation; Snedecor and Cochran 1980).

Salinity had a significant effect on the temperatures at which blue tilapia ceased feeding, lost equilibrium, and died (all $P < 0.005$). The magnitude of the effect was slight, however (Fig. 1). Temperatures at termination of feeding ranged widely within treatments and overlapped broadly among the various salinities (Table 2). Fish lost equilibrium at 6-7 C at 0, 5, and 11.6 ppt, but succumbed at higher temperatures at the higher salinities (Table 3). Fish maintained at intermediate salinities (5 and 11.6 ppt) all died at 5 C (Table 4). The majority of the fish in freshwater died at 6 C; 3 died at 5 C and one at 7 C in the final trial. Death occurred at 6-7 C and 9-10 C at 20 and 35 ppt, respectively (Table 4).

I expected blue tilapia to be most cold tolerant at the isosmotic salinity (11.6 ppt, Beamish 1970) with resistance decreasing as salinity deviated from isosmosity. Correlation of temperature at death versus deviation of salinity from 11.6 ppt proved highly significant

Table 2. Temperatures at which blue tilapia terminated feeding at salinities of 0, 5, 11.6, 20, and 35 ppt NaCl. Subscripts for the 0 ppt assays denote the initial (i) and final (f) trials. Bars below average ranks underline values not significantly different ($\alpha=0.05$; multiple comparisons based on Kruskal-Wallis rank sums).

	Salinity (ppt NaCl)					
	5	0 _f	0 _i	20	11.6	35
Median (C)	13.5	14	14	15	15	17
Range (C)	13-17	12-17	13-17	13-16	13-20	13-20
Average rank	26.96	29.62	30.42	34.92	39.46	57.62

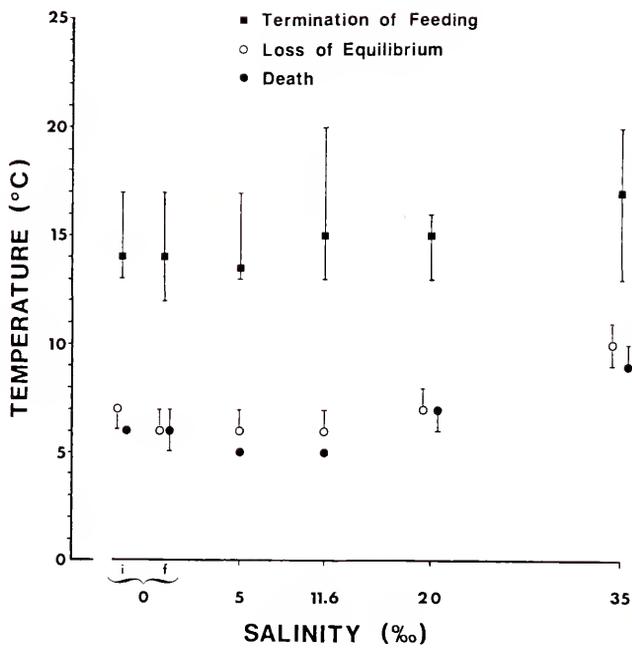
Table 3. Temperatures at which blue tilapia lost equilibrium at salinities of 0, 5, 11.6, 20, and 35 ppt NaCl. Subscripts for the 0 ppt assays denote the initial (i) and final (f) trials. Bars below average ranks underline values not significantly different ($\alpha=0.05$; multiple comparisons based on Kruskal-Wallis rank sums).

	Salinity (ppt NaCl)					
	5	0 _f	11.6	0 _i	20	35
Median (C)	6	6	6	7	7	10
Range (C)	6-7	6-7	6-7	6-7	7-8	9-11
Average rank	21.67	21.67	23.96	37.71	47.50	66.50

Table 4. Lower lethal temperatures of blue tilapia at salinities of 0, 5, 11.6, 20, and 35 ppt NaCl. Subscripts for the 0 ppt assays denote the initial (i) and final (f) trials. Bars below average ranks underline values not significantly different ($\alpha=0.05$; multiple comparisons based on Kruskal-Wallis rank sums).

	Salinity (ppt NaCl)					
	5	11.6	0 _f	0 _i	20	35
Median (C)	5	5	6	6	7	9
Range (C)	5-5	5-5	5-7	6-6	6-7	9-10
Average rank	14.00	14.00	33.75	38.50	52.25	66.50

Fig. 1. Median temperatures at which blue tilapia stopped feeding, lost equilibrium, and died when subjected to a 1 C per day decrease in temperature at salinities ranging from 0 to 35 ppt NaCl. Vertical bars denote ranges. Initial and final assays at 0 ppt NaCl are designated i and f, respectively.



($P < 0.0001$, $r = 0.779$; Spearman rank correlation), supporting this hypothesis.

Effect of Chronic Exposure to Acutely-Sublethal Temperatures

Blue tilapia survived exposure to 12 C for 60 days (at which time the trial was terminated), but eventually succumbed to cold death at all temperatures below 12 C. The ultimate incipient lower lethal temperature (the lowest temperature that can be survived indefinitely, Fry 1947) for blue tilapia is therefore about 12 C. Highly significant differences ($P < 0.0002$) in durations to loss of equilibrium and death were present between treatments at final temperatures below 12 C. Generally, lower temperatures resulted in decreased survival times (Fig. 2). Median survival times were 2, 8, 6, 14, and 31 days at 7, 8, 9, 10, and 11 C, respectively (Table 5). Fish generally lost equilibrium one day prior to expiring. The longer survival times of fish tested at 8 C, compared to 9 C, may have been due simply to experimental error; sample sizes were small and the difference was not significant (Table 5). Conversely, the difference may have resulted from genetic variability in thermal tolerance, as fish in these trials were from two different broods. Considerable heterogeneity in survival times was also apparent within the trials at 10 and 11 C (Fig. 2), indicative of inherent variability in thermal tolerances among test fish.

Effect of Temperature Declination Rate

The rate of temperature declination had a moderately significant effect ($0.010 < P < 0.025$) on the temperature at which experimental

Fig. 2. Survival times of blue tilapia in fresh water subjected to 7, 8, 9, 10, or 11 C following a 1 C/day decrease in temperature. Letters denote frequencies of coincident observations; a = 1 observation, b = 2 observations, etc.

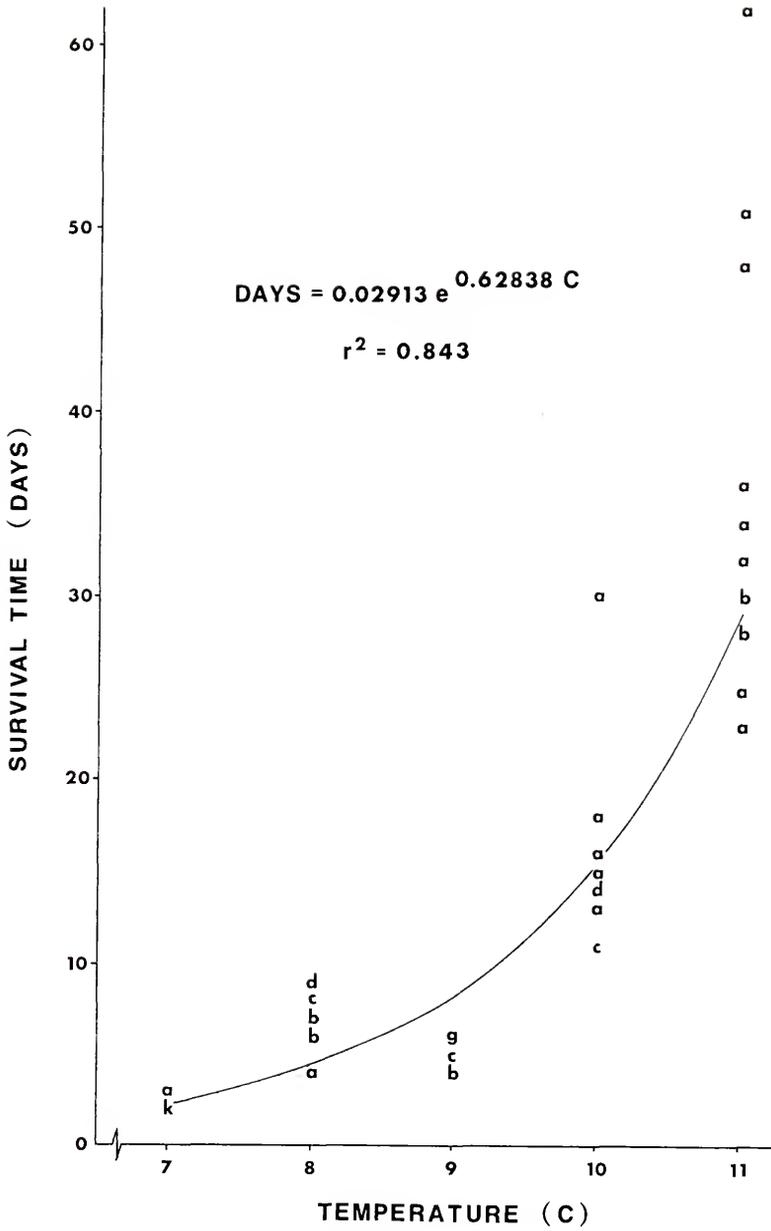


Table 5. Days to loss of equilibrium and death for blue tilapia subjected to chronic exposures to acutely-sublethal temperatures. Bars below average ranks underline values not significantly different ($\alpha = 0.05$; multiple comparisons based on Kruskal-Wallis rank sums).

	Temperature (C)				
	7	9	8	10	11
	Loss of equilibrium				
Median (days)	1	4	7	13.5	31
Range (days)	1-2	3-5	4-8	10-29	22-61
Average rank	<u>6.5</u>	<u>19.0</u>	<u>30.0</u>	<u>42.9</u>	54.1
	Death				
Median (days)	2	6	8	14	31
Range (days)	2-3	4-6	4-9	11-30	23-62
Average rank	<u>6.5</u>	<u>20.0</u>	<u>29.0</u>	<u>42.9</u>	54.1

fish lost equilibrium (Table 6). The directionality of the effect was unclear, however, as the average ranks of the accelerated (1 C/4 h) and retarded (1 C/3 days) rates fell between those of the two assays at 1 C/day. All fish, except one, lost equilibrium at 6 or 7 C regardless of declination rate. The lone exception lost equilibrium at 5 C when subjected to the accelerated rate.

The effect of temperature declination rate on temperature at death was much clearer. Highly significant differences ($P < 0.005$) were noted among treatments. All fish subjected to the accelerated rate died at 5 C whereas the median of those cooled at the retarded rate was 7 C (range 6-7 C) (Table 7). In the 1 C/day assays, median temperature at death was 6 C (range 5-7 C). The temperature at death for fish in the accelerated-rate trial was significantly lower than in the other assays (Table 7).

Discussion

Varying degrees of salinity, particularly at or near isosmosity, expand thermal tolerances in a number of euryhaline species (Loeb and Wasteneys 1912; Gibson 1954; Arai et al. 1963; Craigie 1963; Alabaster 1967; Strawn and Dunn 1967; Garside and Jordan 1968; Allanson and Cross 1970; Allanson et al. 1971; Garside and Chin-Yuen-Kee 1972; Jordan and Garside 1972). Upper lethal temperatures can be elevated as much as 6 C in isosmotic media (Garside and Jordan 1968), but the magnitude of the effect on lower lethal temperatures was heretofore unknown. My data indicate that salinity does have a significant effect on the low thermal tolerance of blue tilapia. Fish maintained in isosmotic media generally succumbed to cold death at lower temperatures than tilapia in

Table 6. Temperatures at which blue tilapia lost equilibrium when subjected to temperature declination rates of 1 C/4 h, 1 C/day, and 1 C/3 days. Two trials were conducted at the intermediate rate. Bars below average ranks underline values not significantly different ($\alpha=0.10$; multiple comparisons based on Kruskal-Wallis rank sums).

	Rate of temperature declination			
	1 C/day (final)	1 C/4 h	1 C/3 days	1 C/day (initial)
Median (C)	6	6.5	7	7
Range (C)	6-7	5-7	6-7	6-7
Average rank	17.83	21.00	27.62	31.54

Table 7. Lower lethal temperatures of blue tilapia subjected to temperature declination rates of 1 C/4 h, 1 C/day, and 1 C/3 days. Two trials were conducted at the intermediate rate. Bars below average ranks underline values not significantly different ($\alpha=0.05$; multiple comparisons based on Kruskal-Wallis rank sums).

	Rate of temperature declination			
	1 C/4 h	1 C/day (final)	1 C/day (initial)	1 C/3 days
Median (C)	5	6	6	7
Range (C)	5-5	5-7	6-6	6-7
Average rank	<u>8.00</u>	<u>24.38</u>	28.00	37.62

water of higher or lower salinities, when subjected to a 1 C/day decrease in temperature. Osmoregulatory failure is the direct mechanism by which temperature-induced mortality is manifested (Houston 1962; Heinicke and Houston 1965; Potts et al. 1967; Solomon and Allanson 1968; Umminger 1969; Allanson and Cross 1970; Allanson et al. 1971; Mackay 1971; Stanley and Colby 1971; Umminger 1971). At isosmotic salinities, osmoregulatory stress is minimized, and temperature-induced osmoregulatory failure is averted at temperatures that would elicit death in hyposmotic or hyperosmotic media. The potential range of blue tilapia in North America can therefore be expected to extend farthest north along the coast, analogous to the restriction of T. mossambica to estuaries at the southern extreme of its distribution in South Africa (Allanson and Noble 1964). The difference in thermal tolerance between fish in fresh water and isosmotic media was small (about 1 C); thus additional habitable range may also be relatively small.

To predict where blue tilapia will survive, on the basis of thermal requirements, necessitates an integrated analysis of the thermal tolerance of the fish. Generally, evaluations of thermal tolerances of fishes have been accomplished using the critical thermal maximum/minimum (CTM) or upper/lower incipient lethal temperature (ILT) methods. Fry (1947, 1967, 1971), Hutchison (1976), and Becker and Genoway (1979) describe the methods in detail and review their relative merits. Neither method is appropriate to determine if tilapia can survive in a given system, as both employ environmentally-unrealistic thermal schedules and discount the ability of fish to thermally acclimate in waters undergoing slow cooling. Decreasing water temperatures by 1 C/day was a convenient technique for evaluating the

effect of salinity on the low thermal tolerance of blue tilapia, and unlike the CTM and ILT methods, the slow cooling rate (SCR) method afforded test organisms opportunity to continuously acclimate to temperatures decreasing at an environmentally relevant rate. However, the actual temperatures at which the fish died are of limited use for determining the suitability of a given body of water for overwintering tilapia, unless the sequence of temperature declination in the system closely follows the regimen enforced in the laboratory. Different rates of temperature declination will result in mortalities at different final temperatures. At declination rates commonly encountered in large natural systems (0.3 to 1.0 C/day), however, this problem is minimized; I did not detect significant differences in temperatures at death for fish subjected to these rates. A more substantial deficiency of the SCR method is demonstrated by the observation that blue tilapia will succumb to cold death at temperatures appreciably above those at which they die in an SCR trial, if subjected to such temperatures for an extended period. For example, in SCR trials in fresh water, the median temperature at death was 6 C. But when temperature declination was terminated at 10 C, tilapia died nevertheless, albeit in about two weeks. Cold death in fishes is not merely a function of temperature and rate of temperature change, but also of time (Fry 1947; Brett 1956). Defining a thermal limit in terms of temperature alone is therefore errant; time must also be considered. In this respect, the ultimate incipient lower lethal temperature may be a thermal milestone of some consequence. By definition, it incorporates both temperature and time. For blue tilapia in fresh water, this temperature is about 12 C. Because cold death can occur at any temperature below 12 C, a safe

assumption might be that a blue tilapia occupying water cooler than 12 C is experiencing some degree of thermal stress. Estimating when such stress will culminate in death may prove useful in evaluating the potential of a given body of water to allow overwintering of tilapia.

I suggest here a methodology incorporating time and temperature that evaluates the thermal stress accrued by an organism when subjected to a given thermal schedule. The chronic-exposure technique (essentially a hybrid of the SCR and ILT methods) provides the necessary data. The cooling rate used in the chronic-exposure trials is environmentally realistic (unlike the CTM) and allows fish to continuously acclimate to decreasing temperatures (unlike the ILT). Because cooling is terminated at a given level in each trial (unlike the SCR), the impact of the final temperature on thermal tolerance can be evaluated. The critical assumption of the methodology is that the rate of dying at a given constant temperature below 12 C is linear with respect to time, i.e. that each day at a certain temperature below 12 C contributes equally to death. Acceptance of this assumption allows calculation of 'daily coefficients of death' for temperatures below 12 C as follows. From the formula given in Figure 2 the predicted time to death for tilapia held at 11 C is 29.3 days. The reciprocal of 29.3, 0.034, is the daily coefficient of death at 11 C. In essence, every day that a tilapia is subjected to 11 C, it draws 3.4 % closer to death (if the preceding assumption is valid). The predicted time to death at 10 C was 15.6 days. Because these fish had been exposed to 11 C for one day, the daily coefficient of death at 10 C is $(1 - 0.034)/15.6 = 0.062$. Similarly, the coefficients for 9, 8, 7, and 6 C are 0.108, 0.179, 0.260, and 0.357, respectively.

To evaluate the impact of a given temperature schedule on blue tilapia survival, multiply the number of days at each temperature below 12 C by the appropriate coefficient of death. Only sets of consecutive days below 12 C should be considered. Mortality of a significant portion of a population of blue tilapia can be expected if the summation of these products exceeds unity. With an adequate data base, coefficients could be calculated for evaluating total mortality using survival times of highly resistant individuals. Because of the nature of the experiments from which the coefficients given here were derived, application of the procedure (in the form presented above) is restricted to environments where daily temperature shifts are less than 1 C.

Temperature schedules for large bodies of water may be in accord with this constraint, but in small systems temperatures may change rapidly and fluctuate widely. Also, fish used in these trials were acclimated to 20 C, then subjected to a 1 C per day temperature declination; lower acclimation temperatures and slower rates of temperature decrease may enhance thermal tolerance in this species. Furthermore, the formula used to derive the coefficients may be unreliable, as considerable variability was apparent in the data. Clearly, the methodology requires further refinement and verification, but the general approach of incorporating both time and temperature appears promising, certainly more so than approaches based on temperature alone.

While thermal tolerance undoubtedly affects the potential geographic distribution of a species, evaluating the suitability of a habitat on the basis of temperature requirements alone may be unsound.

Feeding, resistance to disease, successful reproduction, and sufficient activity to permit existence in the face of competition or predation are all necessary for the continued maintenance of a population. Inability to maintain any one of these activities at moderately extreme temperatures may be as decisive to continued survival as more extreme temperatures are to immediate life (Brett 1956; Kinne 1963, 1970). The tolerances reported here are therefore useful only for designating those habitats that blue tilapia cannot invade, rather than those which the species can successfully colonize.

As the range of blue tilapia extends into north Florida, the opportunity for selection for enhanced cold tolerance may arise, relegating the measures of thermal tolerance reported here obsolete. Considerable heterogeneity in thermal tolerance was apparent among fish sacrificed in the chronic-exposure experiments. Selection for cold tolerance among wild fish is therefore likely.

CHAPTER III
PERIODICITY OF HABITATION OF A STENOTHERMAL SPRING RUN
IN NORTH-CENTRAL FLORIDA BY BLUE TILAPIA

Introduction

Blue tilapia have been observed congregating in heated effluents (Buntz and Manooch 1968; Noble et al. 1975) and stenothermal spring runs (Shafland and Pestrak 1982) during periods when surface-water temperatures are low. McBay (1961) observed that during winter, blue tilapia in ponds occupied shallow water by day and retreated to deeper areas at night in response to diurnal variation in temperature maxima. Temperature is apparently an important directive factor regulating the movements of this species. Fishes are attracted to areas where water temperatures are at, or closest to, their preferred temperatures (Dendy 1945; Ferguson 1958; Gibbons and Bennett 1971; Beitinger 1977; Richards and Ibara 1978; Winkler 1979; Brandt 1980); preferred temperatures closely approximate metabolically-optimal temperatures (Crawshaw 1977). The preferred temperature of blue tilapia is 30 C (Beamish 1970). Water temperatures of spring runs in north-central Florida generally fall within the range 21-24 C (Rosenau et al. 1977), whereas surface-water temperatures can be much lower during winter. Habitation of stenothermal spring runs during winter may therefore afford blue tilapia physiological benefits, as well as offer thermal refugium from lethal temperatures. Accordingly, abundances of blue tilapia in these springs may be expected to be inversely correlated with surface-water

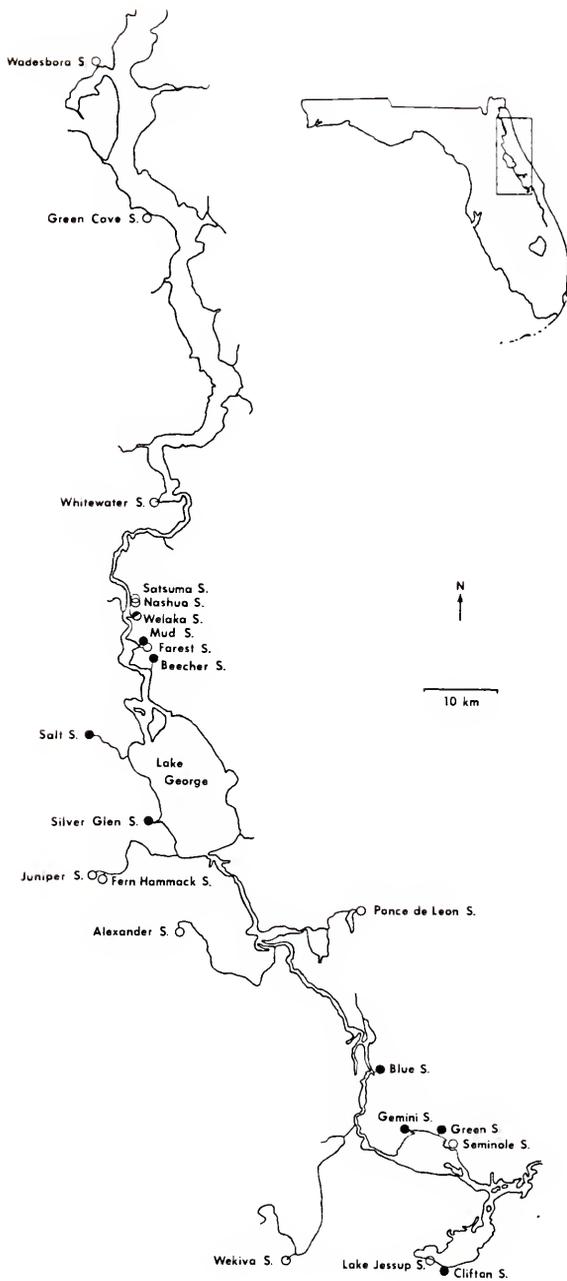
temperatures. If, during winter, blue tilapia actively select habitats where water temperatures are elevated, then locations of these thermal refugia would have to be considered when assessing habitat suitability on thermal criteria.

The general consensus among people residing near springs in north-central Florida, however, is that maximum abundances of blue tilapia in the spring runs are attained not in January (when surface-water temperatures are usually at their annual minimum in Florida; Bradley 1974), but in late February and March, when surface waters have already warmed appreciably. My preliminary observations during 1980-81 led me to concur. In their native range, tilapia migrate to clear waters to spawn (Lowe-McConnell 1953, 1959). Blue tilapia may congregate in the spring runs because of the suitability of these habitats for nesting, not because of thermal considerations. Therefore, it was appropriate to test whether abundances of blue tilapia in stenothermal spring runs were inversely correlated with surface-water temperatures.

Study Area

I conducted a limited survey of 22 stenothermal spring runs in the central and lower sections of the St. Johns River drainage during the winter of 1980-81 to identify suitable study sites. The water clarity of these habitats allowed direct observation of blue tilapia and their distinctive spawning nests from shore, boat, or by snorkeling. Blue tilapia were observed in springs from Lake Jessup north to Welaka (Fig. 3). Major concentrations were found in Blue Spring, Silver Glen Springs, and Mud Spring. These medium to high discharge springs have

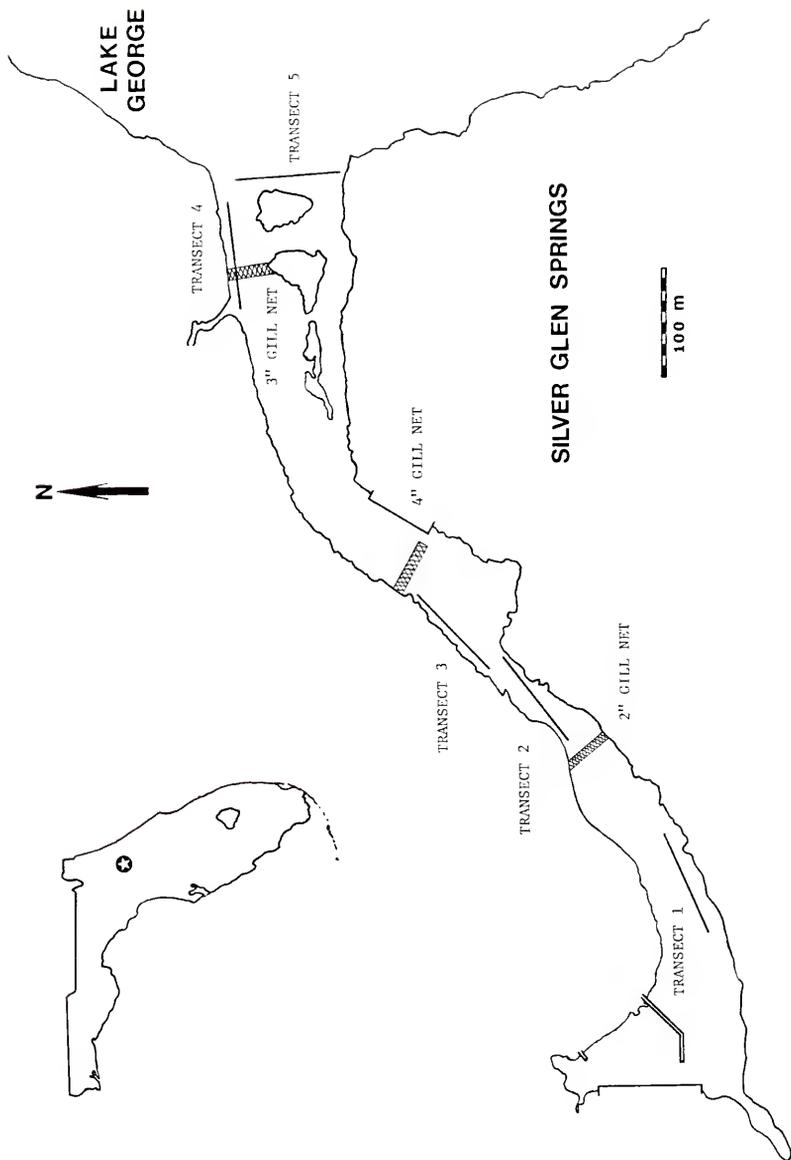
Fig. 3. Locations of stenothermal springs in central and lower sections of the St. Johns River drainage surveyed during the 1980-81 winter. Presence and absence of blue tilapia are denoted by solid and open circles, respectively.



short runs (< 1.0 km) emptying into the river. Other sizable springs in the drainage (e.g. Wekiva, Juniper, Alexander, Ponce de Leon) connected to the river with long runs (> 5 km) attracted no blue tilapia. Springs with short runs but low flow (e.g. Satsuma, Seminole, Forest) also did not attract tilapia. Small numbers of blue tilapia were observed in Clifton Springs, Salt Springs, Gemini Springs, Green Springs, and Beecher Springs. Additionally, a single blue tilapia nest was found in Welaka Spring, but no specimens were observed at this site. I selected Silver Glen Springs for this study because of its large blue tilapia population, easy access, and available support facilities.

Silver Glen Springs is a first magnitude spring in Marion County, north-central Florida (Fig. 4). Discharge averages 3170 liters per second (Rosenau et al. 1977). Water from the spring flows eastward about 1 km through semi-tropical forest to the western shore of Lake George, a widening of the St. Johns River. Silver Glen Springs Run (SGSR) ranges in width from 40 to 130 m with a maximum depth of about 3 m. Substrate is comprised of sand, shell, and muck. Vallisneria americana and Hydrilla verticillata are the predominant submerged macrophytes. Water temperatures at the spring vent ranged from 22.8 to 24.0 C during this study. Because water passage down the run is rapid, temperatures generally do not change appreciably along the course of the run; during exceptionally cool or warm weather, however, a shift of up to 2 C was observed. Depending upon wind direction and force, spring effluent mixes with lake waters at the mouth of the run or extends in a plume up to several hundred meters out into Lake George. During winter, the plume usually spreads out across the surface over the cooler lake water. In summer, run effluent forms a cooler underlying wedge. Blue

Fig. 4. Locations of transects and gill net stations in Silver Glen Springs Run.



tilapia were first observed in SGSR in 1976 or 1977, and have steadily increased in abundance thereafter (J. Morgan, personal communication).

Methods

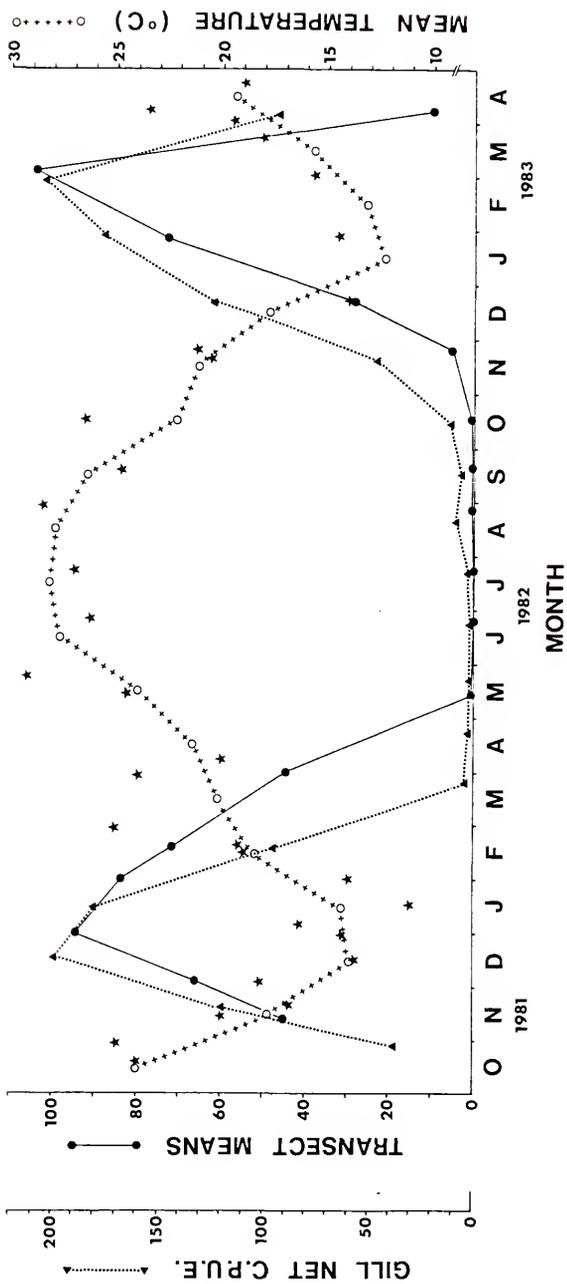
Relative abundances of blue tilapia in SGSR were estimated from October 1981 through April 1983 by gill net catch-per-unit-effort (CPUE) and enumeration along line transects. Sampling was conducted approximately monthly. The two methods were generally employed within a few days of each other. Blue tilapia were counted by snorkeling along five standardized 100-m by 4-m transects (Fig. 4) marked by anchored nylon ropes. I swam each transect three times on each sampling date. Three gill nets (2, 3, and 4 inch bar mesh; 51, 76, and 102 mm, respectively) were set overnight at standardized stations, perpendicular to the current (Fig. 4). The three nets, fished for one night, constituted one unit of effort. Gill nets were pulled at midnight and again at dawn.

Mean monthly air temperatures were used to estimate mean monthly water temperatures (McCombie 1959; Anderson 1975). Water temperatures in Lake George were recorded on each sampling date.

Results

Visual line transects and gill net CPUE were both effective for determining relative seasonal abundances of blue tilapia in SGSR. Estimates derived by the two methods were highly correlated ($P < 0.0001$, $r = 0.904$; Spearman rank correlation) and showed close agreement in discerning seasonal trends in relative abundances (Fig. 5).

Fig. 5. Relative abundances of blue tilapia in Silver Glen Springs Run and water temperatures, October 1981 to April 1983. Stars denote date-specific water temperatures in Lake George.



Relative abundances of blue tilapia in SGSR followed a seasonal pattern (Fig. 5). In late 1981, blue tilapia abundances increased during October and November and peaked in December. The number of fish present declined slightly in January 1982 and was considerably lower in February. Abundances continued to decrease in March and April, and by May very few blue tilapia remained in the run. Tilapia remained scarce in SGSR throughout the summer of 1982. Abundances accrued again during the fall and winter of 1982-83, but peaked later than in 1981-82 correspondent with the difference in temperature trends between the two winters (Fig. 5).

Relative abundances of blue tilapia in SGSR were inversely correlated with surface-water temperatures (Fig. 5). Correlations between relative abundances and mean monthly temperatures were highly significant (transects: $P < 0.0001$, $r = -0.933$; gill net CPUE: $P < 0.0001$, $r = -0.893$), as were correlations between relative abundances and date-specific Lake George water temperatures (transects: $P = 0.0006$, $r = -0.799$; gill net CPUE: $P < 0.0001$, $r = -0.917$).

Discussion

Temperature is a major determinant of fish distributions and movements (Reynolds 1977; Giattina and Garton 1982). Because most fishes are unable to thermoregulate physiologically, they do so behaviorally instead, changing locations to inhabit waters where temperatures are most conducive to optimizing metabolic processes. Tilapia are capable of detecting fine thermal gradients (Kutty and Sukumaran 1975), and accordingly, moved in and out of SGSR to occupy waters where temperatures were at or closest to their preferred

temperature. The temperature differential between Lake George and SGSR was apparently the proximate directive factor governing the habitation of the run by blue tilapia. Tilapia entered the run in large numbers when water temperatures in Lake George fell below those in the run, and emigrated when Lake George became warmer than the run. Delayed immigration in the winter of 1982-83, coincident with delayed onset of cold weather, stressed the significance of temperature in regulating movements of the fish. The apparent increase in abundance of tilapia in the run during early spring, when emigration was already in progress, was simply an artifact of the conspicuousness of male tilapia and their nests in shallow areas of the run.

The few tilapia found in SGSR during summer months may have remained in the run because of the suitability of the site as a nesting area, despite the physiological disadvantages incurred. Non-thermal stimuli (e.g. social interactions, predation, feeding, competition, habitat) can subordinate the influence of temperature considerably (Norris 1963; Javaid and Anderson 1967; Brett 1971; Neill and Magnuson 1974; Kelso 1976; Stuntz and Magnuson 1976; Reynolds 1977; Magnuson and Beitinger 1978; Ross and Winter 1981).

Water temperatures in Lake George did not decline to levels immediately injurious to blue tilapia during this study, but were low enough to cause cessation of feeding and some thermal stress (see Chapter II). The lowest water temperature recorded in Lake George was 11.0 C. For significant cold-induced mortality to result, maintenance of this temperature for at least 3 weeks would be necessary. However, 11 days earlier, water temperature in Lake George was 16.25 C, and 13 days later it was 14.0 C. No evidence of cold-induced mortality was

apparent during this period. Habitation of stenothermal spring runs does not appear to be critical to the survival of populations of blue tilapia in large bodies of water like Lake George in north-central Florida. However, seasonal occupation of SGSR, as opposed to continuous residency in Lake George, would nevertheless appear beneficial. Fish inhabiting SGSR during winter were able to continue to feed (and grow). Gonadal recrudescence was probably accelerated for blue tilapia in the run and habitation of the run extended the reproductive season of blue tilapia, as nesting activity was observed there several months before it commenced in Lake George (see Chapter VII). Also, fish migrating to the run were probably less likely to succumb to disease or predation than were tilapia remaining in Lake George.

The thermophilic tendencies in habitat selection of blue tilapia could result in aversion of cold death during exceptionally cold winters or at higher latitudes. Therefore, locations of potential thermal refugia must be considered when assessing habitat suitability on thermal criteria (Chapter II). Heated water discharges of human origin (e.g. power plants) as well as stenothermal spring effluents may allow considerable range expansion beyond climatically-dictated limits.

All, or even a majority of blue tilapia in the Lake George section of the St. Johns River probably do not enter SGSR during winter. The occurrence of a tilapia in the run depends entirely on its chance encounter of the thermal plume. Tilapia may range widely (tagged individuals have been recaptured as far as 240 km from their release site; Lowe-McConnell 1959), but generally their movements are modest and largely random (Philippart and Ruwet 1982; Rinne and Wanjala 1982). In the course of its movements, a tilapia, upon encountering the

thermal plume in winter would enter the run because of its thermophilic predeliction. A fish that failed to encounter the plume would remain in Lake George. The proportion of Lake George tilapia entering the run would therefore be dependent on the probability of encountering the thermal plume. The size of the thermal plume (relative to the magnitude of Lake George), and the likelihood that blue tilapia movements in Lake George are limited, would suggest that only fish residing within several kilometers of the run would be apt to occupy the run.

The absence of blue tilapia in winter from stenothermal springs connected to the St. Johns River by long runs may be traced to the rheophobic tendencies of the microphagous tilapias (the blue among them). These fishes avoid currents, preferring still waters and pools (Philippart and Ruwet 1982). They would not be expected to ascend swiftly-flowing spring runs in the absence of thermal stimuli; effluent temperatures of long spring runs are not elevated above river temperatures at their outflows into the St. Johns River. Salt Springs Run appears to be the only exception to this rule; despite its length (6.4 km), moderate numbers of tilapia have been observed there each winter for several years. Current velocity in this run is negligible, however, due to its width and low gradient, and may be insufficient to deter tilapia.

Peak abundances of blue tilapia in SGSR during the two winters were similar. Gill net CPUE for December 1981 and February 1983 were 199 and 204 blue tilapia, respectively. Corresponding mean transect counts were 94.5 and 104.5 blue tilapia per transect. The similarity of blue tilapia abundances in SGSR in the two winters may be indicative of

stability in blue tilapia abundances in the Lake George section of the St. Johns River during this study. Conversely, space limitation may restrict the blue tilapia 'carrying capacity' of SGSR. The lack of territoriality among juveniles and females favors the former explanation, however. It may be premature to infer that blue tilapia have attained their maximum abundance in Lake George, on the basis of these data, however.

The visual line transect method proved comparable to gill net CPUE in estimating the relative abundances of blue tilapia in SGSR. This technique has been successfully implemented in enumerating cichlids (McKaye 1977; W. Courtenay, personal communication) and other fishes (e.g. Brock 1954; Bardach 1959; Northcote and Wilkie 1963; Keast and Harker 1977; Goldstein 1978; Colton and Alevizon 1981; Sale and Douglas 1981). The transect method required no costly or specialized equipment, was efficiently accomplished, did not require sacrifice of blue tilapia or non-target species, and did not evoke negative public reaction. The main shortcoming of the method is the necessity of adequate visibility, a requirement limiting its applicability in Florida waters. It is an excellent technique for investigating fish abundances in springs. A shortcoming was the standardization of selected transect locations. Randomization of transect locations would have allowed estimation of the absolute abundance of blue tilapia present in the run.

The habitation of spring runs by blue tilapia affords sportsmen the opportunity to utilize this species by bowfishing and snatch-hooking. It may also provide fisheries managers the opportunity to eradicate portions of blue tilapia populations. Best results, by

both groups, could be expected during, and immediately following, periods when surface-water temperatures are lowest.

CHAPTER IV
A LABORATORY COMPARISON OF GROWTH, SURVIVAL, AND
FORAGING ABILITIES OF EARLY LIFE HISTORY STAGES OF
BLUE TILAPIA AND LARGEMOUTH BASS

Introduction

The range of the blue tilapia in Florida has expanded rapidly since introduction of the species in 1961; it is now the most extensively distributed exotic fish established in the state. Concurrently, populations of blue tilapia have demonstrated an ability to attain high densities and dominate fish communities, often within a few years of colonizing systems (Ware 1973; Germany and Noble 1977). Phytoplanktivory by adults permits such densities to persist, but the rapidity with which these abundances are achieved, often from very small founder populations, and by a species with relatively low fecundity (see Chapter VIII), suggests that recruitment in this species can be relatively high.

Recruitment in fishes is primarily a function of survivorship in early life history stages (LeCren 1962; Braum 1978; Hunter 1980), which in turn is dictated principally by feeding, predation, and abiotic factors (Jones 1973; Eipper 1975; Lett and Kohler 1976). Acquisition of sufficient food not only averts death directly by precluding starvation (Laurence 1977; Hunter 1981), but also deters predation; starvation can increase susceptibility to predation (Ivlev 1961), and suboptimal diets can slow growth rates (Riley 1966; Wyatt 1972; Houde 1975, 1977), thereby protracting vulnerability to predation (Parker 1971; Cushing

1976; Taylor 1980; Hunter 1981). Effective exploitation of trophic resources by young fishes is therefore an essential requisite for survival.

Forage requirements of larvae of marine fishes have been investigated extensively (e.g. O'Connell and Raymond 1970; Saksena and Houde 1972; Wyatt 1972; Laurence 1974, 1977; Houde 1977, 1978) primarily because of the long-standing (Hjort 1914, 1926), but controversial (Marr 1956; May 1974; Laurence 1977), "critical period" concept relating year-class strengths to prey densities at the transition to exogenous feeding. Direct impacts of abiotic factors on early life survival in the ocean tend to be ameliorated by the environmental homogeneity and stability of marine systems (Moore 1966), but heterogeneity of biotic variables (e.g. temporal fluctuations in abundance or patchiness of zooplanktonic prey) can impact larval survival. In freshwater habitats, climatic disturbances (e.g. storms, cold fronts) significantly and rapidly alter aquatic conditions (Ruttner 1966), and differences in year-class strengths of freshwater fishes can often be traced to these abiotic perturbations (e.g. Kramer and Smith 1962; Busch et al. 1975; Summerfelt 1975). Fluctuations of edaphic productivity in freshwater systems are small in comparison to abiotic variability; differences in year-class strengths due to abiotic conditions are therefore much more pronounced. As a result, the forage requirements of early life history stages of freshwater species have received comparatively little attention and are poorly known (but see Laurence 1971; Dabrowski 1975; Li and Mathias 1982). However, limitations in zooplankton abundances can significantly affect survival and growth of young freshwater fishes (Davis 1930; Langlois 1932;

Krumholz 1949; Noble 1975; Lemly and Dimmick 1982; Kashuba and Matthews 1984; Matthews 1984). Food-supply mediated mortality of young fishes in freshwater habitats can be high, but because of relative constancy of productivity between years does not manifest differential year-class strength. However, differential recruitment of sympatric species with dissimilar forage abundance requirements could occur; different species vary in ability to survive under conditions of limited food availability (Braum 1978; Saksena and Houde 1972; Hoagman 1974; May 1974; Houde and Schekter 1980).

I hypothesized that the success of the blue tilapia in colonizing systems and rapidly achieving high abundances is a result of enhanced survivorship and growth during early life history stages conferred by a high relative proficiency in exploiting available trophic resources. I therefore compared the growth, survival, and foraging abilities of early life history stages of blue tilapia and a representative native centrarchid, the largemouth bass (Micropterus salmoides), over a range of food abundances in laboratory experiments. I predicted that if tilapia were more proficient at exploiting available forage, then at equivalent forage abundances survival and growth of tilapia would exceed those of bass and that these differences could be traced to interspecific differences in foraging performance.

Methods

Blue tilapia were spawned in outdoor pools at the Gainesville National Fisheries Research Laboratory in Florida. Embryos were removed from mouths of females shortly after fertilization. Embryos of largemouth bass were collected from nests in spawning ponds at the

Welaka National Fish Hatchery, Welaka, Florida. Embryos of both species were maintained in the laboratory at 27.0-28.0 C until the onset of exogenous feeding.

Food organisms were collected from Lake Alice on the University of Florida campus with 63- μ m-mesh plankton nets. Use of wild zooplankton insured the presence of a natural variety of sizes and species duplicating that encountered by young bass and tilapia in Lake Alice. The aggregate zooplankton concentration in each collection was estimated by counting the numbers of organisms in 3 10-ml aliquots with a dissecting microscope. The mean of the three samples was used as an average concentration for the collection. Generally, several hundred plankters were present in each 10-ml sample, and counts seldom differed by more than 10 %. Appropriate volumes of the daily 'stock solution' were measured and used as needed.

Survival and Growth Trials

Growth and survival of young blue tilapia and largemouth bass were determined separately at prey concentrations of 0, 10, 50, 100, 500, and 1000 zooplankters per liter in 25-liter glass aquaria. Two replicates at each prey density were conducted for each species. Prey concentrations were adjusted daily.

Because relative abundances of specific zooplankters procured from Lake Alice changed daily, the biomass of zooplankton provided to each fish species at numerically equivalent prey concentrations varied. Survivorship was therefore analyzed by both number and biomass of zooplankton provided. Formulae developed by Dumont et al. (1975) were used to determine zooplankter weights. Furthermore, fish were able to

significantly alter nominal zooplankton concentrations between adjustments during the final days of the trials when growth rates were highest; virtually all zooplankters were consumed within 24 hours in some trials. To standardize prey availabilities for growth analyses, an index of prey biomass available to individual fish was derived by dividing zooplankton biomass by the number of survivors in each trial.

Most of the water in each tank was removed daily during adjustment of food concentration and replaced with filtered, dechlorinated tap water. Water was aerated and gently agitated by compressed air supplied through glass pipets. Water temperatures were maintained at 27.0-28.0 C with immersion heaters. A 12:12 light:dark photoperiod was maintained with fluorescent lighting, but other laboratory use precluded strict adherence to the regimen.

Fish were stocked into the tanks at the onset of feeding (10 and 6 days after fertilization for tilapia and bass, respectively). Initial stocking densities of fish were one per liter. Trials were of 16 days duration. Surviving fish were counted every other day, but difficulty was encountered in obtaining accurate counts during the first few days. Dead individuals were removed when noted.

At the termination of the trials, survivors were counted, measured to the nearest 0.05 mm with calipers, and individually weighed to the nearest mg with an electronic microbalance. Interspecific comparisons of growth were made only for weights as morphological differences between species precluded viable comparisons of length. Survival and growth of the two species were regressed against zooplankton concentration and compared. Prey levels required to ensure 10 and 50 %

survival of each species were estimated from the regressions and by probit analysis (Finney 1952).

Relative Foraging Ability Trials

Relative foraging abilities of young blue tilapia and largemouth bass were determined by estimating prey consumption rates at various prey densities; experimental procedures were similar to those of Houde and Schekter (1980).

Fish used in these trials were maintained in a 500-liter fiberglass tank following the onset of feeding. Water temperature was maintained at 27.0-28.0 C. Copious quantities of wild zooplankton were added to the tank daily to insure ad libitum feeding by fish; zooplankton concentrations always exceeded 1000 per liter.

Prey consumption rates were estimated for blue tilapia and largemouth bass at food concentrations of 10, 100, and 1000 zooplankters per liter. Fish were tested 3 days after feeding commenced (DAFC) and every third day thereafter, up to 18 DAFC. Three replicates of each combination of fish species, age, and zooplankton concentration were performed. Trials were conducted in aerated, rectangular, 10-liter, Plexiglas aquaria. For each trial, a small number (3-20) of randomly selected fish were transferred from the rearing tank to a test aquarium. The prescribed quantity of zooplankton was introduced 2 hours later and fish were allowed to feed for a specified interval (1-12 hours). Combinations of durations and numbers of fish were selected to insure that enough prey were eaten to measure consumption rates without reducing prey levels to less than half of initial concentrations. The

longest durations and largest numbers of fish were used in trials with the youngest fish.

At the end of each trial, fish were removed from the experimental aquaria; fish used in trials with prey concentrations of 1000 per liter were fixed in 10 % buffered formalin, others were returned to the rearing tank. At the conclusion of trials with prey levels of 10 and 100 per liter, the entire volume of each tank was filtered and the remaining plankters were counted. The zooplankters remaining in two 1-liter samples were counted for the 1000 prey per liter trials. Reductions in numbers of prey were used to estimate consumption rates. No natural mortality of zooplankton could be detected in exploratory trials without fish; I therefore inferred that reductions in numbers of zooplankton were caused by fish predation. Confer (1971), Houde and Scheckter (1980), and Drenner et al. (1982) similarly found the methodology to be valid.

To convert prey consumption rates from number to biomass of zooplankton ingested per fish per hour, stomach contents of the preserved fish were examined. Zooplankters present were identified and counted. Body lengths were measured to the nearest 10 μm with an ocular micrometer mounted in a dissecting microscope, and dry weights were calculated from these measurements using regression equations developed by Dumont et al. (1975). Gut contents were examined only for fish from the 1000 prey per liter trials; a paucity of test organisms precluded sacrifice of fish from all trials. Because absolute abundance of prey can affect foraging selection (Ivlev 1961; Estabrook and Dunham 1976; Houde and Scheckter 1980; Rajasilta and Vuorinen 1983), the biomass consumption rates calculated for the 10 and 100 prey per liter trials

may be unreliable. Converted consumption rates of bass and tilapia were regressed against ages and weights of fish and compared by analysis of covariance (Snedecor and Cochran 1980). Relative abundances of zooplankters in stomach contents and in daily stock solutions were compared to determine age-specific feeding electivities of both species of fish.

Results

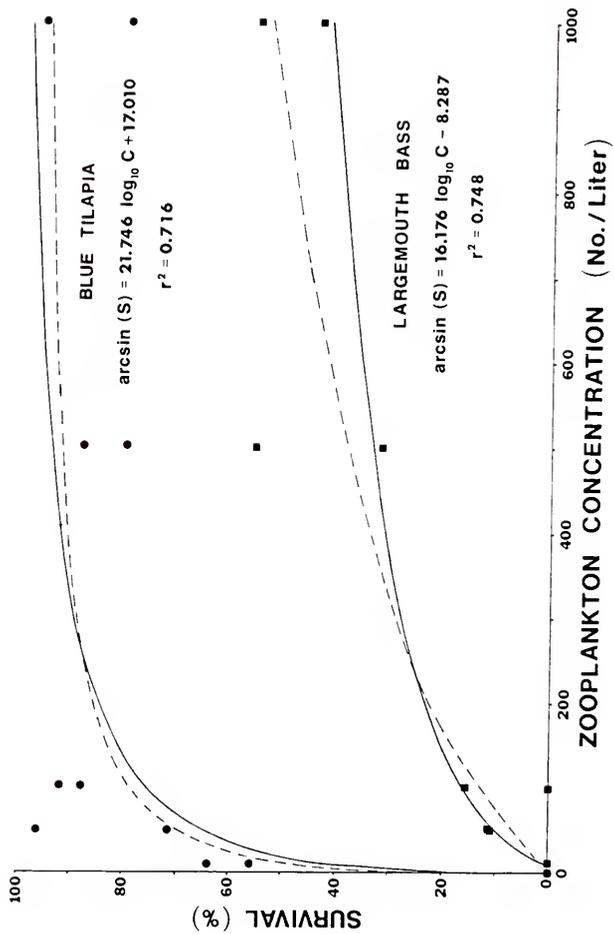
Survival and Growth Trials

Survival rates of both species increased in response to increases in food concentration (Table 8). No individuals of either species survived the 16-day trials in the absence of food, and total mortality was observed among largemouth bass subjected to the 10 zooplankter per liter prey level and in one replicate at 100 zooplankters per liter. Survival of bass was low at or below 100 zooplankters per liter and approached 50 % at the 500 and 1000 zooplankter per liter concentrations (Fig. 6). The least squares fitted regression (arcsin percent survivals on log₁₀ zooplankton concentrations) predicted 10 and 50 % survivorship of largemouth bass at 44.8 and 1965.9 zooplankters per liter, respectively. Probit analysis predicted 10 and 50 % survivorship at 72.3 and 850.1 zooplankters per liter, respectively. Survivorship of blue tilapia exceeded 50 % at all prey levels above 0 zooplankters per liter and became asymptotic at about 90 % at prey levels above 50 zooplankters per liter (Fig. 6). Survivorship of 10 and 50 % was predicted at prey levels of 1.2 and 19.4 zooplankters per liter, respectively, by the arcsin-transformed regression. Probit analysis of tilapia survivorship indicated requirement of 0.5 and 12.7

Table 8. Effect of zooplankton concentration on growth and survival of young blue tilapia and largemouth bass. Two replicates were completed for each species at each prey level. Initial stocking rate was 25 fish per replicate. Experiments were terminated 16 days after the onset of feeding.

Number/liter	Zooplankton concentration		Survival Number	Survival %	Total length (mm)		Met weight of survivors (g)	
	Mean µg/liter	Mean µg/liter/survivor			Mean	SD	Mean	SD
<i>Blue tilapia</i>								
1000	6408	320	20	80	19.38	1.06	0.1006	0.0170
1000	6408	267	24	96	18.55	1.01	0.0898	0.0149
500	3204	160	20	80	15.74	1.19	0.0544	0.0124
500	3204	146	22	88	15.54	0.86	0.0485	0.0031
100	641	29	22	88	11.38	0.60	0.0174	0.0031
100	641	28	23	92	11.46	0.50	0.0178	0.0030
50	320	18	18	72	10.89	0.32	0.0140	0.0020
50	320	13	24	96	10.97	0.55	0.0152	0.0034
10	64	5	14	56	10.56	0.27	0.0110	0.0015
10	64	4	16	64	10.73	0.46	0.0130	0.0020
0	0	-	0	0	-	-	-	-
0	0	-	0	0	-	-	-	-
<i>Largemouth bass</i>								
1000	3176	289	11	44	16.11	2.29	0.0486	0.0213
1000	3176	227	14	56	16.72	2.65	0.0529	0.0203
500	1588	113	14	56	14.78	1.88	0.0290	0.0117
500	1588	198	8	32	17.31	2.34	0.0471	0.0213
100	318	80	4	16	11.28	1.72	0.0138	0.0058
100	318	-	0	0	-	-	-	-
50	159	53	3	12	11.58	1.71	0.0134	0.0060
50	159	53	3	12	9.88	0.68	0.0076	0.0029
10	32	-	0	0	-	-	-	-
10	32	-	0	0	-	-	-	-
0	0	-	0	0	-	-	-	-
0	0	-	0	0	-	-	-	-

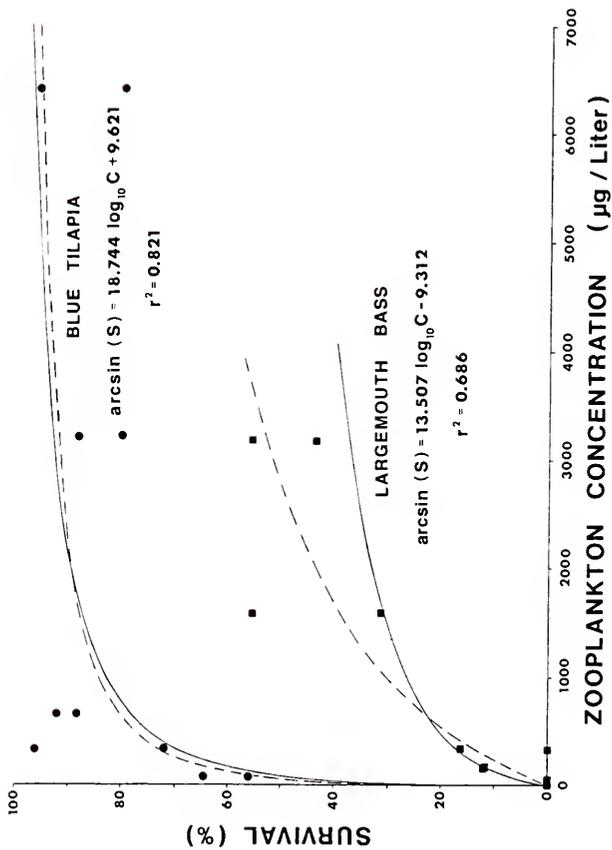
Fig. 6. Percent survival of laboratory-reared blue tilapia (circles) and largemouth bass (squares) at 16 days after feeding commenced in relation to zooplankton concentration (number per liter). Solid lines are based on the arcsin-transformed regressions. Dashed lines were derived by probit analyses.



zooplankters per liter to achieve 10 and 50 % survival, respectively. The elevations of the arcsin-transformed regressions for the two species were significantly different ($P < 0.0001$), inferring enhanced survivorship of blue tilapia over largemouth bass at equivalent prey densities.

Small zooplankters comprised the bulk of potential forage supplied to young largemouth bass. Mean relative abundances of cladocerans and immature copepods (nauplii and copepodids) in the trials with bass were 55.9 and 22.7 %, respectively, whereas the larger adult copepods comprised 19.6 % of potential forage. In trials with blue tilapia, relative abundances of cladocerans, immature copepods, and adult copepods were 28.9, 19.7, and 50.8 %, respectively. At each experimental prey density, blue tilapia were thereby provided with a greater concentration of available zooplankton biomass (Table 8). When regressed against concentration of zooplankton biomass, the survivorship function for blue tilapia was significantly ($P < 0.0001$) elevated above that of largemouth bass (Fig. 7). The least squares fitted regression predicted 10 and 50 % survivorship of largemouth bass at 113.3 and 10496.0 μg of zooplankton (dry weight) per liter, respectively. Probit analysis predicted 10 and 50 % survivorship at biomass concentrations of 229.2 and 2705.0 μg per liter, respectively. The probit relationship appeared to more closely approximate the data; the least squares regression underestimated survival of bass at high prey levels (Fig. 7). Zooplankton biomasses required to elicit 10 and 50 % survivorship of blue tilapia were 3.0 and 77.2 μg per liter, respectively, as predicted by arcsin-transformed regression (Fig. 7).

Fig. 7. Percent survival of laboratory-reared blue tilapia (circles) and largemouth bass (squares) at 16 days after feeding commenced in relation to zooplankton concentration (μg dry weight per liter). Solid lines are based on the arcsin-transformed regressions. Dashed lines were derived by probit analyses.



Similarly, probit analysis predicted 10 and 50 % survivorship of tilapia at 1.4 and 55.6 μg per liter, respectively.

Mortality schedules for bass and tilapia differed considerably (Fig. 8). Especially striking was the difference in longevity of the two species when starved (0 zooplankters per liter). All starved bass died within 7 days (13 days after fertilization); median survival time was 6 days. Total mortality of starved tilapia occurred in 16 days (26 days after fertilization); median survival time was 12 days. Both species suffered some mortality at nearly all prey levels early in the trials, but the rate of death among bass was considerably greater than for tilapia during this period. All bass maintained at 10 zooplankters per liter died within 9 days and the majority of deaths at higher prey levels occurred within the same period. Appreciable mortality of tilapia maintained at 10 zooplankters per liter occurred towards the end of the trials, but at higher prey levels, the few deaths noted occurred within the first week.

Weights and lengths of survivors were directly related to experimental prey levels (Table 8). Mean weights of blue tilapia ranged from 0.0110 g at 10 zooplankters per liter to 0.1006 g at 1000 zooplankters per liter. Mean bass weights ranged from 0.0076 to 0.0529 g at 50 and 1000 zooplankters per liter, respectively. The relationships between survivor weight and forage level were linear for both species (Figs. 9 and 10). Largemouth bass data gave poor fits because of considerable heterogeneity within treatments, but regressions for both species were highly significant (all $P < 0.0001$). At equivalent prey levels, mean weights of surviving tilapia exceeded those of bass (Figs. 9 and 10).

Fig. 8. Mortality schedules of laboratory-reared largemouth bass (upper) and blue tilapia (lower) maintained at six different zooplankton concentrations (number per liter). DAFC = days after feeding commenced.

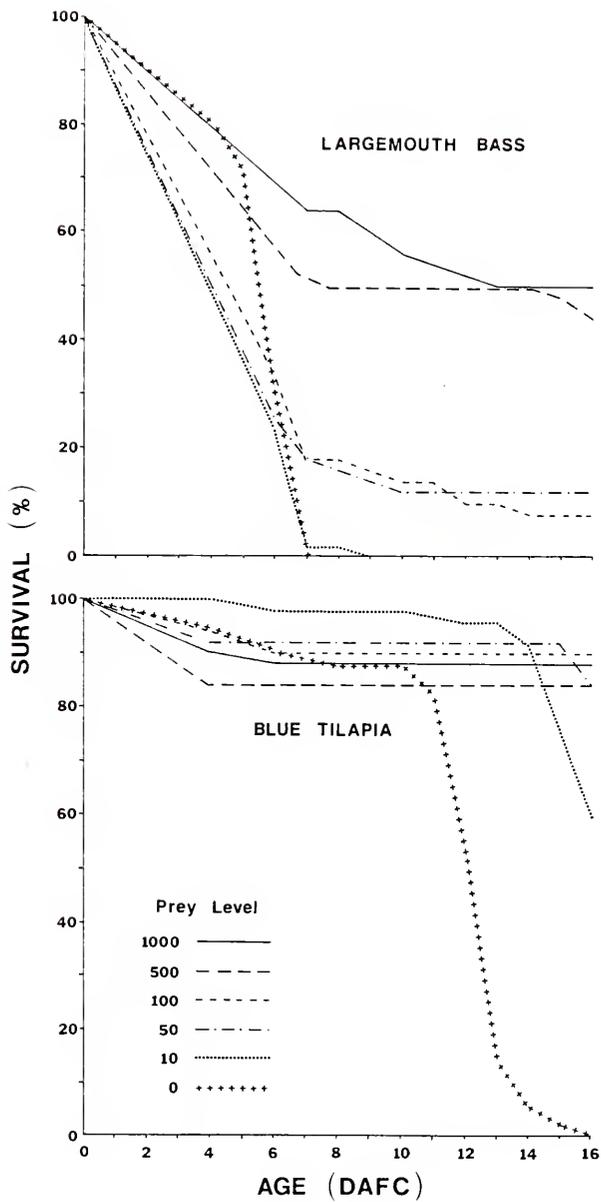


Fig. 9. Mean weights of laboratory-reared blue tilapia (circles) and largemouth bass (squares) at 16 days after feeding commenced in relation to zooplankton concentration (number per liter). Vertical bars represent ± 1 SD. In the regression equations, W and C represent weight and zooplankton concentration, respectively.

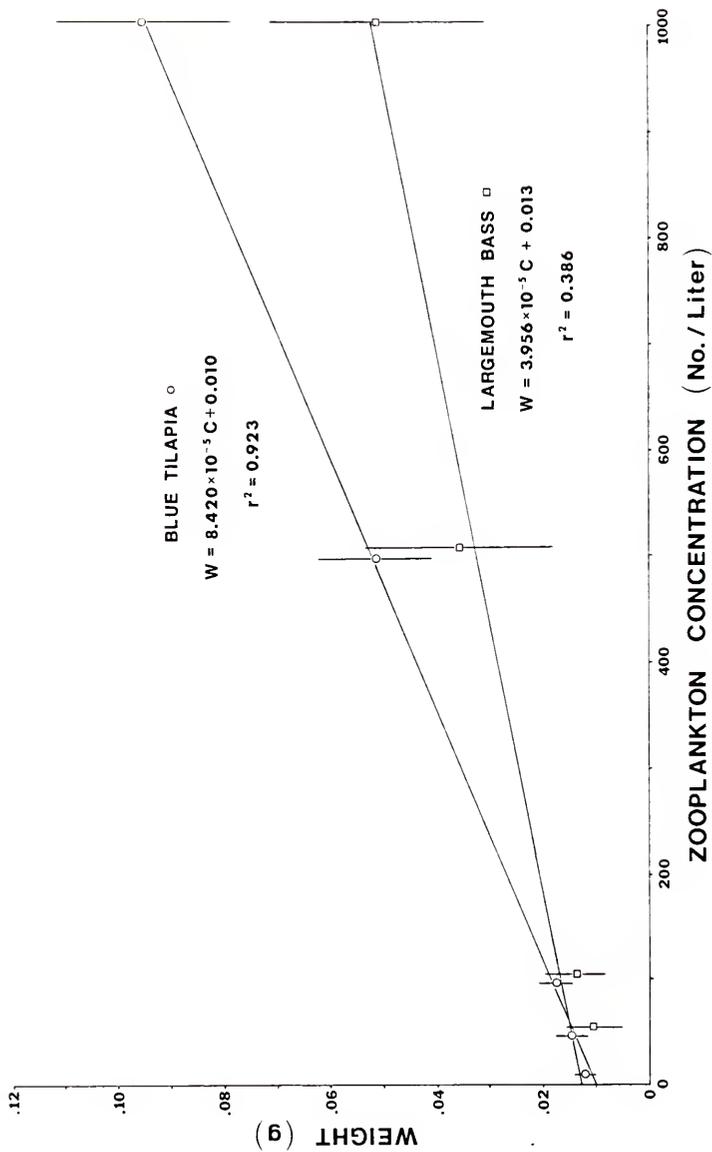
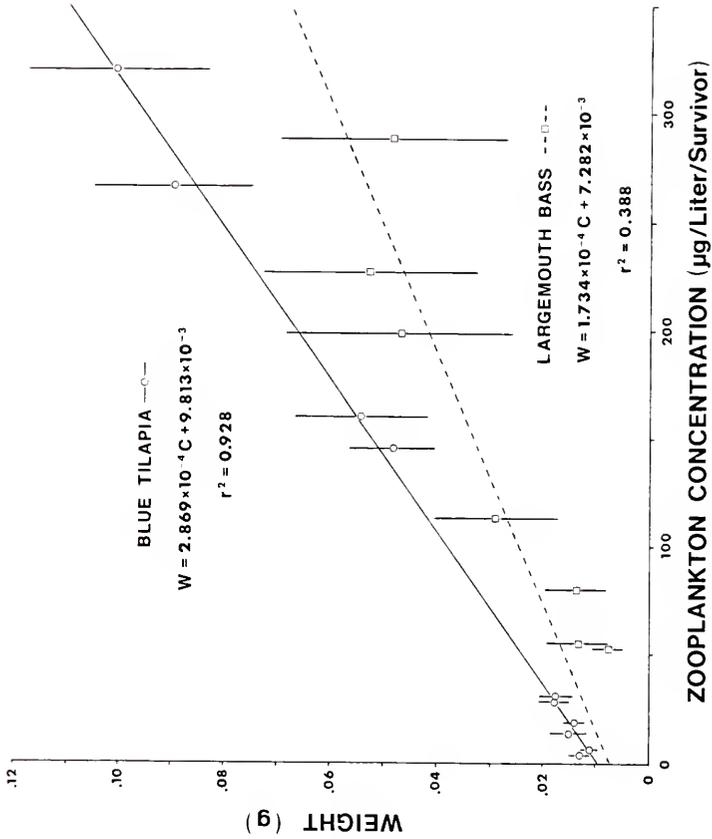


Fig. 10. Mean weights of laboratory-reared blue tilapia (circles) and largemouth bass (squares) at 16 days after feeding commenced in relation to zooplankton concentration (μg dry weight per liter per surviving fish). Vertical bars represent ± 1 SD. In the regression equations, W and C represent weight and zooplankton concentration, respectively.



Relative Foraging Ability Trials

Prey consumption rates (in zooplankters consumed per hour) of blue tilapia increased rapidly with age (Fig. 11). At each age, consumption rates were positively correlated with food concentration. Consumption rates of largemouth bass increased slowly with age initially, but accelerated rapidly after the ninth day of feeding (Fig. 11). At each combination of age and food concentration, tilapia consumed more zooplankters per unit time than did bass. Appreciable feeding by tilapia was measurable at each food concentration and age, but consumption rates of bass were very low or imperceptible (zero zooplankters consumed in 3 trials) at 3 and 6 DAFC at the 10 zooplankter per liter food concentration.

The diet of blue tilapia at 3 DAFC consisted primarily of the small cladoceran Bosmina (Table 9). Accordingly, small zooplankters dominated the size distribution of food items (Fig. 12). Mean weight of forage at 3 DAFC was 1.16 μg . At succeeding ages, tilapia gradually decreased intake of (and selection for) Bosmina and other cladocerans and increased consumption of adult copepods (Table 9). Coincidentally, the relative abundance of large items in the diet increased (Fig. 12). Mean weights of forage at 6, 9, 12, and 15 DAFC were 3.04, 3.66, 6.06, and 7.27 μg , respectively. By 18 DAFC, feeding electivity of tilapia was positive and random for adult calanoid and cyclopoid copepods, respectively, and negative selection was expressed for cladocerans (Table 9). Mean forage weight increased to 10.08 μg .

Bosmina and small Daphnia were the major dietary components of largemouth bass at 3 DAFC (Table 9), and cladocerans continued to be important forage at later ages. Mean weight of bass forage at 3 DAFC

Fig. 11. Prey consumption rates (number of zooplankton per hour) of blue tilapia and largemouth bass at three prey levels (number per liter) in relation to age (DAFC = days after feeding commenced).

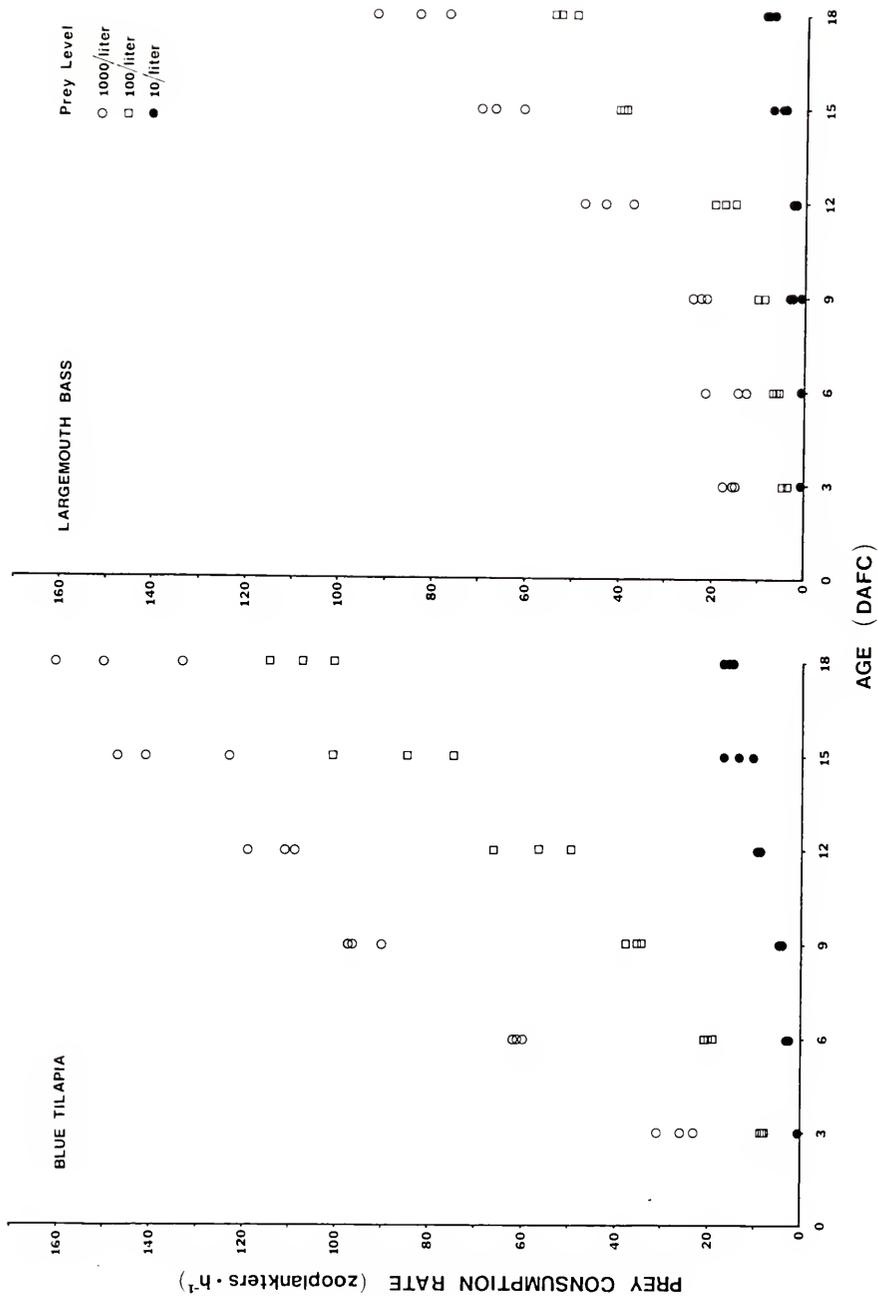
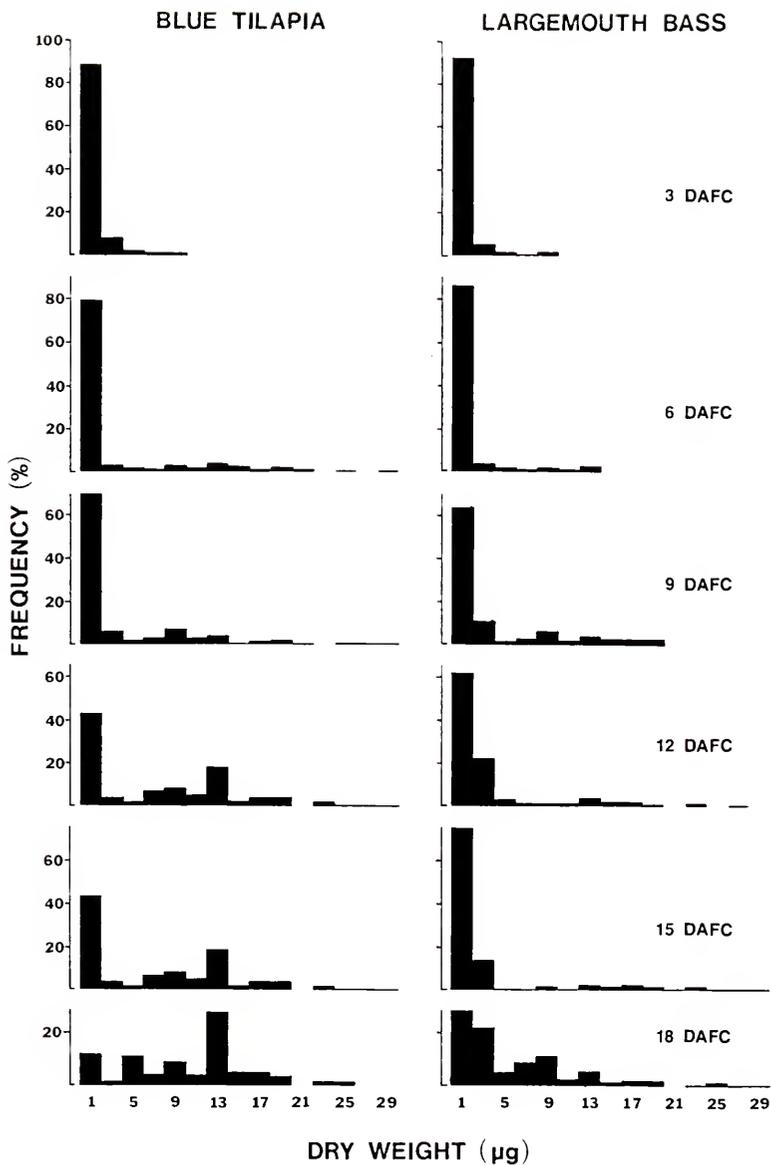


Table 9. Age-specific electivities of blue tilapia and largemouth bass for zooplanktonic prey in laboratory feeding trials. The symbols +, R, and - represent positive, random, and negative selection, respectively. Probability values are given in parentheses. Probability values > 0.05 were judged as indicating random selection (Wilcoxon's signed rank test). The relative abundances of zooplankton available and in the diets of the fish are denoted p and r, respectively.

Zooplankter	Age (days after feeding commences)																	
	3		6		9		12		15		18							
	p	r	p	r	p	r	p	r	p	r	p	r						
<i>Bosmina</i>	0.384	0.932	+ (<0.001)	0.154	0.002	+ (<0.001)	0.150	0.462	+ (<0.001)	0.147	0.412	+ (0.002)	0.254	0.398	R (0.004)	0.330	0.159	- (0.010)
<i>Daphnia</i>	0.005	0.004	- (0.002)	0.009	0.006	- (0.014)	0.015	0.003	- (<0.001)	0.021	0.002	- (0.004)	0.010	0.004	- (0.006)	0.003	0	-
<i>Daphnopsis</i>	0.017	0.004	- (0.002)	0.060	0.003	- (<0.001)	0.046	0.116	R (0.078)	0.031	0.098	+ (0.020)	0.046	0.058	R (1.000)	0.04	0.006	- (0.002)
<i>Glydorus</i>	0.001	0	-	0	0	-	0	0	-	0	0	-	0	0	-	0	0	-
<i>Calanoids</i>	0.024	0.043	- (0.017)	0.251	0.178	R (0.631)	0.366	0.207	- (0.006)	0.482	0.428	R (0.696)	0.399	0.493	R (0.064)	0.393	0.213	+ (0.004)
<i>Cyclopoids</i>	0.373	0.007	- (<0.001)	0.150	0.006	- (<0.001)	0.150	0.065	- (0.002)	0.150	0.022	R (0.004)	0.114	0.043	R (0.130)	0.135	0.111	R (0.770)
<i>Imm. copepods</i>	0.117	0.011	- (<0.001)	0.370	0.006	- (<0.001)	0.268	0.147	- (0.001)	0.165	0.037	- (0.002)	0.174	0.001	- (0.002)	0.016	0	-
<i>Rotifers</i>	0	0	-	0.001	0	-	0	0	-	0	0	-	0	0	-	0.001	0	-
<i>Ostracods</i>	0.008	0	-	0.004	0	-	0.004	0	-	0.004	0	-	0.002	0.001	R (0.004)	0.013	0.011	R (0.412)
<i>Blue tilapia</i>																		
<i>Bosmina</i>	0.548	0.869	+ (0.001)	0.395	0.651	+ (0.009)	0.523	0.568	R (0.912)	0.357	0.465	R (0.556)	0.263	0.747	+ (0.028)	0.255	0.111	- (0.004)
<i>Daphnia</i>	0.015	0.055	R (0.603)	0.029	0.023	R (0.073)	0.064	0.142	+ (0.023)	0.190	0.354	R (0.194)	0.133	0.046	- (0.019)	0.411	0.379	R (0.432)
<i>Daphnopsis</i>	0.010	0	-	0.011	0.032	R (0.575)	0.012	0.020	R (0.263)	0.017	0.016	R (0.276)	0.009	0.019	R (0.432)	0.048	0.016	R (0.316)
<i>Glydorus</i>	0.002	0.009	- (0.014)	0.001	0	-	0.007	0.002	- (0.002)	0.004	0	-	0.054	0.013	- (0.002)	0.008	0	-
<i>Calanoids</i>	0.086	0.023	- (0.002)	0.128	0.005	R (0.093)	0.071	0.162	+ (0.009)	0.061	0.119	R (0.696)	0.069	0.089	R (0.516)	0.059	0.114	R (0.106)
<i>Cyclopoids</i>	0.146	0.018	- (<0.001)	0.172	0.051	- (0.001)	0.108	0.097	R (0.390)	0.106	0.023	- (0.006)	0.094	0.031	R (0.084)	0.075	0.313	R (0.074)
<i>Imm. copepods</i>	0.196	0.027	- (<0.001)	0.236	0.177	R (0.110)	0.182	0.008	- (<0.001)	0.225	0.023	- (0.002)	0.370	0.034	- (0.002)	0.162	0.016	- (0.002)
<i>Rotifers</i>	0.006	0	-	0.078	0	-	0.033	0	-	0.032	0	-	0.006	0	-	0.001	0	-
<i>Ostracods</i>	0	0	-	0	0	-	0	0	-	0	0	-	0.002	0	-	0	0	-
<i>Largemouth bass</i>																		

Fig. 12. Age-specific size frequencies of zooplanktonic forage consumed by blue tilapia and largemouth bass in laboratory feeding trials (DAFC = days after feeding commenced).



was 0.92 μg . Intake of larger forage increased at 6 and 9 DAFC as consumption of adult copepods intensified (Table 9), but then regressed through 15 DAFC (Fig. 12). Mean weights of bass forage at 6, 9, 12, and 15 DAFC were 1.56, 4.05, 3.39, and 2.88 μg , respectively. Consumption of adult copepods increased sharply at 18 DAFC (Table 9) and mean forage weight rose to 5.94 μg coincidentally, but modal forage weight remained $< 2.0 \mu\text{g}$ (Fig. 12).

Rotifers and ostracods were rarely present in the diets of either fish as availabilities of both items were limited (Table 9). Immature copepods were available in appreciable quantities, but were generally minor components of diets of both bass and tilapia (Table 9). Selection for immature copepods was negative by tilapia at all ages, but they comprised a significant portion (14.7 %) of the diet at 9 DAFC. Bass selected against immature copepods at all ages except 6 DAFC when electivity was random for this forage.

Determination of forage weights allowed conversion of prey consumption rates from number to biomass of zooplankton consumed per hour per fish (Fig. 13). Prey consumption rates were described as power functions of age (Table 10) based on the regression of natural logarithm-transformed consumption rates on natural logarithm-transformed ages (Fig. 14). This fitting procedure gave linear regressions from which the back-transformed lines in Figure 13 were derived. The power functions provided excellent fits for the blue tilapia data but underestimated feeding rates of bass at 18 DAFC. The coefficients of determination (Table 10) indicated that the regressions explained a sufficient proportion of total variation in all cases, however. Analyses of covariance and multiple comparisons tests (Zar

Fig. 13. Prey consumption rates (μg dry weight per hour) of blue tilapia and largemouth bass at three prey levels (number per liter) in relation to age (DAFC = days after feeding commenced). Lines are based on least-squares fitted regressions given in Table 3.

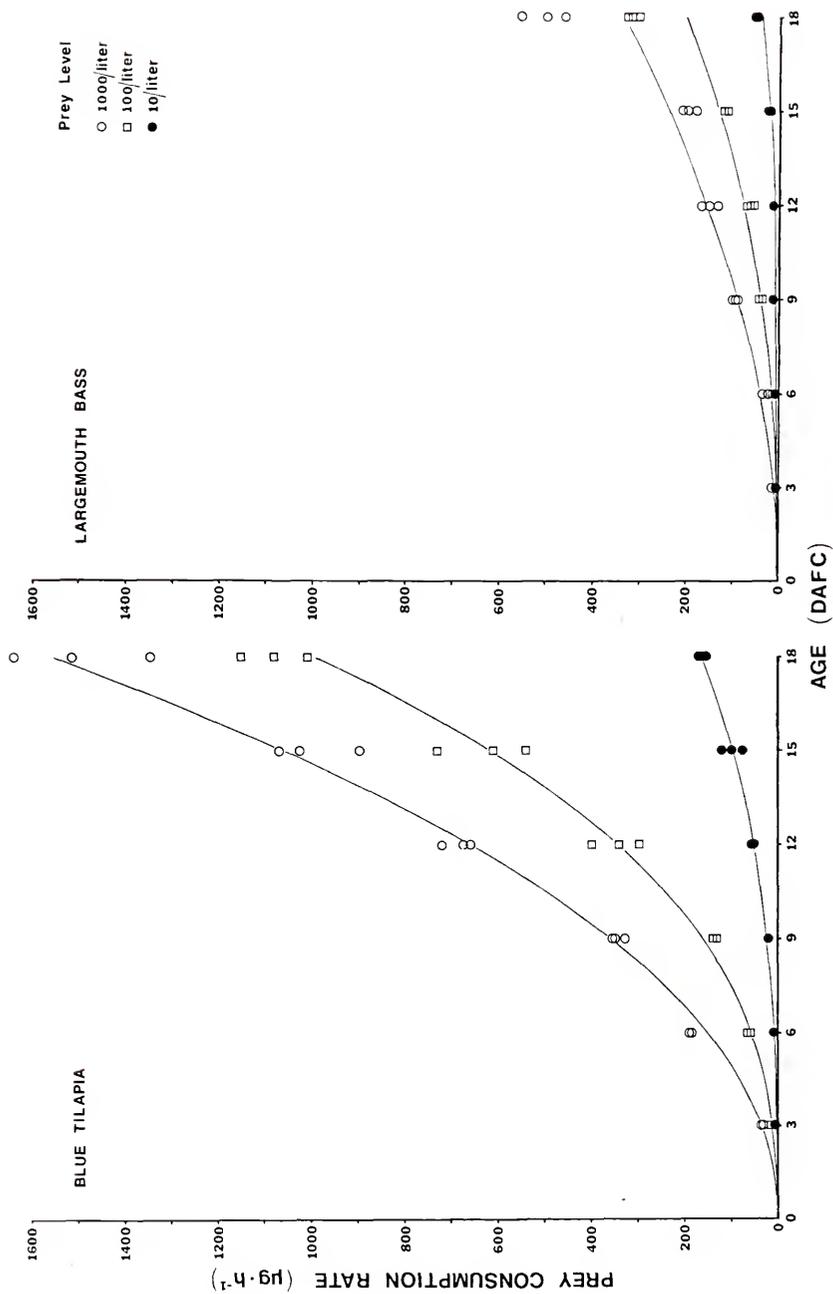
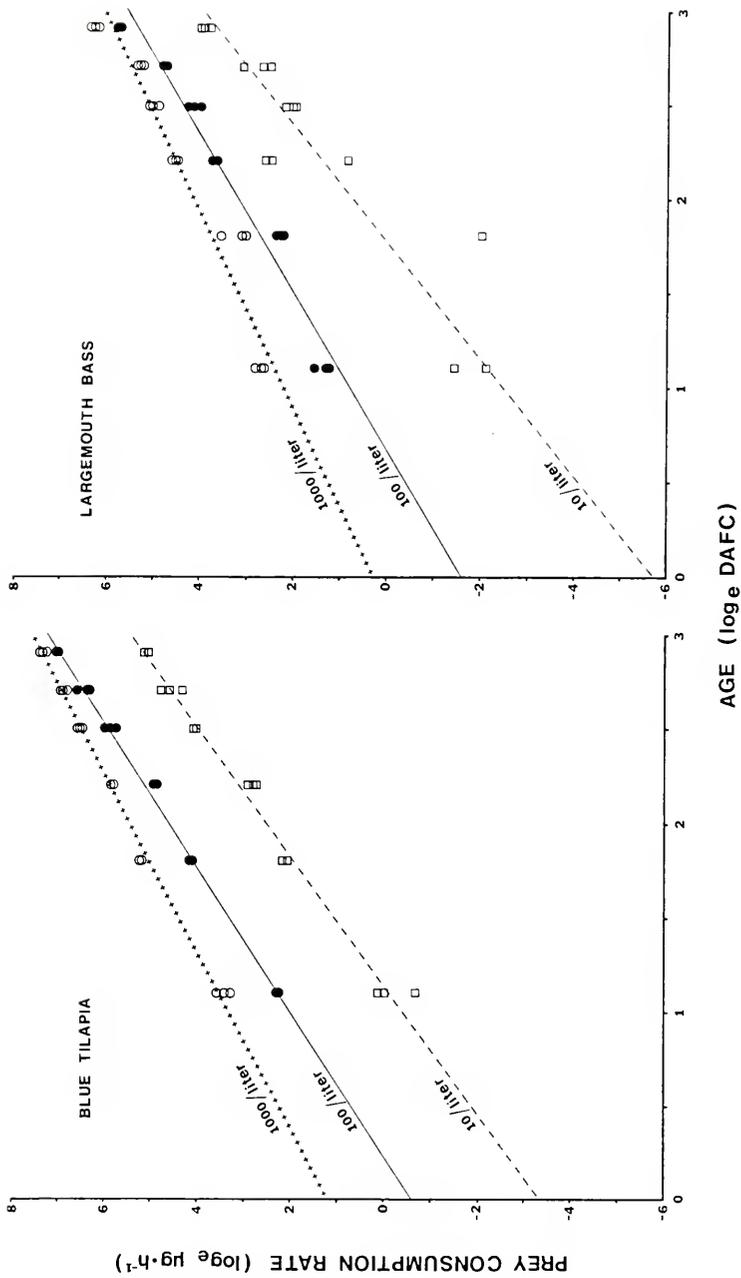


Table 10. Prey consumption rate - fish age relationships of blue tilapia and largemouth bass. Parameter estimates are for data fitted to the power function $C = mt^b$, where C = prey consumption rate ($\mu\text{g prey} \cdot \text{h}^{-1}$), t = age in days after feeding commences, b = power relating the rate of change of prey consumption rate to age, and m = regression constant.

Species	Prey concentration (no./liter)	Parameter estimates		
		m	b	r^2
Blue tilapia	10	0.0346	2.9292	0.984
	100	0.5158	2.6156	0.993
	1000	3.3173	2.1277	0.990
Largemouth bass	10	0.0032	3.2164	0.846
	100	0.1978	2.3910	0.956
	1000	1.2818	1.9256	0.926

Fig. 14. Prey consumption rates ($\log_e \mu\text{g}$ dry weight per hour) of blue tilapia and largemouth bass at three prey levels (number per liter) in relation to age (\log_e days after feeding commenced). Lines are based on least-squares fitted regressions given in Table 3.



1974) were performed on the log-log linear regressions to test for differences in the consumption rates at different food concentrations within species and at equivalent food concentrations between species.

Heterogeneity existed among slopes (b values, Table 10) of the 3 regressions for blue tilapia ($P < 0.0001$). Multiple comparisons indicated that slopes at each prey concentration were significantly different from each other ($P = 0.0025$, < 0.0001 , and < 0.0001 for 10 vs.100, 10 vs.1000, and 100 vs.1000 zooplankters per liter, respectively).

Heterogeneity existed among slopes of the regressions for largemouth bass ($P = 0.0009$), but the slopes of the regressions for 100 and 1000 zooplankters per liter were not significantly different ($P = 0.1201$). The slope of the 10 zooplankter per liter regression was significantly different from each of the others ($P = 0.0131$ for 10 vs.100, $P = 0.0002$ for 10 vs.1000). Elevations of the regressions for 100 and 1000 zooplankters per liter were significantly different ($P < 0.0001$).

Interpreted, these results indicate that prey consumption rates were greater at higher prey concentrations (m increased as prey concentration increased), but that the rate of prey consumption generally increased more rapidly with respect to age at low prey concentrations than at higher prey concentrations (b increased as prey concentration decreased). The slopes of the regressions for largemouth bass at 100 and 1000 zooplankters per liter followed this trend (b = 2.3910 and 1.9256, respectively), but sufficient deviations from the regressions existed to preclude demonstration of a statistically significant difference.

Slopes of the regressions for the two species at equivalent food concentrations were not significantly different in all comparisons ($P = 0.4223, 0.1162, \text{ and } 0.1736$ for 10, 100, and 1000 zooplankters per liter, respectively). In all 3 cases, the elevations of the regressions were different, however (all $P < 0.0001$). Elevations (m values, Table 10) of regressions for blue tilapia exceeded those of bass functions at each prey concentration. Therefore, the developmental response (the rate of change in prey consumption mediated by increasing age) at each prey concentration was similar for both species. At a given age, however, tilapia were capable of higher prey consumption rates than bass at equivalent food concentrations.

The interspecific disparity in age-specific foraging abilities was attributable largely to differences in size between tilapia and bass. Wet weights of individual eggs of tilapia and bass used in these experiments were about 7.4 and 2.8 mg, respectively. At 3 DAFC, mean wet weight of tilapia was 12.1 mg whereas bass larvae weighed about 3.3 mg each. At subsequent ages, the disparity in sizes expanded as growth of tilapia exceeded that of bass under ad libitum feeding conditions (Fig. 15). Cubic regression models (Table 11) provided optimum fits for regressions of prey consumption rates on weights (Fig. 16). The cubic term significantly improved accuracy of the regression model for each data set; inclusion of a quartic term did not ($\alpha = 0.05$). Prey consumption rates of bass and tilapia were reasonably comparable at equivalent weights (Fig. 16), but the regression lines for bass generally were elevated above those of tilapia, particularly in the 10 and 100 zooplankter per liter trials. Tests for coincident multiple regressions (Zar 1974) indicated that each pair of sample regression

Fig. 15. Mean wet weights (g) of blue tilapia (squares) and largemouth bass (circles) used in laboratory foraging ability trials in relation to age (days after feeding commenced). Vertical bars represent ± 1 SD.

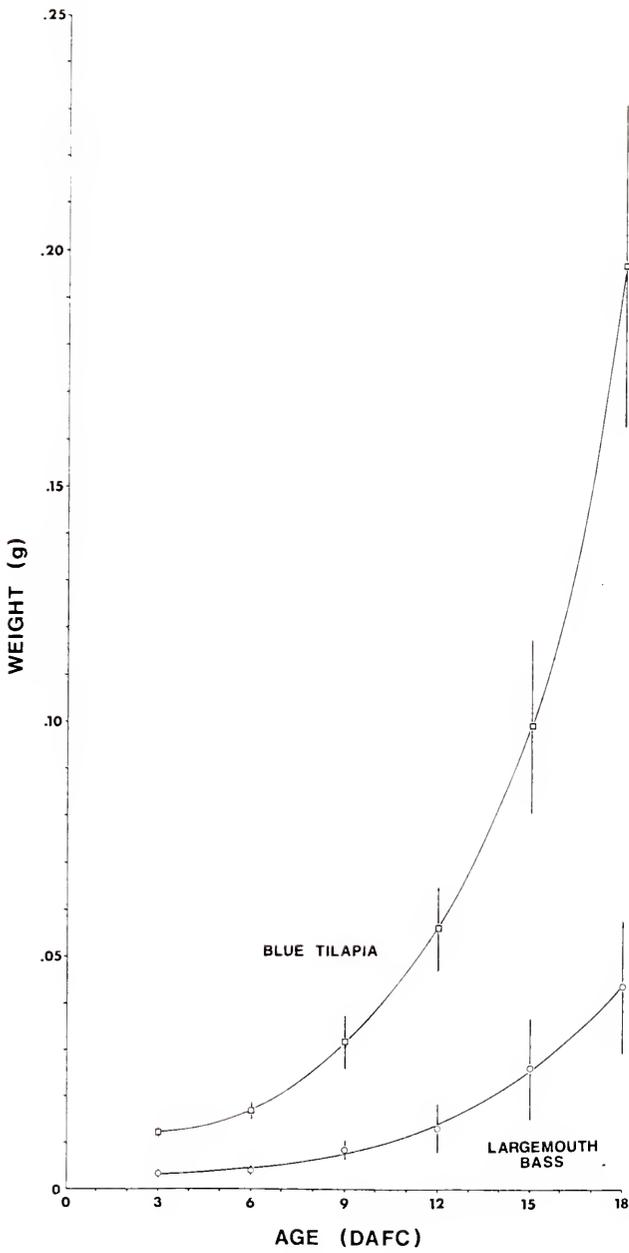
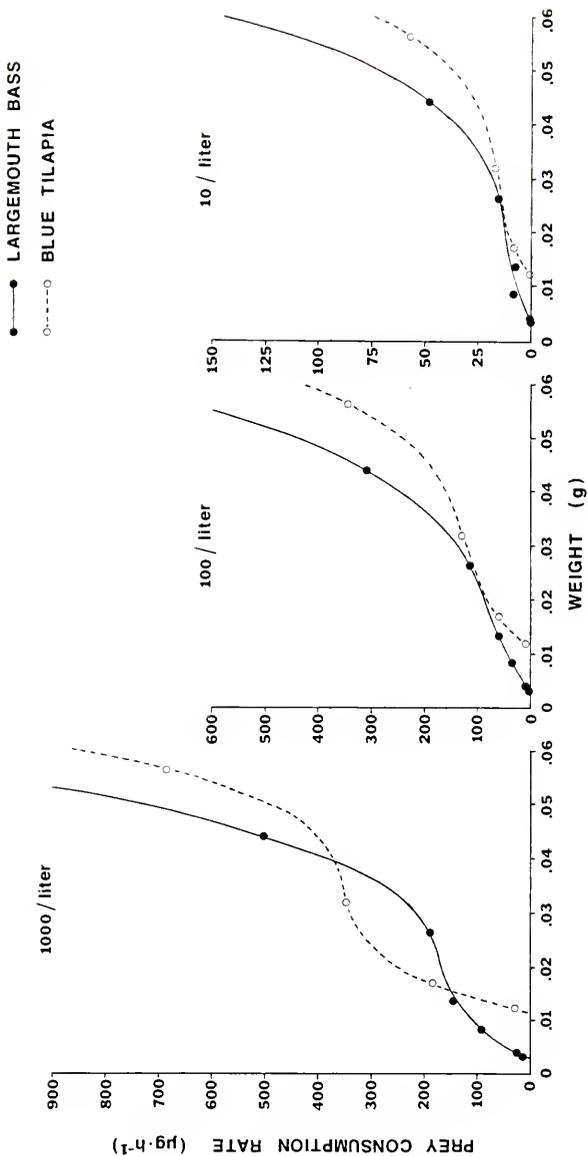


Table 11. Prey consumption rate - fish weight relationships of blue tilapia and largemouth bass <0.06 g. Parameter estimates are for data fitted to the cubic function $C = aW^3 + bW^2 + cW + d$, where C = prey consumption rate ($\mu\text{g prey} \cdot \text{h}^{-1}$), W = weight in g, and a , b , c , and d are regression constants.

Prey concentration (no./liter)	Parameter estimates				r^2
	a	b	c	d	
<i>Blue tilapia</i>					
10	1716462.8	-151668.6	4807.0	-38.1	0.997
100	9130631.3	-852207.3	29452.3	-238.4	0.974
1000	25503611.1	-2600564.5	90808.8	-732.5	0.996
<i>Largemouth bass</i>					
10	1688994.6	-94615.3	2115.5	-5.9	0.957
100	6822369.1	-347586.9	9700.4	-24.3	0.997
1000	20323581.7	-1255617.4	28927.3	-70.4	0.989

Fig. 16. Prey consumption rates (μg dry weight per hour) of blue tilapia and largemouth bass at three prey levels (number per liter) in relation to wet weight (g). Lines are based on least-squares fitted regressions given in Table 4. The ordinate scale for the 10 zooplankton per liter concentration is different from those used for the other prey levels.



functions did not estimate the same population regression (all $P < 0.001$). Plateaus in the developmental response coincided approximately with metamorphosis to the juvenile period for both species.

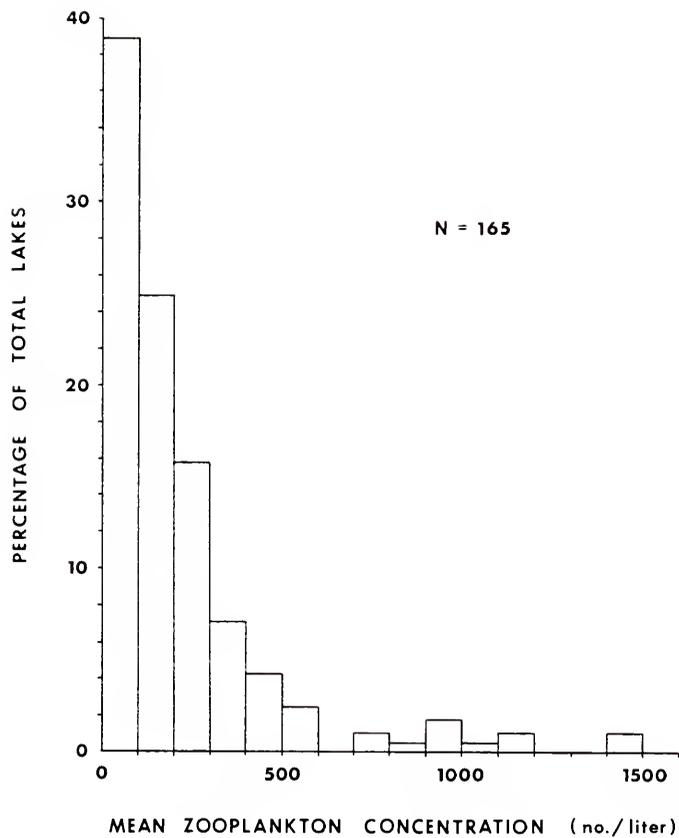
Discussion

My results show that at equivalent ages, young blue tilapia were more proficient than largemouth bass at exploiting zooplanktonic food and thereby were conferred enhanced survival and growth in the laboratory during the critical early life history period. Extrapolation of these findings to natural waters may explain, at least in part, the success of the species in colonizing new habitats and rapidly achieving high abundances in Florida. Essentially, tilapia are able to survive under conditions of food availability detrimental to survival of young bass.

The advantages of enhanced foraging proficiency would be largely, if not altogether, inconsequential in influencing survivorship in the presence of abundant forage. However, zooplankton concentrations in most Florida lakes (Fig. 17) encompass a range wherein survivorship of blue tilapia would be expected to exceed considerably that of largemouth bass and other native species with similar food abundance requirements.

Even in lakes with high zooplankton concentrations tilapia may still have the advantage. Zooplankton assemblages in these eutrophic systems are typically dominated by rotifers (Reid and Squibb 1971; Cowell et al. 1975; Blancher 1979), an infrequent and unpreferred forage of centrarchid larvae (Chew 1974; Lemly and Dimmick 1982). Abundances of microcrustacea in these lakes are often similar to those

Fig. 17. Frequency distribution of mean annual zooplankton concentrations (number per liter) for 165 lakes in Florida. Data courtesy of D. Canfield (by permission).



found in systems with lower total zooplankton abundances (Cowell et al. 1975; Blancher 1979). Additionally, rotifers appear to be an important first food of blue tilapia (see Chapter V).

Critical food concentrations for survival appear to be limiting only for a brief interval following the onset of active feeding (Hunter 1972; Laurence 1977; Houde 1978; Houde and Scheckter 1980; Li and Mathias 1982). Mortality schedules reported here provide concurring evidence; most bass deaths at low food concentrations occurred within the first week after initiation of feeding, coinciding with deaths of starved fish and with very low (or negligible) prey consumption rates in the 10-zooplankton-per-liter foraging trials.

Even at the highest food concentrations, survival of bass was only about 50 %. Similarly, survival of first-feeding walleye (Stizostedion vitreum) studied by Li and Mathias (1982) did not exceed 60 %. Conversely, survival of tilapia levelled-off at about 90 % at zooplankton concentrations above 50 per liter. Schulmann (1965) suggested that larvae may discontinue feeding (and die) if initially unsuccessful. High mortalities among bass larvae may therefore have been due to low initial prey capture success.

Appreciable mortality occurred among fed tilapia only at the 10 zooplankton per liter food level but did not coincide with deaths due to starvation. These fish probably did not die from an inability to capture available food items, but rather were unable to meet metabolic requirements with the supplied daily ration. These mortalities likely would not have occurred had a truly constant food level been maintained (i.e. if zooplankton concentrations had been adjusted more frequently).

Advantages of Large Initial Size

The interspecific disparity in age-specific foraging ability between bass and tilapia was apparently attributable to their difference in initial size; foraging abilities of the two species were similar at equivalent weights. Ova of the bearing tilapias are larger and have a higher yolk density than the eggs of most fishes (Noakes and Balon 1982). Within species, larger, denser eggs produce larger embryos, larvae, and juveniles (Blaxter and Hempel 1963; Bagenal 1969, 1971; Taylor 1980) and generally, similar correlations hold true interspecifically (Shirota 1970; Balon 1977; Philippart and Ruwet 1982).

Large larvae tend to be more successful in initial feeding attempts (Rosenthal and Fonds 1973; Hunter 1980); the enhanced survivorship of tilapia therefore may have been the product of higher prey capture success rates at the initiation of exogenous feeding due to larger initial size. Conversely, the smaller bass larvae may have been unable to procure sufficient forage at low prey levels and therefore starved. Similarly, egg sizes tend to be larger in initial broods of fishes with extended spawning seasons (Cushing 1967; Bagenal 1971; Southward and Demir 1974), apparently enhancing foraging ability and therefore survival early in the reproductive season when food abundances are low.

Larger size at the initiation of exogenous feeding enhances foraging ability, because swimming speed is correlated with size (Blaxter 1969; Blaxter and Staines 1971; Laurence 1972; Hoagman 1974; Hunter and Kimbrell 1980), thereby allowing search of a greater volume of water for food (Blaxter 1969; Hunter 1980, 1981; Gerritsen 1984).

Tilapia, because of their larger initial size, were probably able to search greater volumes of water than could bass and thereby acquired sufficient food at prey levels that were deleterious to bass survival. The superior locomotory ability of tilapia probably also increased their rate of capture success for prey encountered, especially for the larger, more mobile forms. Similarly, larger individuals are able to more efficiently handle food items because mouth sizes of young fish increase with body size (Lebour 1919; Shirota 1970; Wong and Ward 1972; de Mendiola 1974). I did not measure mouth widths, but at corresponding ages, mouth sizes of tilapia probably exceeded those of bass, enabling more efficient prey handling.

Embryos used in my experiments were taken from small (about 200 mm TL) tilapia spawning for the first time. Because egg weights of mouthbrooding tilapias may increase four-fold or more depending on the size of the female (Peters 1963), the initial and ensuing sizes and corresponding feeding rates of tilapia reported here are probably conservative. Performance of progeny from larger fish may be considerably enhanced. Egg and female weights of bass are also correlated (Merriner 1971), but sizes of larvae used here were probably representative of the species; bass embryos were collected from a spawning pond at Welaka National Fish Hatchery stocked with 2-year-old brood-stock averaging 1.4 kg (J. I. Maxwell, personal communication).

Large initial size may also enhance survival in natural waters by means not directly addressed by my experiments. Larger larvae are able to survive longer without food (Blaxter and Hempel 1963; Bagenal 1969, 1971; May 1971; Hunter 1980, 1981) because the weight-specific rate of energy loss of large animals is less than that of small organisms

(Gerritsen 1984). Large larvae are therefore more likely to encounter food before starving in habitats where food concentrations are low or zooplankton distributions are patchy. Survival times of starved blue tilapia exceeded those of largemouth bass.

Large initial size can also act as a deterrent to predation and thereby enhance survivorship. Predation is widely considered to be one of the greatest causes of early life mortality in fishes (Cushing 1974; Lett and Kohler 1976; Laurence 1977; Hunter 1981), and considerable laboratory and field evidence supports this assumption (e.g. Bennett 1950; Theilacker and Lasker 1974; Stevenson 1962; Fraser 1969; Aggus and Elliott 1975). Because starvation increases vulnerability to predation (Ivlev 1961), enhanced foraging capabilities afforded by large size indirectly reduce predation. More directly, size itself is a principal determinant of susceptibility to predation (Murphy 1968; Ware 1975; Balon 1984a, 1984b; Brodie and Formanowicz 1983); not only do larger organisms have fewer predators (Cushing 1974), but they are also better able to evade them. Therefore, an increase in initial size is accompanied by a decrease in the number of potential predators. Furthermore, enhanced foraging abilities and larger digestive surface area afforded by larger initial size allowed growth rates of tilapia to exceed those of bass. Similarly, Atlantic herring (Clupea harengus) and jack mackerel (Trachurus symmetricus) hatched from large eggs grow faster with the same feeding treatment than those hatched from small eggs (Blaxter and Hempel 1963; Theilacker and Dorsey 1980). Faster growth diminishes the number of potential predators at an accelerated rate and thereby decreases the probability of death due to predation (Parker 1971; Cushing 1976; Taylor 1980).

Feeding Strategies

Differences in feeding strategies may have also contributed to the superior foraging and growth rates of tilapia. A growing fish may satiate its increasing food demand by eating more, larger, or more-valuable (energetically) zooplankters, or a combination thereof (Hartmann 1983). Consumption rates of blue tilapia increased rapidly with age because both the numbers and sizes of zooplankters consumed progressively increased. Numbers of zooplankton consumed by largemouth bass increased with age (albeit slowly at first) but prey sizes stagnated from 9 to 15 DAFC. Steadiness in increase of prey size with fish age has generally been considered typical (Marak 1960, 1974; de Mendiola 1974; Last 1980), but stagnation thereof, possibly as a result of conditioning (Ivlev 1961) mediated by earlier gape-limitations (Wankowski 1979) or zooplankton evasion ability (O'Brien 1979), may occur (Brooks 1968; Furnass 1979; Hansen and Wahl 1981; Hartmann 1983). Stagnation of food sizes by largemouth bass may have precluded maximization of consumption rates and thereby contributed to the disparity in relative growth rates of the two species. Additionally, by progressively increasing prey sizes, blue tilapia exploited adult copepods extensively at an earlier age than did bass. Accelerated transition to a diet consisting mainly of copepods is energetically beneficial because the weight-specific calorific content of copepods exceeds that of cladocerans by about 20 % (Comita and Schindler 1963).

Evolutionary Considerations

Large initial size appears to confer clear survival advantages upon young fish; however, it also has one distinct disadvantage: egg

sizes and development times (from activation to exogenous feeding) are positively correlated (Blaxter and Hempel 1963; Rosenthal and Folds 1973; Ware 1975; Balon 1977; Theilacker and Dorsey 1980). Fish derived from larger eggs spend more time as highly vulnerable embryos and therefore are at greater risk to death by predation or through the actions of inclement abiotic factors. Natural selection minimizes durations of life-history stages that confer low survivorship (Williams 1966). Therefore, it appears advantageous for fish eggs released in hostile environments to be small. For example, eggs released in pelagic waters, where predatory pressures are high, are uniformly small in a wide variety of species (Bagenal 1971; Ware 1975) although their adult sizes can vary widely. Embryos of centrarchids, though vigorously guarded by male parents, are nevertheless subject to intense predation (Swingle and Smith 1943; Eckblad and Shealy 1972; Keenleyside 1972; Gross and Nowell 1980; Bain and Helfrich 1983; Goff 1984) and extreme temporal variation in physical conditions (Kramer and Smith 1962; Eipper 1975; Summerfelt 1975). Small egg sizes, and consequent rapid development, decrease duration of the most vulnerable life-history stage.

Blue tilapia avert the perils of a long development period by mouthbrooding. Mouthbrooding probably was a precursor to the evolution of large egg size in tilapias. Eggs of non-brooding (guarding) tilapias are smaller than those of brooders and develop at an accelerated rate (Lowe-McConnell 1955, 1975; Peters 1963; Oppenheimer 1970; Ishibashi 1974; Balon 1975; Noakes and Balon 1982; Philippart and Ruwet 1982); the resulting embryos are subject to the same dangers experienced by centrarchids. Mouthbrooding may have evolved as a result of both

reduced predation on embryos (Shaw and Aronson 1954; Lowe-McConnell 1969; Oppenheimer 1970; Balon 1975, 1977) and reduced impacts of abiotic phenomena (Baylis 1981; Philippart and Ruwet 1982).

Mouthbrooding offers a distinct survival advantage by transforming the most dangerous life-history stage into one of the most secure.

Occasional brooding for several days following the initiation of exogenous feeding whenever external stimuli of danger are apparent (Baerends and Baerends-van Roon 1950; McBay 1961; Fishelson 1966) compounds this advantage. In mouthbrooding species the free-living juvenile phase is therefore the life-history stage with the lowest expected survivorship. Life history traits increasing survival during, and decreasing the longevity of, the juvenile phase are therefore adaptive in mouthbrooding species. For reasons mentioned earlier, large initial size is one such stratagem. Whereas a slight increase in egg size would reduce overall offspring survivorship in a guarding or pelagic-spawning species by elongating development time, an increase in egg size by a mouthbrooder would increase overall offspring survivorship by increasing size at the initiation of exogenous feeding (Shine 1978). Evolution of larger eggs would continue until increases in offspring survivorship no longer compensated for the concomitant reduction in parental fecundity (Shine 1978).

Evolutionarily-advanced reproductive tactics such as mouthbrooding and large egg size are probably necessary to ensure adequate offspring survivorship in the species-rich tropical habitats to which blue tilapia are native. Competitive and predatory pressures in these habitats are intense (Dobzhansky 1950). Expression of such tactics in Florida waters, where biotic pressures are decidedly less rigorous, may

well explain the considerable success exhibited by the species in colonizing systems and rapidly achieving very high abundances. Biomass of tilapia may exceed 2,000 kg/ha in U.S. waters (Ware 1973; Germany and Noble 1977); abundances in native systems are much lower (Lowe-McConnell 1982).

In retrospect, the observed population and colonization dynamics of the blue tilapia in Florida would appear to have been predictable in light of the evolutionarily-advanced reproductive tactics exhibited by the species. The ecological literature abounds with theory concerning life history strategies and tactics. Fishery biologists might do well to take this theory into consideration, and apply it, when evaluating species for possible introduction.

Potential Impacts

Introductions of planktivorous species have deleteriously impacted established fish populations (von Geldern 1971; von Geldern and Mitchell 1975; Li et al. 1976; Wydoski and Bennett 1981), presumably by depleting zooplanktonic resources. At present, it is unknown if the introduction of blue tilapia has impacted native fish populations in Florida in this way. However, the following observations suggest that such an interaction is plausible. Zooplankton abundances typically decline during late spring and early summer (Cowell et al. 1975; Lemly and Dimnick 1982), possibly as a result of suppression by larval and juvenile fish (Shireman and Martin 1978; Keast 1980), suggesting that the zooplanktonic resource is limited. Additionally, larvae of different species occur sequentially (Anundrud et al. 1974; Keast 1980; R. Conrow, personal communication), possibly to avoid competition by

temporally partitioning this resource (Keast 1980). Introduction of an additional zooplanktivore, particularly one that is relatively large and effective, may increase demand upon the zooplanktonic resource. Resultant decreases in zooplankton abundances may directly affect survival of larvae of native fishes. Gerritsen (1984) showed that under exploitative competition for food in aquatic habitats, larger organisms will exclude smaller animals. More subtly, decreased food supply may retard growth of native species, thereby protracting time spent at vulnerable sizes, decreasing age-specific fecundities, and delaying age at first reproduction.

Adult blue tilapia may also feed intensively on zooplankton (Cowell et al. 1975; Spataru and Zorn 1978; Hendricks and Noble 1979), thereby further depleting available zooplankton. Supporting evidence is provided by pond experiments conducted by Shafland and Pestrak (1983); adult female blue tilapia did not inhibit nesting by bass, but nevertheless suppressed production of young-of-the-year bass. Zooplankton abundances may have been reduced by the tilapia, causing a decrease in bass survivorship.

CHAPTER V
THE TROPHIC ECOLOGY OF EARLY LIFE HISTORY STAGES OF
BLUE TILAPIA IN LAKE GEORGE, FLORIDA:
OVERLAP WITH SYMPATRIC SPECIES

Introduction

A potential impact of the blue tilapia, heretofore not considered, concerns exploitative competition between early life history stages of blue tilapia and native species for trophic resources. Because zooplanktonic resources appear to be limited and young blue tilapia are extremely capable zooplanktivores (see Chapter IV), trophic overlap between the young of blue tilapia and native species could deleteriously affect survival of larvae of native fishes. However, evaluation of this possibility has been hindered by the lack of information on food habits of young blue tilapia in natural systems. Information on the food habits of the young of other tilapias is also lacking, save the qualitative observations of Fryer (1961) on Tilapia variabilis. I therefore examined the food habits of young blue tilapia and sympatric species in Lake George, Florida, to a) characterize the trophic ecology of young blue tilapia under natural conditions, and b) determine the extent of interspecific overlap for food between young blue tilapia and native fishes.

Methods

Ichthyoplankton was sampled along the west shore of Lake George, Florida, from May to July 1983 to characterize the feeding ecology of

young blue tilapia in a natural system. Three tows were made on each of 6 sampling dates with a 0.5-m-diameter, 0.5-mm-mesh tow net. Tow speed was about 100 m/minute. On each date, two tows were made in littoral vegetation; the third sample was taken in open water. All tows were 5 minutes in duration, but because macrophytes quickly clogged the net in the littoral zone, volumes of water sampled per tow in the two habitats were probably unequal. Collections were preserved in 10 % buffered formalin. Zooplankton was sampled concurrently (triplicate 1-minute tows) with a 63- μ m-mesh plankton net. Zooplankton in stomach contents of young blue tilapia and native fishes collected coincidentally were identified and enumerated. Selective predation on zooplankton was evaluated for each species by comparing the relative abundances of prey in gut contents and in the water column using the Wilcoxon's signed-rank test (Kohler and Ney 1982). Similarity of diets was quantified using Hurlbert's (1978) measure of niche overlap.

Fortuitous capture of a brooding female blue tilapia in Lake George by gill-netting in May 1983 provided opportunity to characterize the feeding ecology of young blue tilapia prior to entering independent stages of development. The young were removed from the buccal cavity of the female and preserved in 10 % buffered formalin. Stomach contents of the brooded young were identified and integrated with the aforementioned trophic analyses.

Results

Few blue tilapia were captured in Lake George during ichthyoplankton sampling. Only 35 and 6 specimens were taken on 12 May and 19 May, 1983, respectively. All blue tilapia caught on each date

were taken in a single tow. No blue tilapia were collected on 4 sampling dates in June and July 1983. Both successful tows were conducted in shallow littoral waters, heavily vegetated with Vallisneria and Hydrilla. No blue tilapia were collected in open-water tows. Larval tidewater silversides (Menidia beryllina) and shad (Dorosoma spp.) were captured concurrently with blue tilapia on 12 May 1983. Silversides dominated the catch (98.1 %); shad and tilapia comprised 0.4 and 1.5 % of the sample, respectively. Silversides continued to dominate catches on later dates; several thousand were usually collected in each littoral tow. Larval shad and various juvenile and larval centrarchids were usually collected, but in very low numbers compared to silversides. Based on uniformity of size, the tilapia in the 12 May sample appeared to be from a single brood. Tilapia in this collection ranged from 9.9 to 12.8 mm TL (mean = 10.8 mm, S.D. = 0.54). The 6 fish taken 19 May 1983 were slightly larger (mean = 12.3 mm TL, range 10.7-13.8 mm) and more heterogenous in size (S.D. = 1.19).

The brooding female blue tilapia (397 mm TL and 1175 g in weight) was caught 12 May 1983 in littoral vegetation and yielded 101 young. The young had large yolk sacs and averaged 9.4 mm TL (range 8.7-9.9 mm, S.D. = 0.28).

Because a sufficient sample of blue tilapia was taken only on 12 May 1983, complete analysis of food habits was restricted to this date. The stomach contents of 30 randomly-selected individuals of each species caught with the tow net on this date were examined. Additionally, 30 young blue tilapia from the brooding female were dissected. Rotifers (primarily Keratella) and immature copepods were

the dominant zooplankters numerically in the littoral vegetation on 12 May 1983; cladocerans and adult calanoid and cyclopoid copepods were present in low abundances, and ostracods and harpacticoid copepods constituted minor components of the zooplankton community (Table 12).

Immature copepods, Bosmina, and rotifers comprised the bulk of the diet of independent blue tilapia, but of these prey, only Bosmina was positively selected for (Table 12). Rotifers were taken in significantly lesser numbers than if tilapia were feeding indiscriminantly. Diaphanosoma and calanoid copepods were taken more frequently than expected. About 10 % of the volume of the gut contents of these tilapia consisted of planktonic algae and particulate detritus.

Although zooplankters were fed upon by all but one of the blue tilapia examined from the brooding female, phytoplankton and detritus comprised about 90 % of the gut contents of these fish volumetrically. Rotifers were the most common zooplankter ingested, and both rotifers and Bosmina were positively selected for (Table 12).

Silversides fed almost entirely upon immature copepods but also selected positively for Bosmina (Table 12). Algae and detritus were absent from guts of larval silversides.

Trophic analysis of shad larvae was hindered by the presence of very few or no food items in their guts; 6 shad contained no food, and a mean of only 4.5 zooplankters was present in specimens with food. Clupeiform larvae may partially or completely void their digestive tracts when captured and preserved (Houde and Scheckter 1980). Adult copepods comprised a large fraction of the pooled diet of larval shad, but the absence of these zooplankters from the guts of many specimens

Table 12. Relative abundances of zooplankters in littoral vegetation and in gastric tracts of fish, and feeding electivities of fish, 12 May 1983, Lake George, Florida. The symbols +, R, and - represent positive, random, and negative selection, respectively. Probability values are given in parentheses. Probability values > 0.05 were judged as indicating random selection (Wilcoxon's signed rank test).

Zooplankter	Fish							
	Blue tilapia ^{a/} (n=30)		Blue tilapia ^{b/} (n=29)		Silversides (n=30)		Shad (n=24)	
	% in habitat	% in diet Electivity	% in diet Electivity	% in diet Electivity	% in diet Electivity	% in diet Electivity	% in diet Electivity	
<u>Bosmina</u>	1.54	24.98 + (<0.001)	13.36 + (0.015)	3.51 + (0.039)	0.92 - (<0.001)			
<u>Daphnia</u>	0.09	0.70 R (0.057)	0 -	0.02 - (<0.001)	0 -			
<u>Diaphanosoma</u>	0.28	8.62 + (<0.001)	0 -	0 -	2.78 - (0.021)			
Calanoids	1.38	3.36 + (0.047)	0.38 - (<0.001)	0.05 - (<0.001)	31.48 R (0.197)			
Cyclopoids	0.42	0.82 R (0.057)	0 -	0 -	7.41 R (0.087)			
Harpacticoids	0.02	0 -	0.76 - (<0.001)	0 -	0 -			
Imm. copepods	31.15	38.30 R (0.052)	4.96 - (<0.001)	93.81 + (<0.001)	56.63 + (0.002)			
Rotifers	65.11	23.21 - (<0.001)	80.53 + (<0.001)	2.61 - (<0.001)	2.78 - (<0.001)			
Ostracods	0.02	0 -	0 -	0 -	0 -			

a/ free-living tilapia captured in tow net.

b/ brooded tilapia taken from mouth of female captured in gill net.

resulted in neutral selection for them overall (Table 12). Positive selection for immature copepods by shad was observed. Shad did not feed on algae or detritus.

Stomach contents of only 4 of the 6 tilapia collected 19 May 1983 could be examined; 2 fish were overly mutilated. Briefly, these fish fed chiefly upon cladocerans (89.9 %); immature and adult copepods were minor dietary components (6.2 and 2.3 %, respectively). A single ostracod and one rotifer (each 0.8 %) were ingested. Significantly, algae and detrital material were absent from the guts of these fish.

Hurlbert's measure of overlap assumes a value of zero when no resource is shared by 2 species, a value of 1.0 when both species use each resource in proportion to its abundance, and a value > 1.0 if each species uses less common resources more intensively than others and the preferences of the 2 species tend to coincide (Hurlbert 1978).

Dietary-overlap indices for zooplanktivory were computed for fish collected 12 May 1983 (Table 13). Dietary similarity of silversides and independent tilapia was moderate as Bosmina and immature copepods were the two most important items in the diets of both. The high relative abundance of immature copepods decreased the intensity of overlap. Similarity of diets of shad and tilapia was relatively high as both species coincided in the consumption of a variety of less-abundant items. A high degree of similarity for brooded and independent tilapia resulted entirely from the intense use of Bosmina by both. Overlap in the diet of brooded tilapia with those of shad and silversides was negligible. Dietary similarity of shad and silversides was moderate, as overlap was notable only for the relatively-common immature copepods.

Table 13. Diet overlap matrix for fishes captured 12 May 1983,
Lake George, Florida.

	Blue tilapia ^{a/}	Silversides	Shad
Silversides	1.733		
Shad	2.596	1.679	
Blue tilapia ^{b/}	2.592	0.492	0.282

^{a/} free-living tilapia captured in tow net.

^{b/} brooded tilapia taken from mouth of female captured in gill net.

Discussion

Juvenile tilapia feed on zooplankton, especially microcrustacea (LeRoux 1956; McBay 1961; Yashouv and Chervinski 1961; Drenner et al. 1982), and it has been assumed therefore that early life history stages do so also (Bowen 1982). However, Fryer (1961) noted that first-feeding T. variabilis consumed large quantities of planktonic algae. Planktonic algae and detrital particles were important components of the gut contents of young blue tilapia in Lake George also, particularly in the brooded fish. The relative importance of these items declined rapidly with increases in size, however. Algae and detritus probably do not contribute significantly to the nutrition of these fish; the digestive physiology necessary to extract nutrients from these materials, although present in adults (Bowen 1982), is almost certainly lacking during early stages of development (Fryer 1961). No evidence of algal digestion was apparent. In all likelihood, the tilapia initially were feeding indiscriminantly on all available particles which they were capable of ingesting. With experience, they shifted to more nutritionally-valuable forage.

Findings reported in Chapter IV indicate that when provided with zooplankton consisting almost entirely of microcrustaceans, young blue tilapia will consume these organisms readily and grow rapidly. In Lake George, microcrustaceans comprised a large portion of the diet of tilapia, but rotifers were also a major forage, especially in the brooded fish. Utilization of rotifers declined with fish size, however. As in the laboratory trials, independent tilapia in Lake George expressed positive selection for cladocerans and calanoid copepods. Immature copepods comprised a larger fraction of the diets of Lake

George fish than of laboratory-reared tilapia, but their relative abundance in the environment was also greater.

Dietary overlap of independent blue tilapia and tidewater silversides was moderate and approximated the relationship between shad and silversides. However, similarity of diets of shad and tilapia was relatively high. Declines in shad abundances following the introduction of blue tilapia (Babcock and Chapman 1973; Germany 1977) have been attributed to the trophic similarity of adults of these species (Foote 1977; Hendricks and Noble 1979). Perhaps overlap during the early life period, when mortality is highest and definition of year-class strength is most pronounced (Hjort 1914, 1926; LeCren 1962; Braum 1978; Hunter 1980), also influences this phenomenon (see also Chapter IV).

Materialization of overlap-mediated effects could only occur if tilapia consumed sufficient zooplankton to significantly deplete the trophic resources available to other species. This was certainly not the case in Lake George during the summer of 1983; young tilapia comprised a minute fraction of the ichthyofauna present. Similarly, seining in Lake George during August 1983 captured no juvenile tilapia at locations that yielded moderate numbers in the preceding summer (see Chapter VI). These findings imply that reproductive success of blue tilapia in Lake George during 1983 was substandard. Elevated water levels and increased turbidity due to excessive precipitation may have suppressed spawning; in native habitats, mouthbrooding tilapias spawn in clear waters, usually prior to the rainy season (Lowe-McConnell 1953, 1959). Nesting activity, relative to other years, could not be ascertained due to poor water transparency. Flushing of acidic waters from wooded swamps surrounding Lake George into littoral habitats by

heavy rainfall may have depressed fertilization success and/or embryonic survivorship; tilapia may be relatively intolerant of low pH (Lovshin in Chervinski 1982).

CHAPTER VI
RELATIVE PREFERENCE OF LARGEMOUTH BASS FOR
BLUE TILAPIA AND BLUEGILL AS FORAGE

Introduction

Because the blue tilapia has proved to be neither an effective aquatic vegetation control agent nor a sport fish in Florida (Buntz and Manooch 1968), its introduction generally has been considered inexpedient and undesirable. However, evidence suggests that the species may manifest some benefit by serving as forage for important native sport and food fishes. Noble et al. (1975) reported that blue tilapia served as an important forage for largemouth bass (Micropterus salmoides) in Trinidad Lake, Texas, and were partly responsible for rapid bass growth rates. Similar observations have been made in Florida (V. P. Williams, personal communication). Swingle (1960) reported that largemouth bass readily fed on tilapia in experimental polyculture ponds. In Africa, tilapia are consequential forage for a variety of piscivores (Jackson 1961; Munro 1967; Donnelly 1969; Bruton 1979; Lowe-McConnell 1982) including the introduced largemouth bass (Ludbrook 1974). Utilization of juvenile blue tilapia as forage may be particularly consequential if blue tilapia displace native forage species. The largemouth bass, a popular and economically valuable sport fish in Florida, is a top predator and could potentially be affected by changes in forage fish assemblages. To evaluate the suitability of blue tilapia as forage for bass, I conducted laboratory electivity

experiments to determine the relative preference of largemouth bass for juvenile blue tilapia and bluegill (Lepomis macrochirus). The bluegill is a native centrarchid often prominent in the diet of largemouth bass (McLane 1948; McCammon et al. 1964; Bennett and Gibbons 1972; Chew 1974; Cochran and Adelman 1982).

Methods

Electivity experiments were conducted in 2-m diameter, circular, white, fiberglass tanks housed indoors at the Gainesville National Fishery Research Laboratory. Water clarity was maintained by recirculation through a biological filter.

Most of the largemouth bass were collected locally by electrofishing; several were raised at the laboratory. Bass were acclimated to laboratory conditions for at least one week prior to experimentation. During the acclimation period bass were fed mosquitofish (Gambusia affinis). Blue tilapia were selected from stocks maintained at the laboratory. Bluegill were collected locally by electrofishing or seining, or were procured from the Welaka National Fish Hatchery. Forage 50-60 mm TL were used, as the body depth to length ratios of bluegill and tilapia are equal within this range (Shafland and Pestrak 1981). Larger bluegill (> 60 mm TL) have a greater body depth to length ratio than do blue tilapia of equal length. Body depths of forage (14-18 mm) were within the range ingestable by the smallest bass used (Lawrence 1957; Shafland and Pestrak 1981).

In each trial, 15 blue tilapia and 15 bluegill were introduced to the experimental tank one day prior to the addition of a single bass.

Experiments were terminated when about one-third to one-half of the forage were consumed; trials were generally 7 to 10 days in duration. Forage found dead in the tanks were replaced with fresh individuals. If 3 or more forage fish died in a trial, the trial was aborted. Trials in which bass failed to feed were discarded from further analysis. At the termination of each trial, the experimental tank was drained and remaining forage were counted. Ten acceptable trials were completed.

Two additional trials were conducted in which bass were offered bluegill and tilapia of equal weight (6.0-7.0 g). Lengths of blue tilapia and bluegill were 70-75 and 75-80 mm TL, respectively. Body depths of bluegill (25-27 mm) exceeded those of tilapia (20-22 mm).

An attempt was made to evaluate the relative importance of blue tilapia as forage of largemouth bass in Lake George, north-central Florida, during August 1983. Ten seine hauls were made with an 18-m bag seine at randomly-selected littoral locations along the west shore of Lake George to determine the relative abundances of forage species. Seining locations encompassed the major habitat types present including open water. Forage fishes were fixed in 10 % buffered formalin and enumerated in the laboratory. Concurrently, largemouth bass were collected by electrofishing at the same locations. Bass stomachs were excised immediately and preserved in 10 % buffered formalin. Ingested prey were identified and enumerated in the laboratory.

Results

In 10 trials (1-10) with 50-60 mm TL forage, bass consumed more tilapia than bluegill in 8 cases (Table 14). Overall, bass consumed about twice as many tilapia as bluegill, but selection was not

Table 14. Prey consumed by largemouth bass in laboratory electivity experiments. Blue tilapia and bluegill of equal length and body depth were offered in trials 1 through 10. Forage of equal weight were used in trials 11 and 12.

Trial	Total length of largemouth bass (mm)	Number consumed and percent of diet			
		blue tilapia		bluegill	
		n	%	n	%
Forage of equal length and body weight					
1	189	2	16.7	10	83.3
2	274	5	35.7	9	64.3
3	190	11	78.6	3	21.4
4	203	7	87.5	1	12.5
5	196	7	63.6	4	36.4
6	222	11	64.7	6	35.3
7	211	13	92.8	1	7.1
8	225	9	64.3	5	35.7
9	174	8	61.5	5	38.5
10	294	9	100.0	0	0.0
Forage of equal weight					
11	294	10	83.3	2	16.7
12	298	13	72.2	5	27.8

significantly different from random ($P = 0.095$; Wilcoxon's signed-rank test; Kohler and Ney 1982). A tendency to preference for tilapia could be inferred, however, in consideration of the small sample size. Similarly, Strauss' linear food selection index indicated positive selection for tilapia ($L = + 0.151$; Strauss 1979), but the standard deviation of the measure (0.218) did not allow inference of clear preference. In the two trials (11 and 12) with forage of equal weight, bass consumed more tilapia than bluegills in both experiments (Table 14).

The attempt to evaluate the importance of blue tilapia as forage for largemouth bass in Lake George proved futile. No tilapia were captured by seining (Table 15) and none were recovered from bass stomachs. Stomachs of 13 of 22 bass collected were empty; the remaining 9 fish contained 7 tidewater silversides (Menidia beryllina), 6 shad (Dorosoma spp.), 1 spotted sunfish (Lepomis punctatus), 1 bluegill, 1 golden shiner (Notemigonus crysoleucas), and 5 fish too digested to identify.

Discussion

When offered blue tilapia and bluegill of equal length and body depth, bass tended to consume tilapia preferentially. Optimal foraging theory (Emlen 1966; Schoener 1971; Werner and Hall 1974; Pyke 1979) would predict selection for tilapia in this instance, as the weights of tilapia exceeded those of bluegill. Within the 50-60 mm TL range, blue tilapia (1.9-3.9 g) are heavier than bluegill (1.4-2.8 g). Largemouth bass are ambush predators; ingestion time represents nearly all their handling time (cost) during foraging (Savitz and Janssen 1982). As body

Table 15. Species, numbers, and relative abundances of forage fishes collected in 10 seine hauls, west shore of Lake George, Florida, August 1983.

Common name	Scientific name	n	%
Shad	<u>Dorosoma</u> spp.	450	18.2
Golden shiner	<u>Notemigonus crysoleucas</u>	3	0.1
Atlantic needlefish	<u>Strongylura marina</u>	14	0.6
Seminole killifish	<u>Fundulus seminolis</u>	79	3.2
Tidewater silverside	<u>Menidia beryllina</u>	1654	66.7
Bluegill	<u>Lepomis macrochirus</u>	215	8.7
Redear sunfish	<u>Lepomis microlophus</u>	1	+
Spotted sunfish	<u>Lepomis punctatus</u>	3	0.1
Largemouth bass	<u>Micropterus salmoides</u>	12	0.5
Black crappie	<u>Pomoxis nigromaculatus</u>	23	0.9
Blue tilapia	<u>Tilapia aurea</u>	0	0
Freshwater goby	<u>Gobionellus shufeldti</u>	20	0.8
Naked goby	<u>Gobiosoma bosci</u>	3	0.1
Clown goby	<u>Microgobius gulosus</u>	1	+
		2478	

depths of both forage species were equal, so would be the costs of ingestion. The greater calorific value of a tilapia (assuming comparable energy per unit weight) would make it energetically more profitable to ingest than a bluegill of equal body depth. In the two trials where forage of equal weight were offered, the greater cost of ingesting bluegill due to their greater body depth may have caused bass to select tilapia. Savitz and Janssen (1982) showed that largemouth bass are able to ingest green sunfish (Lepomis cyanellus) more efficiently than bluegill of equal weight because of morphological differences between the two prey species. Bass can probably ingest tilapia more efficiently than bluegill also, as the body shapes of green sunfish and tilapia are similar, at least in comparison to bluegill.

Vulnerability can also depend on the armament and behavior of prey (Ivlev 1961; Hatton 1977). The spines of bluegill are proportionately longer than those of tilapia and may have affected bass foraging choice. Prey motion can influence feeding by bass (Moehn 1959; Hatton 1977; Howick and O'Brien 1983). Tilapia are generally more active than bluegill and may have more readily attracted the attention of bass.

The value of blue tilapia as forage for largemouth bass would appear to be comparable or better than that of bluegill. Swingle (1960) found that growth of bass stocked with tilapia exceeded that of bass stocked with bluegill. In a pond study, Lewis and Helms (1964) reported that bass utilized tilapia as forage to a greater extent than bluegill, green sunfish, or golden shiners. Only black bullhead (Ictalurus melas) were preferred to tilapia. However, gizzard (Dorosoma cepedianum) and threadfin shad (D. petenense) generally are considered to be the

premier piscine forage for largemouth bass (Dubets 1954; Schneidermeyer and Lewis 1956; von Geldern and Mitchell 1975; Jenkins 1979) and it is these species which have been displaced by blue tilapia (Horel 1969; Babcock and Chapman 1973; Ware 1973; Germany 1977) possibly because of dietary similarity (Hendricks and Noble 1979) or selective predation by largemouth bass (Shafland and Pestrak 1981). Shad have greater length and weight to body depth ratios than tilapia because of their more elongate shape and could therefore be expected to be preferred forage (Shafland and Pestrak 1981). The extended spawning season of tilapia may partially nullify this effect however, as indicated by continued rapid growth rates of bass coincident with displacement of shad by tilapia in Trinidad Lake, Texas (Noble et al. 1975). Also, in Lake Kyle, Rhodesia, large bass (> 30 cm) showed a preference for tilapia over compressed fusiform/elongate species morphologically analogous to shad (Ludbrook 1974). Research is needed to elucidate the relative suitabilities of tilapia and shad as forage for largemouth bass, especially with respect to the size-distribution dynamics of the two forage species in natural systems.

Clearly, my experiments provide little information on the ultimate suitability of blue tilapia as forage, except to indicate that bass tend to consume tilapia preferentially over bluegill. Because numerous bass populations have subsisted entirely on bluegill, a diet of tilapia probably would not be disastrous. The distribution, accessibility to predators, size-distribution, relative abundance, and density of blue tilapia in a system compared to other forage will influence their utilization. Only by evaluating these factors can the relative value of blue tilapia as forage be determined. Long-term, intensive studies in

natural systems are needed to determine if juvenile tilapia are spatially available to predators and how their rapid growth and extended reproductive season affect temporal availability.

CHAPTER VII
NEST-SITE SELECTION BY BLUE TILAPIA AND LARGEMOUTH BASS
IN SILVER GLEN SPRINGS RUN:
CIRCUMSTANTIAL EVIDENCE OF COMPETITIVE EXCLUSION

Introduction

Buntz and Manooch (1968) collected spawning blue tilapia, bluegill, and redear sunfish sympatrically along the shoreline of Lake Parker, Florida, and therefore inferred that competition for spawning grounds occurred between these species. Although sympatric spawning may be more indicative of an absence of competition, their observations showed that such competition is conceivable as the nesting habitats of these fishes overlapped. Noble et al. (1975) observed that year classes of largemouth bass apparently failed to recruit in Trinidad Lake, Texas, in the presence of high densities of blue tilapia. They postulated that tilapia suppressed reproduction by bass. Subsequent pond studies (Noble et al. 1975; Shafland and Pestrak 1983) established that high densities of blue tilapia may inhibit or suppress nesting activity of largemouth bass under experimental conditions.

Competition with centrarchids for nesting habitat has therefore often been invoked as a major ecological impact of blue tilapia in U.S. waters (e.g. Ware 1973; Courtenay et al. 1974; Taylor et al. 1984). However, no studies have been conducted to investigate this interaction under field conditions.

I investigated the impacts of blue tilapia on nesting by largemouth bass in Silver Glen Springs Run (SGSR). A description of the

study site is presented in Chapter III. Historically, SGSR has been a major spawning area for largemouth bass in Lake George. In a comprehensive survey of nesting areas of largemouth bass in Lake George during the 1951 spawning season, Horel (1951) located 46 bass nests throughout the lake. Of these, 28 were found in SGSR. All bass nests in the run were associated with stands of eelgrass (Vallisneria americana) situated on sand substrates. Mean depth of nests was 0.75 m (range 0.58-0.94 m, S.D.= 0.10). Blue tilapia were first observed nesting in SGSR in 1976 or 1977 (J. Morgan, personal communication); many tilapia nests are now readily apparent in the run during late winter and early spring.

Spawning by largemouth bass is behaviorally suppressed in crowded environments (Chew 1972) in response to high rates of interspecific encounter (Barwick and Holcomb 1976; Smith 1976; Smith and Crumpton 1977). In the presence of high fish abundances, male largemouth bass elect not to construct nests, and therefore forego reproduction. Aggregations of nesting blue tilapia, in habitats suitable for nesting by bass, would therefore be expected to inhibit nesting by bass. Suppression would be expected to vary as a function of the density of tilapia.

I characterized nest-site selection by blue tilapia in SGSR using Horel's (1951) criteria (depth, substrate and vegetation) and compared these preferences to those of bass prior to the presence of tilapia (i.e. Horel's data). If microhabitat preferences of blue tilapia for nest sites corresponded to those of bass in allopatry, then behavioral suppression of nesting by bass could be inferred. Conversely, if nest

sites of bass and tilapia were mutually exclusive, nesting activity of bass in sympatry would be expected to be undisturbed.

Furthermore, I predicted that if tilapia were interfering with nesting by bass in SGSR, then nest densities of bass in the run would be depressed from prior abundances and/or locations of bass nests would be displaced from microhabitats formerly occupied. However, because populations and environments vary over time, such changes would not conclusively demonstrate interspecific competition (Connell 1983); without replicates and controls, inference of competition would be tenuous.

The seasonal timing of nesting in SGSR was also determined. Discontemporaneous spawning by bass and tilapia would obviate competition for nest sites.

Methods

The periodicity of nesting by blue tilapia in SGSR was determined from November 1982 through August 1983 at roughly monthly intervals. All blue tilapia nests within 3 standardized areas (cells) were counted from a boat. The cells were selected from shallow areas used by nesting tilapia in previous years where floating vegetation and other obstructions did not hinder vision. Cells were delineated by natural, static landmarks and were unequal in area. Counts were made only when wave action was minimal. Only active nests (lacking accumulations of detritus) were counted.

Nest-site selection by tilapia was evaluated by comparing relative abundances of active nests in various habitats within the run to the availability of these habitats. Habitats were classified by water

depth, vegetation, and substrate. SGSR was divided into 21 50-m sections numbered sequentially 1 to 21, the latter located at the confluence of the run with Lake George. Depth contours (0.5 m) and substrate/vegetative characteristics were mapped for 5 randomly-selected sections (sections 5, 11, 15, 16, and 20). The following four substrate/vegetation types were recognized: 1) open sand, no vegetation; 2) hydrilla (Hydrilla verticillata) and eelgrass, sand interspersed with pockets of detrital material (H/E/S/D); 3) hydrilla and eelgrass, surface of substrate comprised of detritus only with no sand evident (H/E/D); and 4) emergent (Scirpus sp., Nuphar luteum, Pontederia lanceolata, Sagittaria lancifolia, Hydrocotyle umbellata) and floating (Eichhornia crassipes, Pistia stratiotes, Salvinia rotundifolia) vegetation, sand and detritus (E/F/S/D). Areas (in square meters) encompassed by each depth class, substrate/vegetation type, and combination thereof were determined from the maps with a digitizing pad linked to a microcomputer. Tilapia nests within each combination of depth and substrate/vegetation type were counted within each of the 5 sections during March 1983. Most nests were counted from a boat, but I also snorkeled in densely-vegetated areas to ensure detection of all nests.

I surveyed the entire run for bass nests at least once monthly from January to April 1983 by boat and snorkeling. Depth and substrate/vegetation type were recorded for each bass nest encountered.

Results

No tilapia nests were observed in the 3 nesting-periodicity cells in November or December 1982, but several shallow excavations, believed

to be incipient nests, were present elsewhere in the run in December. From January through March 1983, many tilapia nests were counted in the cells (Fig. 18). Nesting intensity appeared to be relatively constant during this period. In April and May, nest abundances declined, and very few nests remained in June. No nests were found anywhere in the run in August. Nest abundances declined as tilapia emigrated from the run (see Chapter III). Concurrently, tilapia nests appeared along the shorelines of Lake George.

Depth appeared to be an important factor influencing nest-site selection by tilapia (Fig. 19). In each section, and in aggregate, the depth distributions of nests and available area were significantly different (all $P < 0.005$, chi-square test). Tilapia nested in shallower waters than would be expected if nest-site selection was independent of depth.

Highest nest densities observed were in the 0-0.5 m depth classes of sections 5 and 20 (Fig. 20); with all sections combined, nest densities were highest within this depth range. However, in sections 11, 15, and 16, nest densities were highest between 0.5 and 1.0 m (Fig. 20). In section 11, no nests were found in water shallower than 0.5 m. At depths greater than 1.0 m, nest densities progressively decreased in all sections. The greatest number of nests was found between 1.0 and 1.5 m, but the area at this depth within the 5 sections also comprised the largest proportion (Fig. 19), resulting in low densities.

The relationship between nest-site selection by tilapia and substrate/vegetative characteristics appeared to be largely mediated by depth. Highest nest densities were found in E/F/S/D habitat (Fig. 21); this habitat was restricted to water less than 1.5 m in depth (Fig.

Fig. 18. Temporal changes in tilapia nest abundances within 3 standardized cells (A, B, and C) in Silver Glen Springs Run, November 1982 to August 1983.

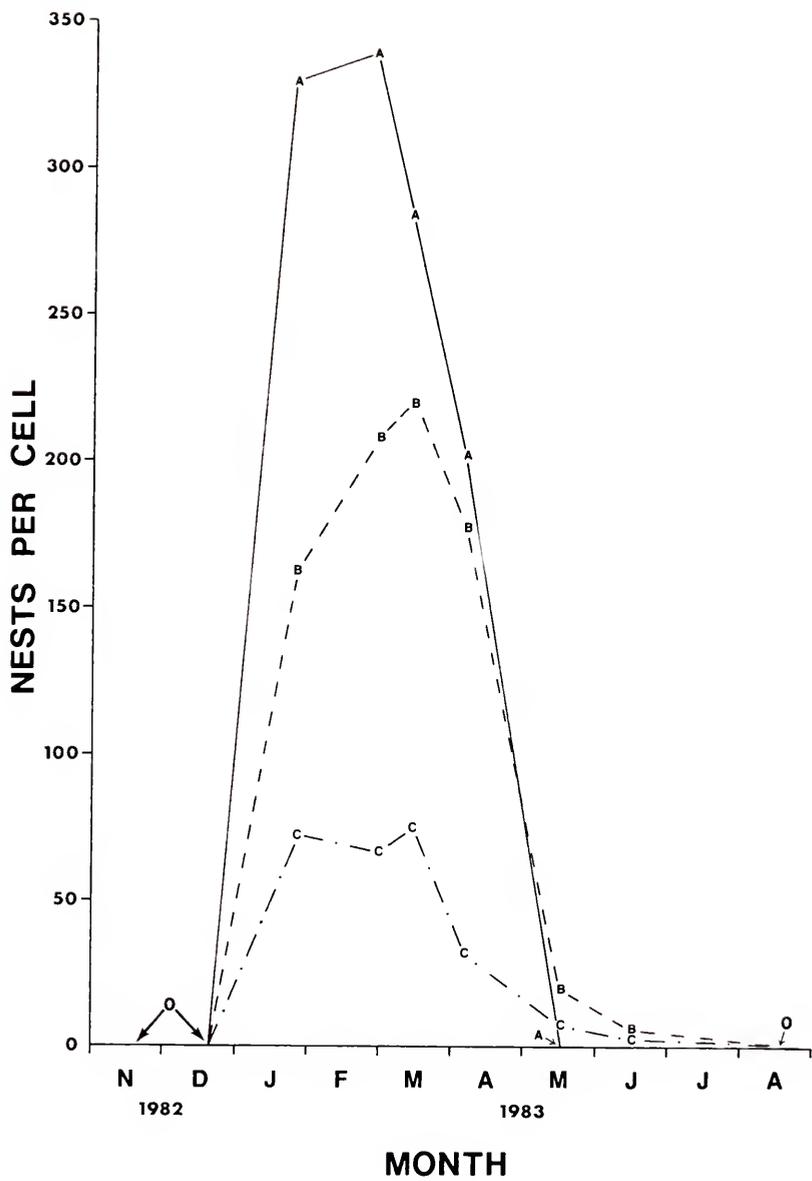


Fig. 19. Frequency distributions of tilapia nests (shaded) and available areas (open) within 0.5-m depth classes in five 50-m sections of Silver Glen Springs Run, March 1983. The final (lower right) graph is an aggregate of the five sections.

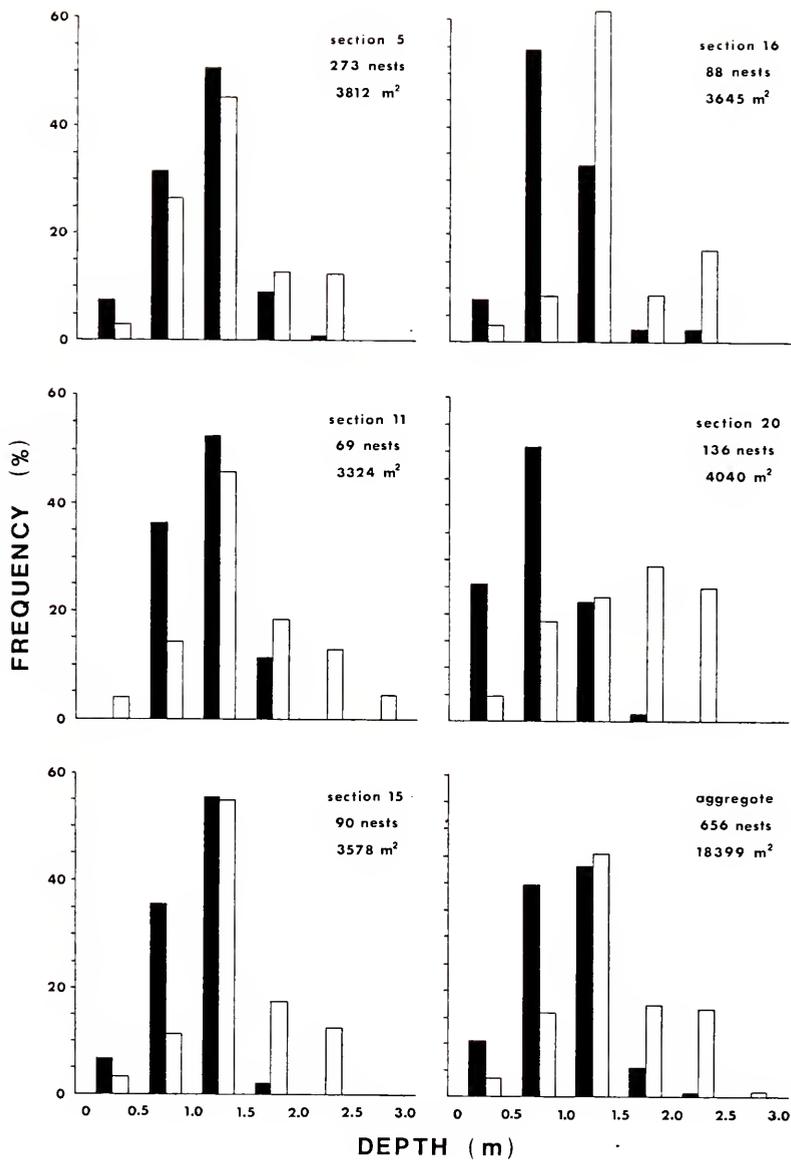


Fig. 20. Densities (per m^2) of tilapia nests within 0.5-m depth classes in five 50-m sections of Silver Glen Springs Run, March 1983. The final (lower right) graph is an aggregate of the five sections.

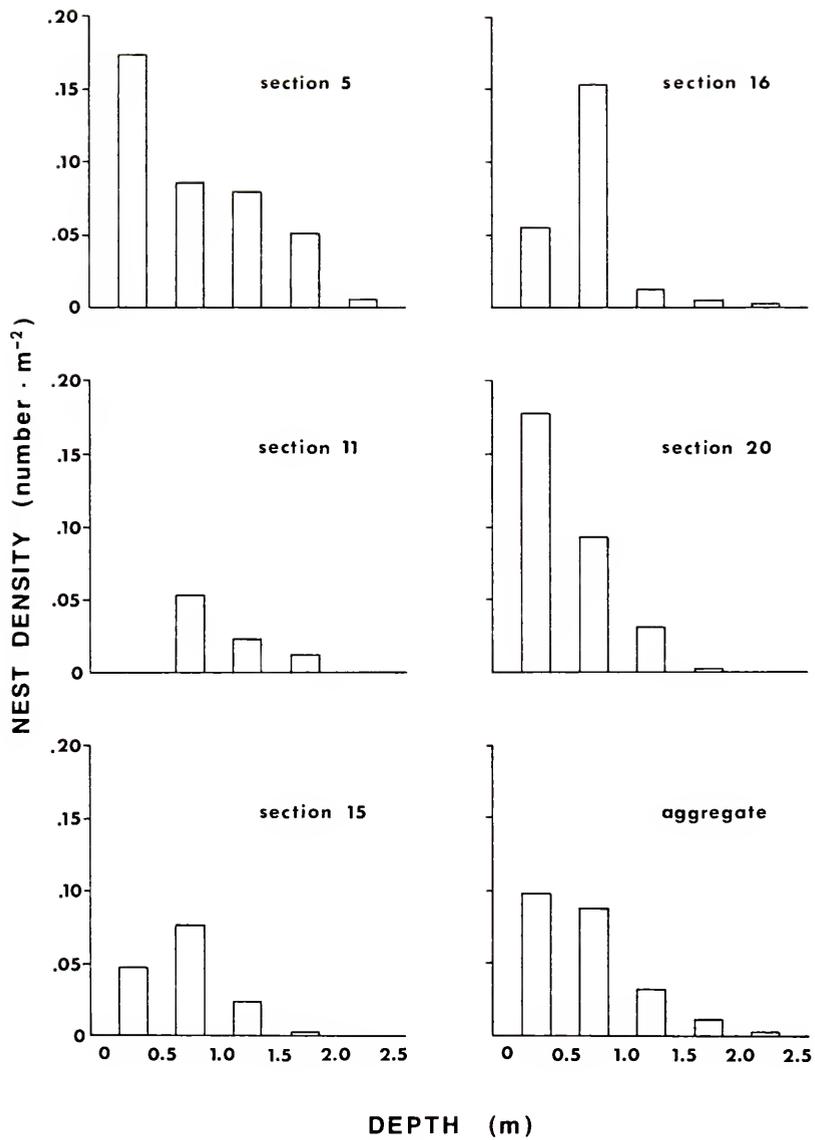
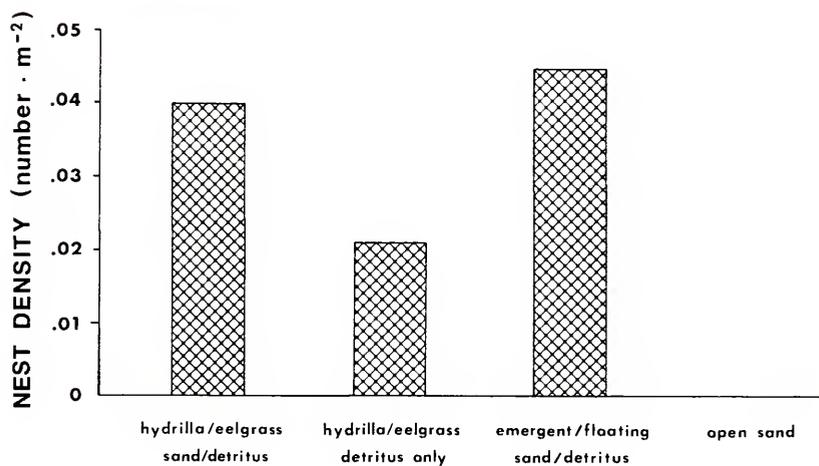
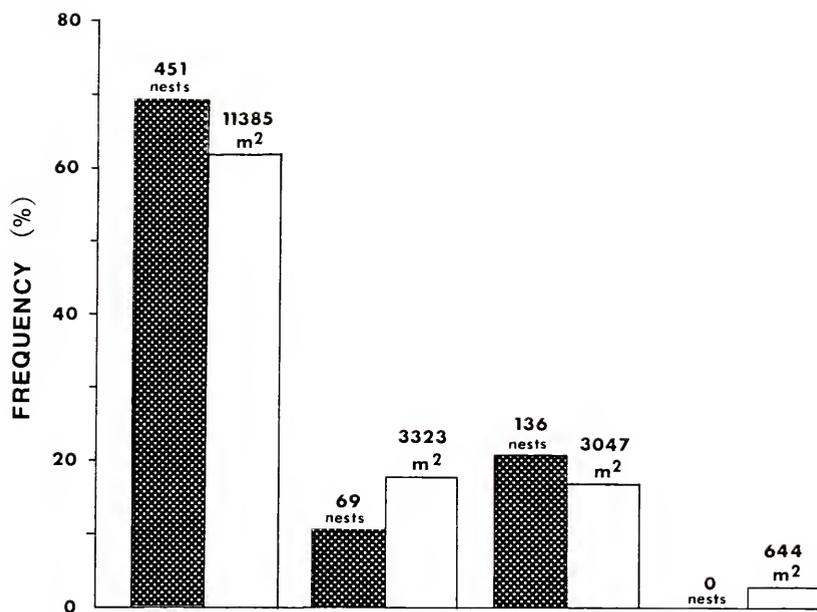


Fig. 21. Pooled frequency distributions of tilapia nests and available areas (upper) and nest densities (lower) within 4 substrate/vegetation types in five 50-m sections of Silver Glen Springs Run, March 1983.



22). Nest densities were slightly lower in H/E/S/D habitat (Fig. 21) as this habitat type encompassed a wide range of depths (Fig. 22). Most of the nests in the 5 sections (451 of 656) were found in this habitat. Relatively low nest densities occurred in H/E/D habitat (Fig. 21); these areas were generally located in deeper water (Fig. 22). An exception to the interaction between depth and habitat was evident on open sand. Although this habitat was restricted to a 0.5-1.0 m deep sand bar in section 5, no tilapia nested there (Fig. 21).

Considering both depth and habitat type simultaneously, nest densities were highest in H/E/S/D habitat at depths less than 1.0 m (Fig. 22). Moderate densities of nests occurred at 0.5-1.0 m in H/E/D and E/F/S/D habitats (Fig. 22), but densities at depths less than 0.5 m in the latter habitat were relatively low. Dense vegetation may have decreased the suitability of these sites.

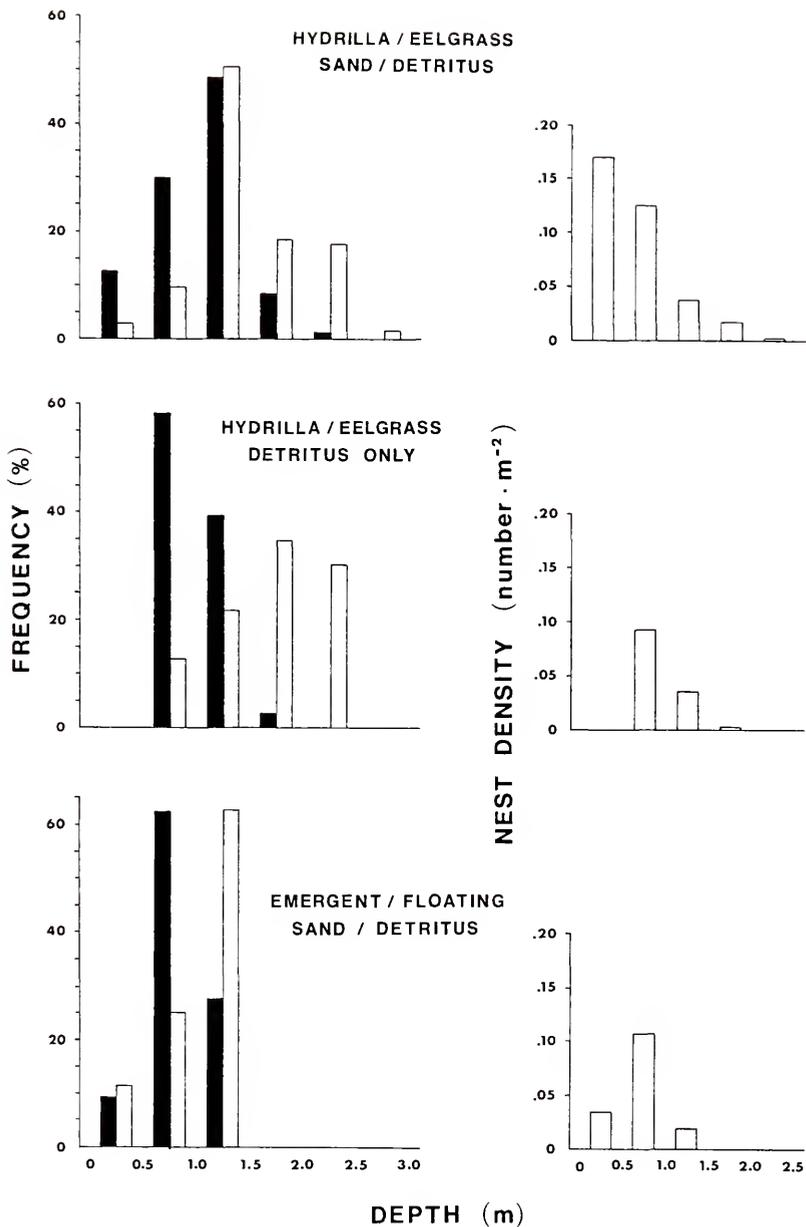
The total number of tilapia nests in SGSR was estimated at 2962 (95 % CI = 2761-3164) by extrapolating depth-stratified nest density estimates to the total area of the run.

Only 2 bass nests were located in SGSR in 1983, both on 3 March. Both were located in H/E/S/D habitat at depths of 1.5 and 1.8 m. In February 1982, I noted 2 bass nests while swimming transects. These were also located in H/E/S/D habitat, both in 1.2 m of water.

Discussion

Blue tilapia and largemouth bass nested concurrently in SGSR and therefore did not avoid competition for nest sites through temporal partitioning of the run. However, the degree of temporal overlap may be somewhat less overt in variable-temperature environments in

Fig. 22. Pooled frequency distributions of tilapia nests (shaded) and available areas (left) and nest densities (right), segregated by substrate/vegetation types, within 0.5-m depth classes in five 50-m sections of Silver Glen Springs Run, March 1983.



north-central Florida. Blue tilapia require water temperatures of 22-24 C to initiate reproductive activities (Yashouv 1958; McBay 1961; Fishelson 1966; Payne and Collinson 1983). Water temperatures in SGSR (22.8-24.0 C) barely exceeded this criterion. Nesting by blue tilapia in Lake George was observed only after water temperatures in the lake exceeded 22 C, usually in late March or April. Spawning in the lake appeared to peak in May. The peak period of spawning for largemouth bass in this section of the St. Johns River generally occurs in March and April (McLane 1948; Horel 1951), and spawning may occur as early as January (McLane 1955). Horel (1951) reported that bass began spawning in Lake George when water temperatures attained 18.3 C, and Chew (1974) observed peak nesting activity at 15.6-18.3 C in nearby Lake Weir. Clugston (1966) reported that largemouth bass in south Florida commenced spawning in winter when water temperatures decreased to 15.6 C. The Florida subspecies therefore appears to spawn at slightly lower temperatures than do northern largemouth bass (Chew 1975); northern bass typically spawn at 19-22 C (Coutant 1975). Significant temporal segregation of spawning bass and tilapia may therefore occur in eurythermal surface-waters, thereby reducing overlap considerably. Over time, selection for early spawning among bass may occur where tilapia and bass are sympatric, if early spawning significantly enhances reproductive success. Complete overlap probably occurs only in systems, like SGSR, with unusual thermal properties. In stenothermal spring runs in Florida, largemouth bass spawn at the same time as bass in variable-temperature environments (Caldwell et al. 1957).

Tilapia preferentially selected nest sites in vegetated, shallow-water areas in SGSR. However, nest densities in the shallowest

areas (< 0.5 m) were variable; areas where the entire water column was densely vegetated or where the bottom sloped steeply, were avoided. Low nest densities in water less than 0.5 m deep in sections 11, 15, and 16 were probably related to these factors, particularly the latter. In these sections, most of the area within this depth range consisted of a steeply-sloping thin band (< 1 m wide) immediately adjacent to the shoreline. Sections 5 and 20, which had higher nest densities, were characterized by wide expanses of gently-sloping or flat, moderately-vegetated habitat less than 0.5 m deep.

Reports describing habitats used by blue tilapia for nesting are few and lack detail, but are in general agreement with my findings in SGSR. McBay (1961) noted that blue tilapia nested on sand at depths of about 0.6 m in experimental ponds. In Lake Parker, Florida, nests were on sand in shallow water along the shoreline (Buntz and Manooch 1968). Shafland and Pestrak (1983) reported that blue tilapia preferred sand substrate to gravel for nesting in experimental ponds. Payne and Collinson (1983) noted that nests of blue tilapia were restricted to "shallow-water weedy areas" in the Nile Delta, Egypt.

Habitat preferences of other mouthbrooding tilapias are similar to those of blue tilapia in SGSR. Lowe-McConnell (1956) reported that I. karomo nested at depths of 0.5 to 1.5 m on sand/detritus substrate near submergent vegetation in the Malagarasi Swamps, Tanzania. In Lake Kyoga, Uganda, I. variabilis nest on sand/detritus substrate in 0.15 to 1.0 m deep water (Lowe-McConnell 1956). In Lufira Reservoir, Zaire, I. macrochir nest at a depth of 0.8 to 1.5 m (mode, 1.2-1.3 m) on flat bottom (Ruwet 1962). Whyte (1975) reported finding nests of I. multifasciata at depths of about 1 to 3 m on sandy substrates among

weed beds or in open water in Lake Bosumtwi, Ghana. In Lake Sibaya, South Africa, Bruton and Boltt (1975) located nests of T. mossambica at depths ranging from 0.4 to 8.5 m, but densities were highest between 0.5 and 1.0 m. Nest densities were highest in moderately-vegetated areas, lower where macrophytes were dense, and lowest in non-vegetated areas. In Parakrama Samudra, Sri Lanka, nest densities of T. mossambica were highest between 0.4 and 0.6 m (DeSilva and Chandrasoma 1980).

Prior to invasion of SGSR by tilapia, largemouth bass nested exclusively on sand substrates near vegetation at depths between 0.5 and 1.0 m in the run (Horel 1951). This habitat now supports high densities of tilapia nests. Because nesting by largemouth bass is behaviorally suppressed under crowded conditions (Chew 1972; Barwick and Holcomb 1976; Smith 1976; Smith and Crumpton 1977), the presence of numerous nesting tilapia has probably impacted use of the run by spawning bass. Accordingly, the number of bass nests in the run has declined (from 28 to 2), and the few remaining nests are in deeper water (where tilapia nest densities are lower). Tilapia appear to have effectively excluded bass from nesting in the habitat they formerly occupied. Harris (1978) reported anecdotal evidence of a similar decline in bass nest abundances (from about 20-30 nests to one) following colonization by tilapia in DeBary Creek, a spring run flowing from Gemini Springs to Lake Monroe in Volusia County, Florida.

These findings should not be construed to be definitive evidence of competitive exclusion; the observed changes in abundances and locations of bass nests may have developed through other means. Correlative observations are prone to misinterpretation, especially in the absence of replication.

The physical environment of SGSR (and other spring runs) is conducive to nesting by largemouth bass. Constant temperature and sheltered surroundings preclude temperature fluctuations and excessive wave action caused by cold fronts and storms. The effects of these factors during the nesting period appear to be the primary causes of variation in year-class strength in largemouth bass populations (Kramer and Smith 1962; Miller and Kramer 1971; Allan and Romero 1975; Eipper 1975; Summerfelt 1975). If blue tilapia deter bass from nesting in spring runs, impacts on bass populations may be considerable, particularly during years in which the spawning season is characterized by inclement weather.

CHAPTER VIII
REPRODUCTIVE BIOLOGY OF BLUE TILAPIA IN
SILVER GLEN SPRINGS RUN / LAKE GEORGE, FLORIDA

Introduction

Aspects of the reproductive biology of many species of tilapia have been documented (see reviews by Philippart and Ruwet 1982 and Jalabert and Zohar 1982), but little such information exists on the blue tilapia, especially for free-living populations in open waters. Because knowledge of the reproductive biology of an exotic species is essential for its effective management, I investigated this component of the life history of the blue tilapia population of Silver Glen Springs Run / Lake George, Florida.

Methods

Blue tilapia were collected in Silver Glen Springs Run (SGSR) by gill-netting (see Chapter III for details) from November 1981 to April 1983 at about monthly intervals. Fish were also collected in Lake George (LG) at a site about 1 km south of SGSR from May 1982 to August 1982, and again from April 1983 to July 1983 to supplement sample sizes; abundances of tilapia in the run were low during summer.

Total and standard lengths (TL and SL, respectively) were measured to the nearest mm; fish were weighed to the nearest g. Gonads were excised, sexed, weighed to the nearest 0.001 g, and preserved in 10 %

buffered formalin. Gonadosomatic index (GSI) values were calculated ($GSI = (\text{gonad weight}/\text{total weight}) \times 100$) using fresh weights.

Size-frequency distributions of intraovarian oocytes were determined for 3 or 6 randomly-selected females from each month from December 1981 to December 1982. An absence of females in the March and April 1982 samples necessitated substitution with fish from 1983 for these months. Only fish weighing 1000-1300 g were used in this analysis, as egg sizes are correlated with female weight in tilapia (Peters 1963). About 500 oocytes from the central portion of one preserved ovary of each fish were measured to the nearest 0.1 mm using an ocular micrometer mounted in a dissecting microscope. Preliminary analyses showed that oocyte size distributions were homogeneous throughout each ovary and did not differ between pairs of ovaries. Only oocytes > 0.5 mm were measured; smaller oocytes were previtellogenic and constituted a fixed distribution throughout the year.

Fecundities of 75 ripe females were determined by gravimetric estimation. After weighing both preserved ovaries, a portion (about 25 %) of one was cut off and weighed. The number of fully-developed ova within the portion was counted, and the total contained in both ovaries was estimated by simple extrapolation.

Results

Plots of GSI's against total weights by month indicated that gonad weights of age-0 tilapia (both sexes) tended to comprise a slightly smaller proportion of total body weight than in older (larger) fish. Fish weighing more and less than 600 g were therefore treated separately. This weight approximates the size of individuals in this

population at the transition from age-0 to age-I (Chapter IX). GSI's and body weights were not correlated within the two weight groups.

Mean GSI values for both sexes cycled annually in synchrony. For fish weighing > 600 g, mean GSI's increased during fall and early winter, declined in spring and summer, and reached an annual low in September (Fig. 23). A similar sequence was apparent among age-0 fish through 1982 (Fig. 24), but gonadal recrudescence lagged behind that of larger fish in 1983.

Considerable heterogeneity in GSI values was apparent within some months, especially for the female component of the population. Much of this variability was reflected in the size-frequency distributions of intraovarian oocytes. As GSI's increased from December 1981 through February 1982, a single class of yolked ova broke away from the reserve of primary oocytes and increased in size (Fig. 25). In March, this class of large eggs was still extant in the ovaries of many fish, but had disappeared in others (Fig. 26), indicating commencement of spawning by some individuals. A second wave of vitellogenic oocytes was forming in the ovaries of the recently-spawned fish, and several unconsolidated, yolky masses, presumably unspawned eggs undergoing resorption, were also present. The oocyte size distribution in the ovaries of a brooding female captured in May 1983 was similar (Fig. 27). Oocyte size-frequency distributions remained variable through June, with both ripe and ripening females present (Figs. 28-30), indicative of continued spawning and recrudescence. In July and August (Figs. 31 and 32), samples yielded some ripening females, but the ovaries of others were entering quiescence; no new wave of vitellogenic oocytes was forming in these fish. No ripe females (GSI's > 2.0) were

Fig. 23. Seasonal variation in mean gonadosomatic index (GSI) values of female (solid circles) and male (open circles) blue tilapia >600 g total weight from Silver Glen Springs Run and Lake George, Florida, November 1981 to July 1983. Vertical bars represent ± 1 SD. Numbers adjacent to means represent the number of observations in each sample.

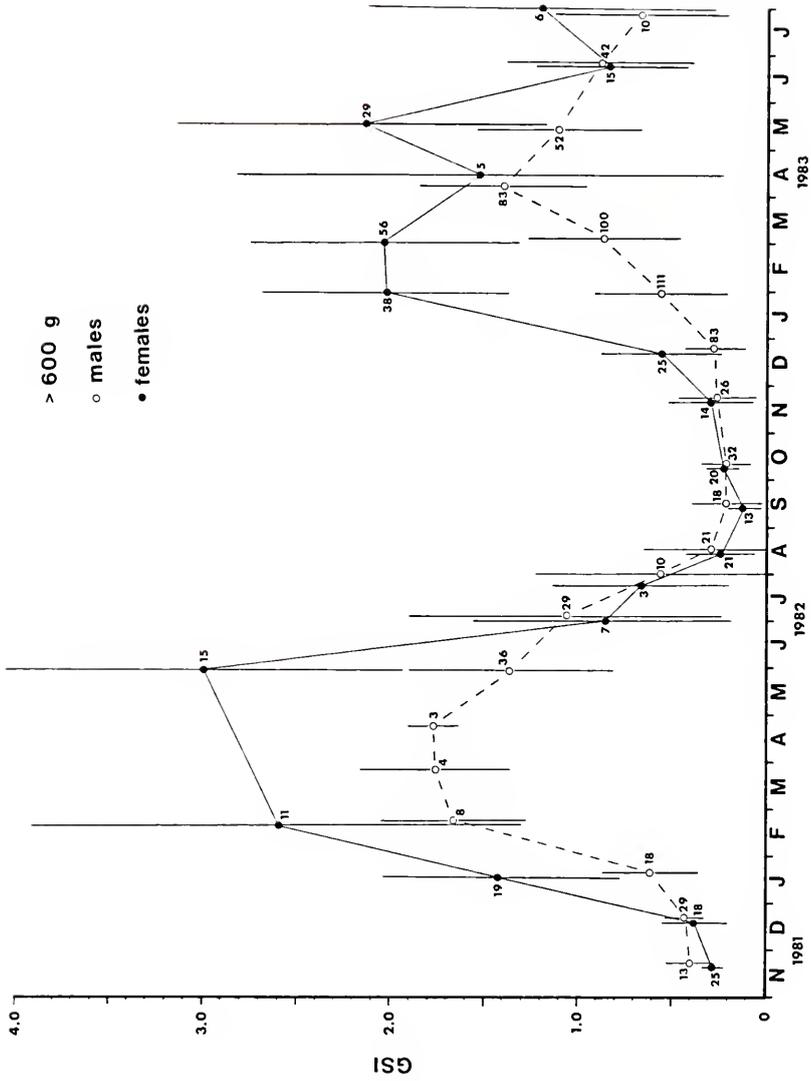
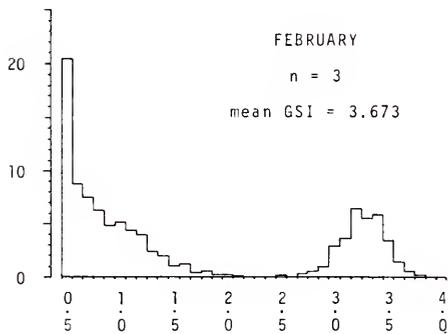
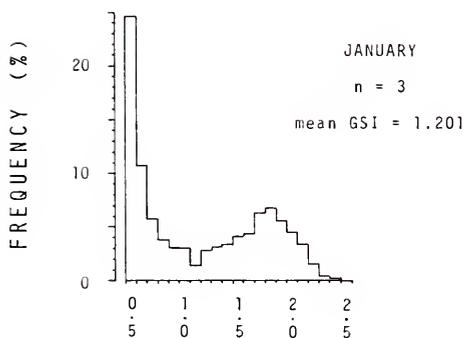
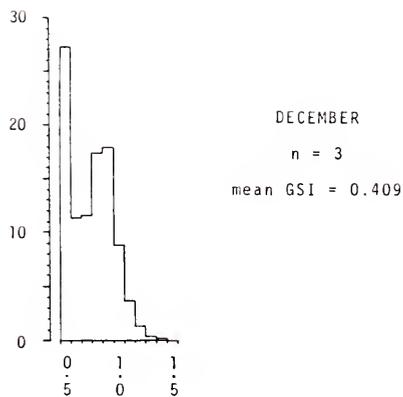


Fig. 24. Seasonal variation in mean gonadosomatic index (GSI) values of female (solid circles) and male (open circles) blue tilapia <600 g total weight from Silver Glen Springs Run and Lake George, Florida, November 1981 to May 1983. Vertical bars represent ± 1 SD. Numbers adjacent to means represent the number of observations in each sample.

Fig. 25. Size-frequency distributions of intraovarian oocytes for female blue tilapia 1000-1300 g total weight from Silver Glen Springs Run, Florida, December 1981 to February 1982. Each distribution is a composite for 3 females, averaged by interval (individual distributions were homogeneous within these months).



DIAMETER (mm)

Fig. 26. Size-frequency distributions of intraovarian oocytes for individual female blue tilapia 1000-1300 g total weight from Silver Glen Springs Run, Florida, March 1983.

MARCH

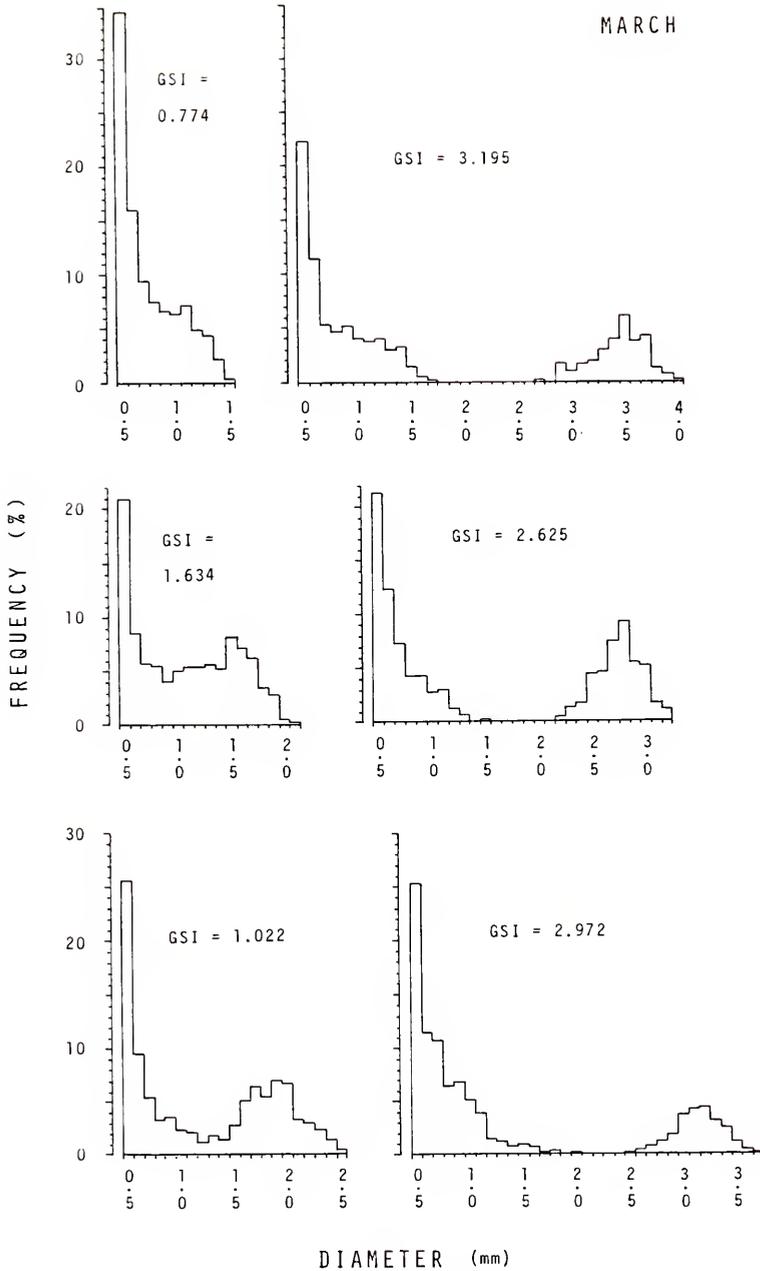


Fig. 27. Size-frequency distribution of intraovarian oocytes for a brooding female blue tilapia 1175 g total weight captured 12 May 1983, Lake George, Florida. Based on the stage of development of the brooded young, the female was estimated to have spawned about 10 days prior to capture.

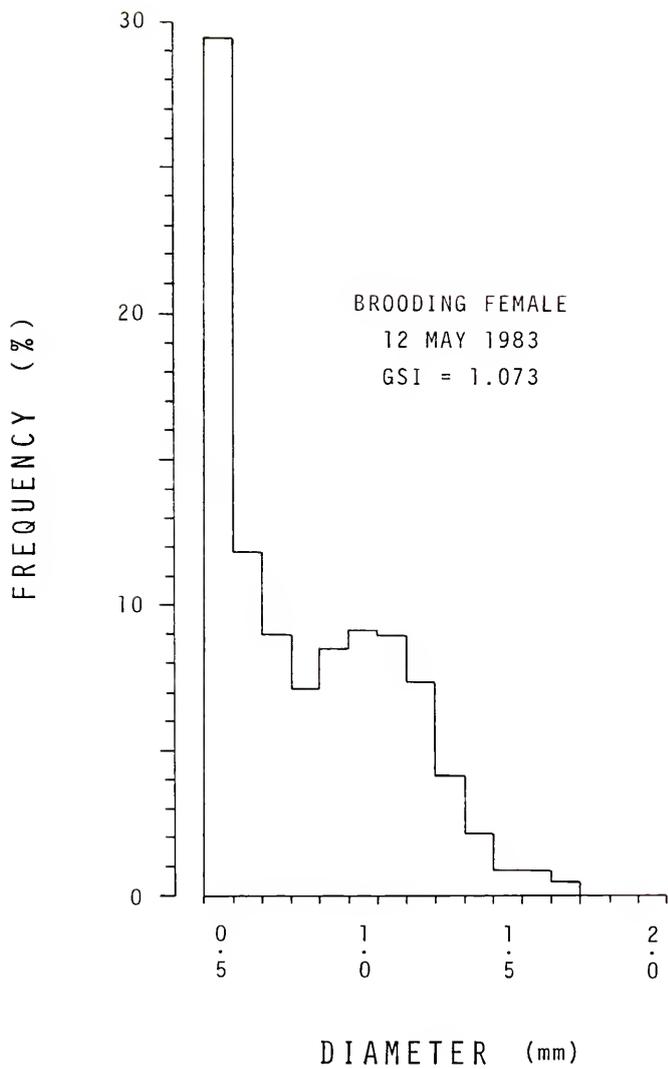
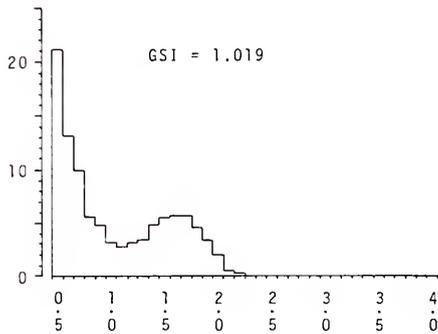
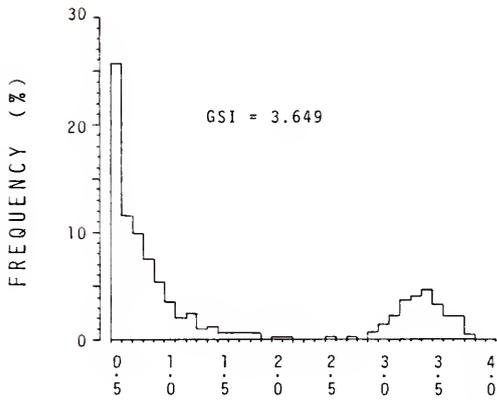
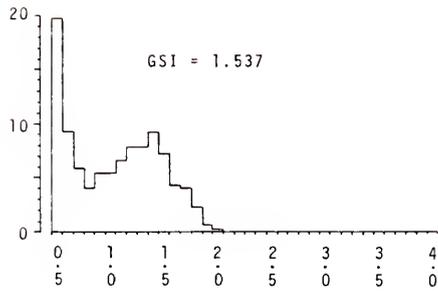


Fig. 28. Size-frequency distributions of intraovarian oocytes for individual female blue tilapia 1000-1300 g total weight from Lake George, Florida, April 1983.

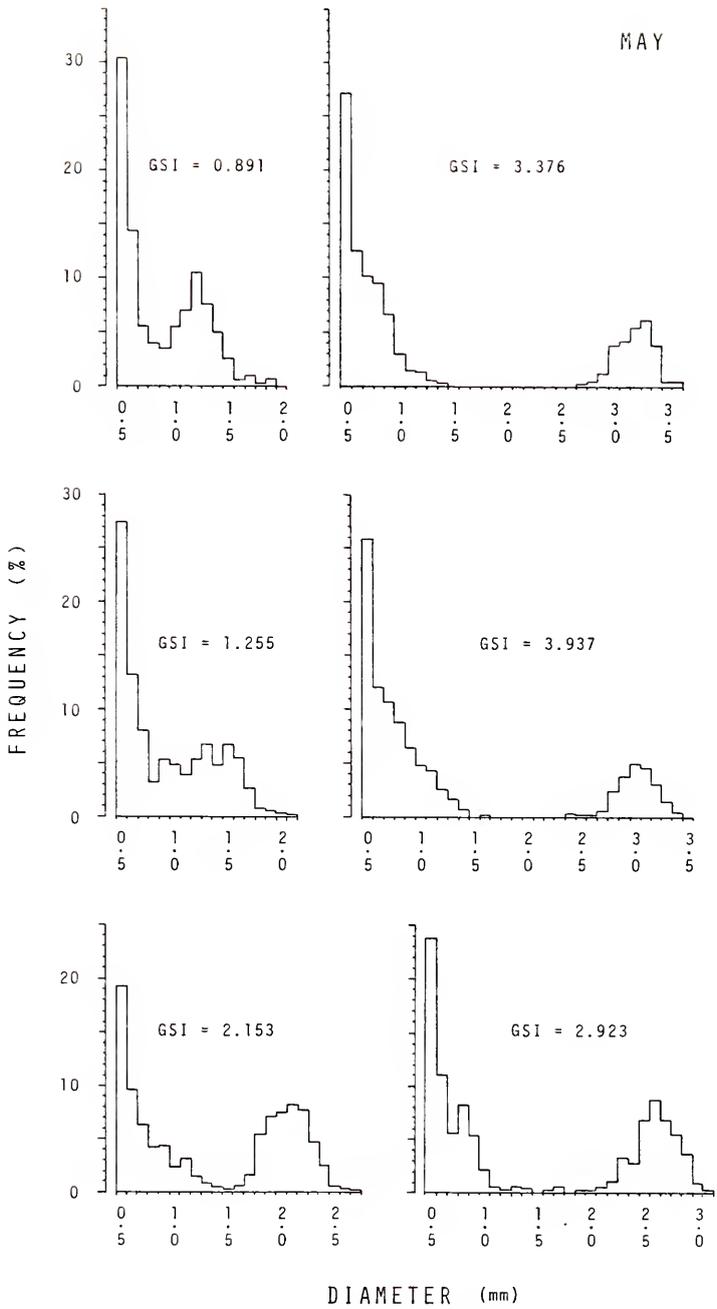
APRIL



DIAMETER (mm)

Fig. 29. Size-frequency distributions of intraovarian oocytes for individual female blue tilapia 1000-1300 g total weight from Lake George, Florida, May 1982.

MAY



DIAMETER (mm)

Fig. 30. Size-frequency distributions of intraovarian oocytes for individual female blue tilapia 1000-1300 g total weight from Lake George, Florida, June 1982.

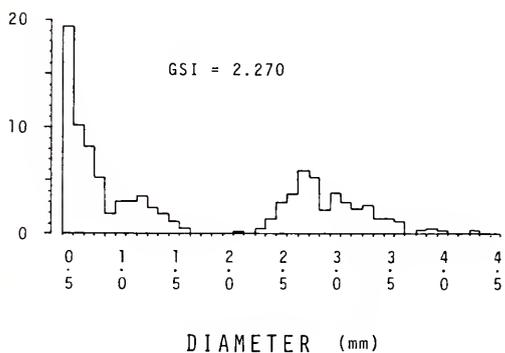
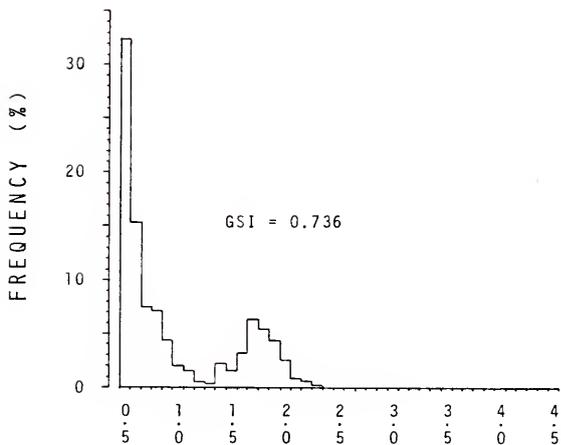
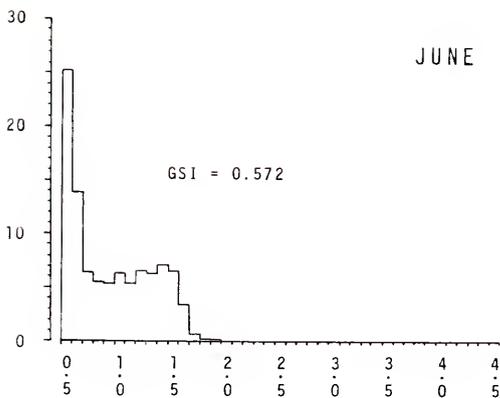


Fig. 31. Size-frequency distributions of intraovarian oocytes for individual female blue tilapia 1000-1300 g total weight from Lake George, Florida, July 1982.

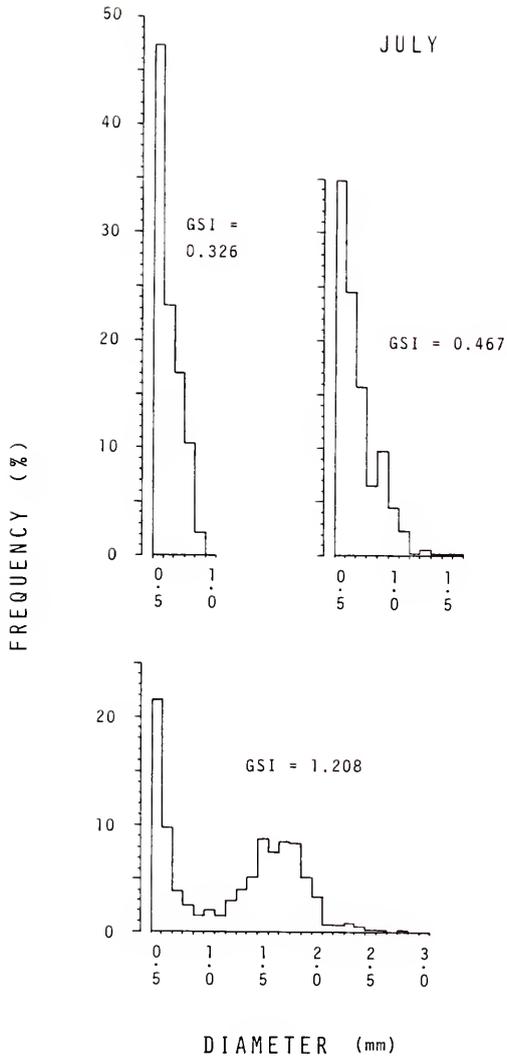
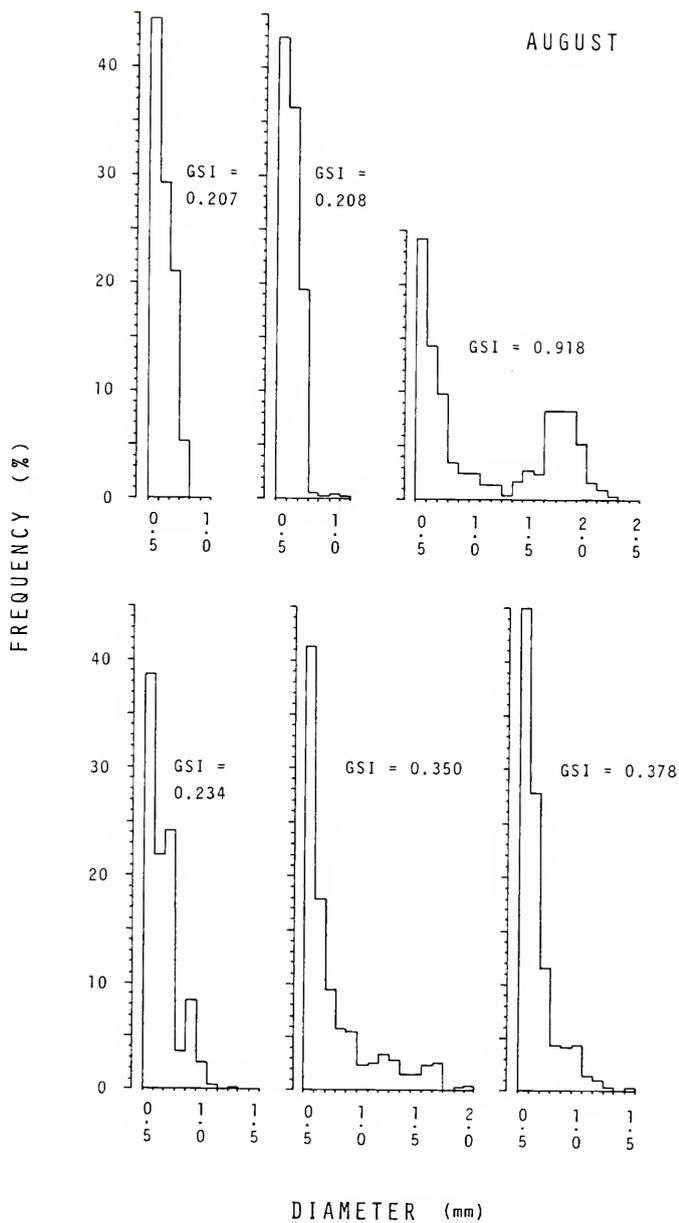


Fig. 32. Size-frequency distributions of intraovarian oocytes for individual female blue tilapia 1000-1300 g total weight from Lake George, Florida, August 1982.

AUGUST



collected in July or August. All examined ovaries appeared to be quiescent from September through November (Fig. 33), coinciding with low GSI values. Gonadal recrudescence was again evident in December 1982 (Fig. 33).

Fecundity estimates for ripe females ranged from 1359 to 8599. These estimates included only the large size-class of yolked eggs. Fecundity increased curvilinearly with length (Figs. 34 and 35) and linearly with weight (Fig. 36). Considerable deviation from the estimated regressions was evident; fecundities of 6 fish, all about 400 mm TL, were higher than expected.

Discussion

The simultaneous presence of ripe, ripening, and recently-spawned females from March through June, and concurrent gradual decline in relative testes weights, infer that spawning by the blue tilapia population in SGSR/LG extended primarily through spring and early summer. The large decreases in mean GSI's of females from May to June indicate that recrudescence of ovaries declined thereafter, but the presence of some ripening females in July and August infers that some spawning may have occurred through mid-summer.

Temperature and photoperiod are the primary proximate environmental factors influencing the reproductive cycle in fishes (de Vlaming 1972, 1974; Crim 1982). In this population, the annual cycle of gonadal maturation appeared to be influenced more by photoperiod than temperature. Ovarian and testicular recrudescence were initiated in December, following the winter solstice, and continued through spring as daylength increased. Although temperatures in Lake George remained

Fig. 33. Size-frequency distributions of intraovarian oocytes for female blue tilapia 1000-1300 g total weight from Silver Glen Springs Run and Lake George, Florida, September to December 1982. Each distribution is a composite for 3 females, averaged by interval (individual distributions were homogeneous within these months).

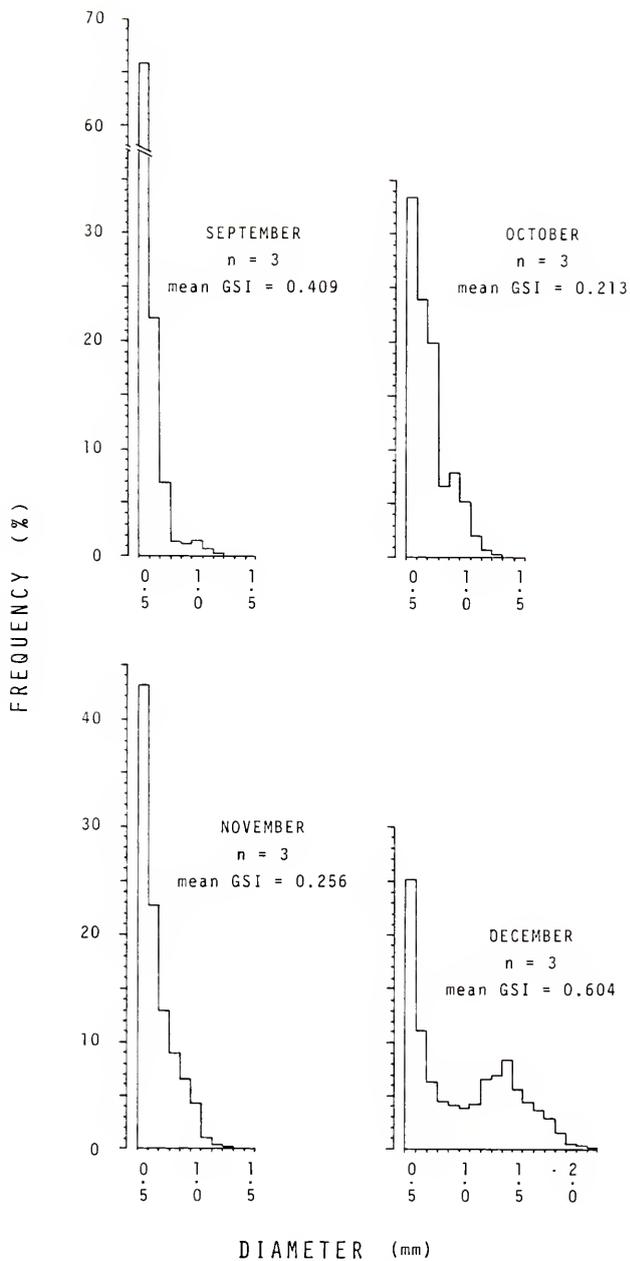


Fig. 34. Relationship of ovarian fecundity to total length (mm) for 75 ripe female blue tilapia from Silver Glen Springs Run and Lake George, Florida.

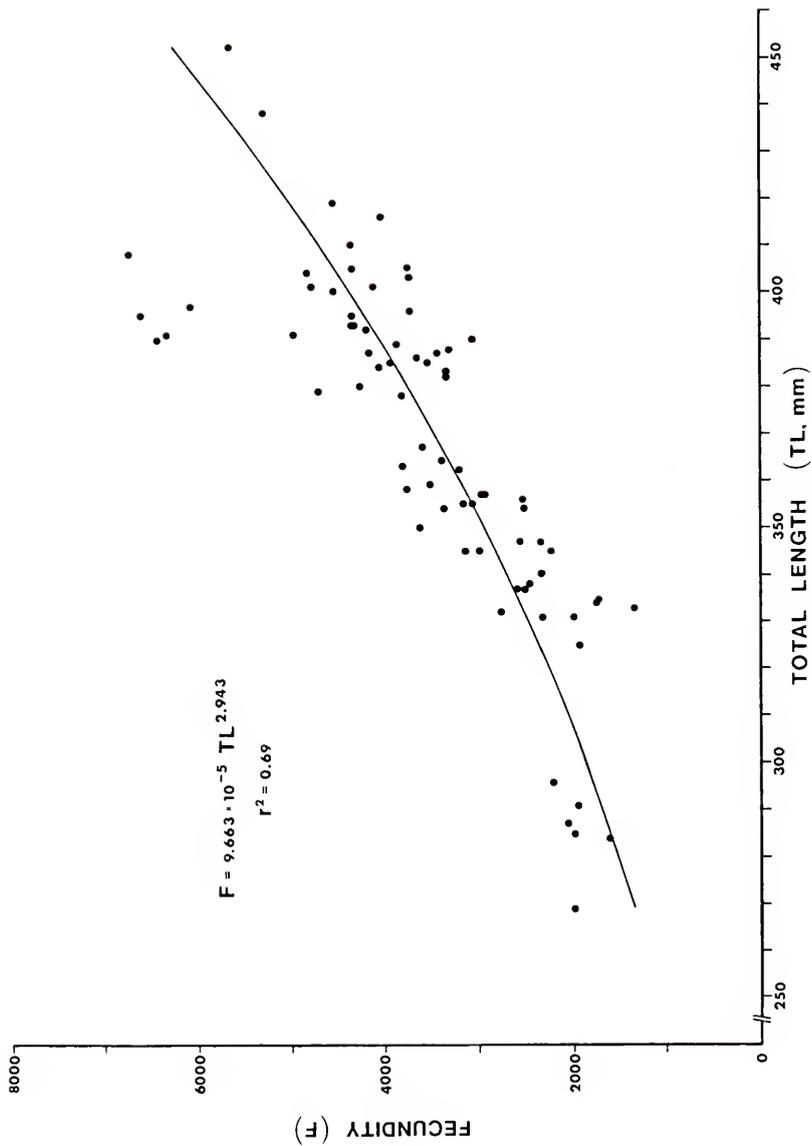


Fig. 35. Relationship of ovarian fecundity to standard length (mm) for 75 ripe female blue tilapia from Silver Glen Springs Run and Lake George, Florida.

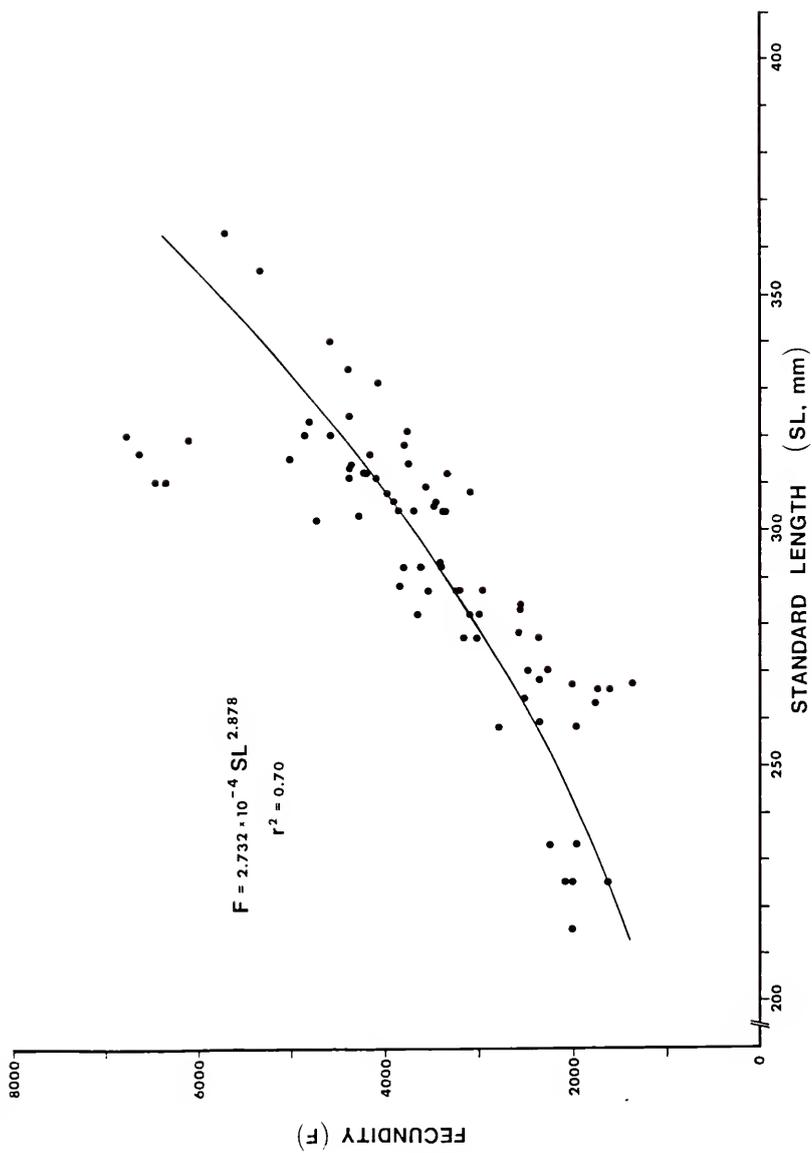
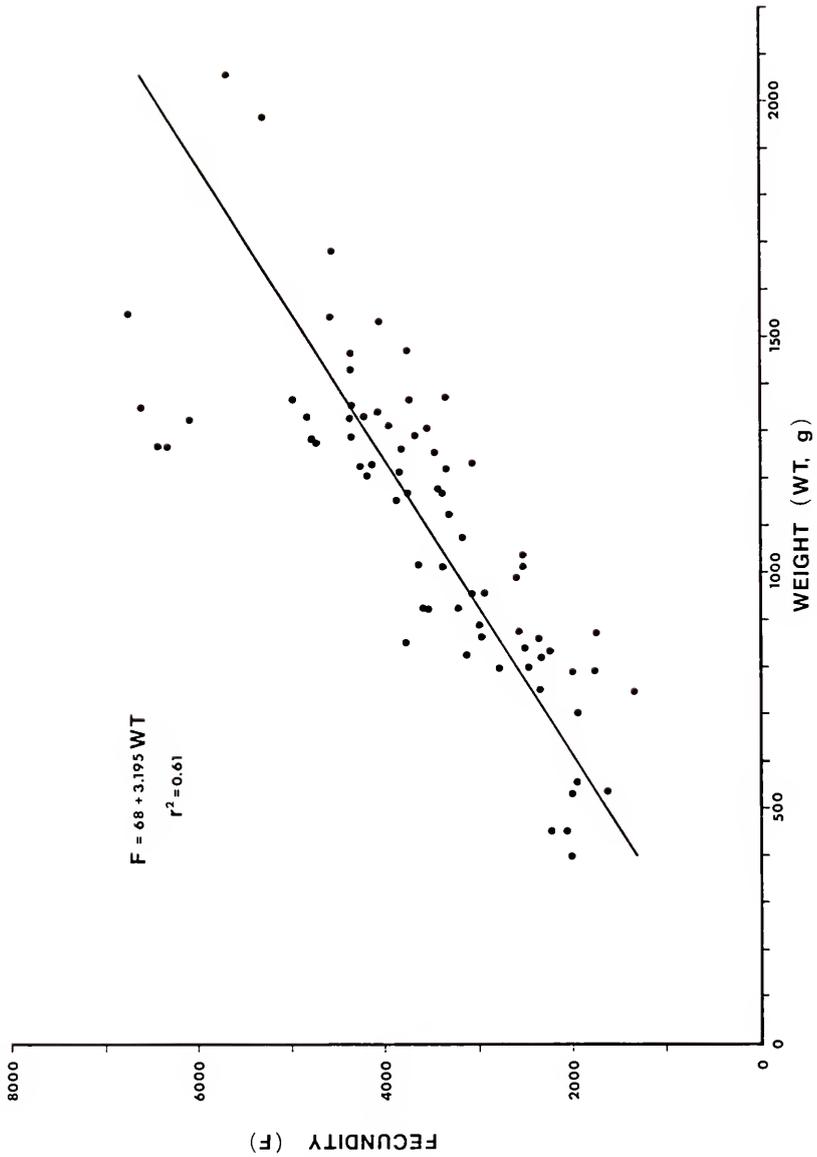


Fig. 36. Relationship of ovarian fecundity to total weight (g) for 75 ripe female blue tilapia from Silver Glen Springs Run and Lake George, Florida.



suitable for spawning through October, gonadal regression was evident beginning in July, concurrent with decreasing photoperiod. Gonadal development therefore appeared to be correlated with increasing daylength; gonads became refractory as daylength decreased, even at high temperatures. However, fish considered here were always at temperatures above 22 C; certainly, some threshold temperature exists below which gonads will not develop, irrespective of trends in daylength. For example, golden shiners (Notemigonus crysoleucas) require both warm temperatures and long photoperiod to stimulate gonadal development; either factor alone is insufficient (de Vlaming 1975). A similar relationship probably exists for tilapia. Gonadal development of tilapia remaining in Lake George through the winter may be retarded relative to fish inhabiting SGSR. Fish overwintering in the run are probably able to spawn earlier than lake-dwelling individuals.

Males began constructing nests in the run in late December and nested intensively in January and February (Chapter VII), but no evidence of actual spawning prior to March was found. At about the same time that spawning commenced, tilapia were leaving the run for the rapidly-warming waters of Lake George (Chapter III). Therefore, SGSR does not appear to be a major spawning site for blue tilapia in this system, despite the impressive density of nests evident there during winter (Chapter VII). The behavior of the males may be a result of the stenothermal properties of the run. Although the males are physiologically incapable of spawning during winter because their testes are undeveloped, the water temperatures in the run (22.8 to 24.0 C) may act as a stimulus initiating nesting behavior; blue tilapia require temperatures of 22-24 C to initiate reproductive activities

(Yashouv 1958; McBay 1961; Fishelson 1966; Payne and Collinson 1983). Spawning did not occur, however, until ovarian maturation in females was complete.

In non-equatorial regions, tilapia are generally believed to spawn for as long as temperatures are favorable but with a peak during the period of maximum water temperature and maximum daylength (Jalabert and Zohar 1982). Blue tilapia in the SGSR/LG system deviate from this generalization, spawning primarily in spring and early summer (March to June) as photoperiod increases. Similar reproductive schedules have been noted for various tilapias in some large bodies of water (Ben-Tuvia 1959; Bruton and Boltt 1975; Marshall 1979; Payne and Collinson 1983) but not in others (Hodgkiss and Man 1978; Payne and Collinson 1983). In small ponds, spawning appears to continue as long as temperatures remain high and may not be overtly influenced by photoperiod (Yashouv 1958; Pelren and Carlander 1971; Payne and Collinson 1983). In stenothermal aquaria, seasonal cycling in response to natural variations in photoperiod has been observed (Aronson 1951; Rothbard 1979). Controlled experiments investigating environmental regulation of reproductive cycles in tilapia are needed; findings could have aquacultural applications.

Lowe-McConnell (1955) stated that the number of spawnings by a female tilapia in a reproductive season can be predicted by examination of ovarian oocyte size frequency distributions. She reported that 4 or more separate batches of eggs can be seen in various east African tilapias, but provided no supporting data. My findings, and those of others who have depicted oocyte size frequency distributions of tilapia (Siddiqui 1977; Babiker and Ibrahim 1979; DeSilva and Chandrasoma 1980)

indicate that only the most advanced class of oocytes is evident in ripe or ripening females. Almost all of this batch is spawned simultaneously (McBay 1961; Peters 1963; Welcomme 1967; Pelren and Carlander 1971; Siddiqui 1977; Hodgkiss and Man 1978; Silverman 1978; Babiker and Ibrahim 1979; DeSilva and Chandrasona 1980), and the few residual yolked oocytes are resorbed rapidly (Welcomme 1967). The next wave of yolked oocytes begins to develop from the stock of primary oocytes at about the time of spawning (or the ovary can enter quiescence). Reported spawning intervals of reproductively-active female blue tilapia range from 4 to 9 weeks (Yashou 1958; McBay 1961; Dadzie 1970). Given a March through June breeding season, individual females in the SGSR/LG system may spawn about 2 to 4 times per year.

Ovarian fecundities of mouthbrooding tilapias have been found to increase proportionally with the square of maternal length (Welcomme 1967; Siddiqui 1977; Babiker and Ibrahim 1979) rather than the cube as is usual in fishes (Bagenal 1978). However, the relationship was close to cubic for blue tilapia from SGSR/LG; accordingly, fecundity increased linearly with body weight. Payne and Collinson (1983) concluded that fecundity increased in proportion to the square of length in blue tilapia, but examined only 7 small (100-135 mm SL) fish, which they pooled with I. nilotica for their regression; Babiker and Ibrahim (1979) showed that the relationship for I. nilotica is proportional to the square of maternal length.

Fecundities of blue tilapia from SGSR/LG were much higher than those previously reported for this species, but this may largely be an artifact of the large size of the fish I examined. In the laboratory, McBay (1961) reported fecundities ranging from 64 to 655 eggs in blue

tilapia 128-168 mm TL, and Dadzie (1970) recorded 68 to 2052 eggs in females between 135 and 287 mm TL. Fecundities of Dadzie's largest fish, which were comparable to the smallest individuals I examined, approximated values expected from my regression. Payne and Collinson (1983) observed fecundities of about 350 to 930 in blue tilapia 100 to 135 mm SL from the Nile delta in Egypt. Fecundities of blue tilapia 220-250 mm TL in Lake Tiberias, Israel, ranged from 2100 to 4300 (Ben-Tuvia 1959). The latter figure, which greatly exceeds fecundities of similarly-sized fish from SGSR/LG, represents the maximum number of ovarian eggs previously reported in any mouthbrooding cichlid (Fryer and Iles 1972). The 8599 eggs I found in a 420 mm TL specimen establish a new maximum. Five other females (390-408 mm TL) yielded estimates of 6096 to 6754 eggs. These 6 females were all captured at the Lake George sampling station during May, albeit in 3 different samples in 2 different years (2 in 1982, 4 in 1983). Except for having larger ovaries than usual, they were indistinguishable from other females of similar size taken in the same or different samples. McBay (1961) and Dadzie (1970) observed large fluctuations in numbers of eggs spawned by individual blue tilapia in the laboratory; fecundal heterogeneity may be common in this species. Fecundity can vary in response to quantity and/or quality of food (Scott 1962; Bagenal 1966); the high productivity of the St. Johns River system may promote elevated fecundities.

The number of young successfully brooded to the free-living stage can be considerably less than the ovarian fecundity (Lowe-McConnell 1955; Riedel 1965; Welcomme 1967; Fryer and Iles 1972). A small percentage of eggs is not spawned (Welcomme 1967) and some may be lost

during spawning; all eggs may not be successfully fertilized and some embryos probably do not develop normally. Nevertheless, the maximum number of 1300 embryos reported by Liebman (1933) in the mouth of a blue tilapia from Lake Tiberias, Israel, is probably regularly exceeded by females in Lake George.

CHAPTER IX
AGE, GROWTH, AND MORPHOMETRIC RELATIONSHIPS OF BLUE TILAPIA
IN SILVER GLEN SPRINGS RUN / LAKE GEORGE, FLORIDA

Introduction

Knowledge of the life history characteristics of a species is essential for its effective management. From an applied fisheries perspective, age and growth information is fundamental. I conducted the investigation described here because age and growth relationships of blue tilapia in open waters in the U.S. are poorly known.

Methods

Blue tilapia were collected in Silver Glen Springs Run (SGSR) by gill-netting (see Chapter III for details) from October 1981 to April 1983 at about monthly intervals. Fish were also collected in Lake George (LG) at a site about 1 km south of SGSR from May 1982 to August 1982, and again from April 1983 to July 1983 to supplement sample sizes; abundances of tilapia in the run were low during summer.

Fish were sexed, weighed to the nearest g, and total and standard lengths (TL and SL, respectively) were measured to the nearest mm. Several scales were removed from the left side of each fish directly below the appressed tip of the pectoral fin. Scale impressions were made on acetate strips with a roller press. Scale radii (focus to anterior scale edge) and anterior radii of putative annuli were measured to the nearest 0.1 mm with a microprojector.

Morphometric relationships (weight vs. TL, weight vs. SL, TL vs. SL, and TL vs. scale radius) were computed for each sex and for both sexes combined. Analysis of covariance (Snedecor and Cochran 1980) was used to test for differences between sexes for each of these relationships.

Total lengths at annuli were back-calculated using the Whitney and Carlander (1956) modification of the Lee method (Lagler 1956; Carlander 1981, 1983). Least-squares estimates of parameters of sex-specific von Bertalanffy growth equations (Ricker 1975) were fitted to the back-calculated lengths using a canned computer program (procedure NLIN, SAS Institute Inc. 1982). The von Bertalanffy growth equation is $L_t = L_\infty(1 - \exp[-k(t - t_0)])$ where L_t is total length (mm) at age t (years), L_∞ is asymptotic total length (mm), k is the Brody growth coefficient, and t_0 is the hypothetical time at which the fish would be zero length.

Results and Discussion

Morphometric Relationships

Significant differences between sexes were found for all morphometric relationships except weight vs. TL (Table 16). The differences for the weight vs. SL and TL vs. SL relationships were small, however, and probably were due largely to the large sample sizes involved. For most purposes, the combined-sex relationships should suffice. However, the sex-related difference in intercept estimates for the TL vs. scale radius relationships was relatively large (> 15 mm) and required separate back-calculations of length at age for each sex. Morphometric relationships reported for other blue tilapia populations

Table 16. Morphometric relationships for blue tilapia from Silver Glen Springs Run/Lake George, Florida. Weight in g; lengths and scale radii in mm.

Sex	Relationship	n	r ²
Weight (WT) vs. Total Length (TL) ^{a/}			
Female	$WT = 3.04 \times 10^{-5} TL^{2.956}$	605	0.962
Male	$WT = 2.63 \times 10^{-5} TL^{2.981}$	1018	0.959
Combined	$WT = 2.79 \times 10^{-5} TL^{2.971}$	1623	0.961
Weight (WT) vs. Standard Length (SL) ^{b/}			
Female	$WT = 1.08 \times 10^{-4} SL^{2.849}$	605	0.964
Male	$WT = 6.79 \times 10^{-5} SL^{2.936}$	1018	0.958
Combined	$WT = 8.05 \times 10^{-5} SL^{2.904}$	1623	0.960
Total Length (TL) vs. Standard Length (SL) ^{c/}			
Female	$TL = 14.032 + 1.199 SL$	647	0.992
Male	$TL = 8.149 + 1.233 SL$	1045	0.989
Combined	$TL = 10.285 + 1.220 SL$	1692	0.989
Total Length (TL) vs. Scale Radius (S) ^{d/}			
Female	$TL = 4.084 + 49.257 S$	631	0.904
Male	$TL = 19.862 + 46.446 S$	1031	0.884
Combined	$TL = 14.857 + 47.432 S$	1662	0.892

^{a/} no significant difference between sexes ($P = 0.3998$).

^{b/} significant differences between sexes ($P = 0.0028$).

^{c/} significant differences between sexes ($P < 0.0001$).

^{d/} significant differences between sexes ($P = 0.0006$).

in Florida (Foote 1977; Shafland et al. 1980) were similar to those reported here, but length-specific weights of SGSR/LG fish were slightly greater.

Validation of Aging Technique

Marginal increments (distances from the last scale ring to the anterior scale edge) cycled annually in both sexes (Fig. 37), indicating that scale rings may serve as annular marks. Ring formation occurred primarily from March through June, concurrent with spawning (Chapter VIII), suggesting that scale-ring formation may be associated with physiological stresses related to spawning. Payne and Collinson (1983) also observed coincident spawning and scale-ring formation in blue tilapia in Egypt. Foote (1977) and Shafland et al. (1980) reported that peak annulus formation in other blue tilapia populations in Florida occurred from March through May.

Whereas the number of scale rings increased regularly with body size in females (with a few exceptions), the relationship for males was inconsistent (Fig. 38). Larger males generally had more rings, but a significant proportion of males corresponding in size to fish with one ring bore no scale rings (Fig. 38). Also, the radius of the first ring in some males corresponded to that of the second ring in others. Formation of the first scale ring appeared to vary among males, occurring at either 1 or 2 years of age. Scale rings were therefore not valid annuli for males of this population of blue tilapia.

Male blue tilapia nest colonially in leks and actively compete for nesting territories and mates. Small males may be unable to obtain or defend optimal nest sites or may be perceived to be sub-optimal sexual

Fig. 37. Mean marginal increments from last scale ring to anterior scale edge of female (solid) and male (open) blue tilapia collected October 1981 to July 1983 from Silver Glen Springs Run and Lake George, Florida. Circles denote fish with one scale ring; squares represent fish with two rings.

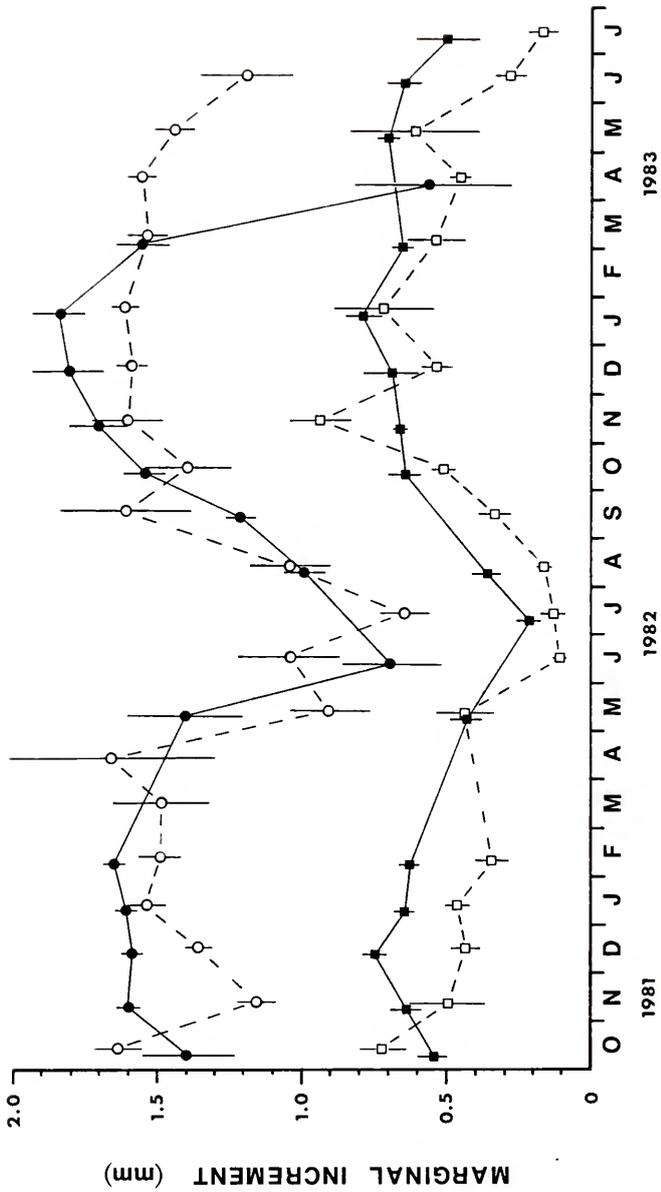
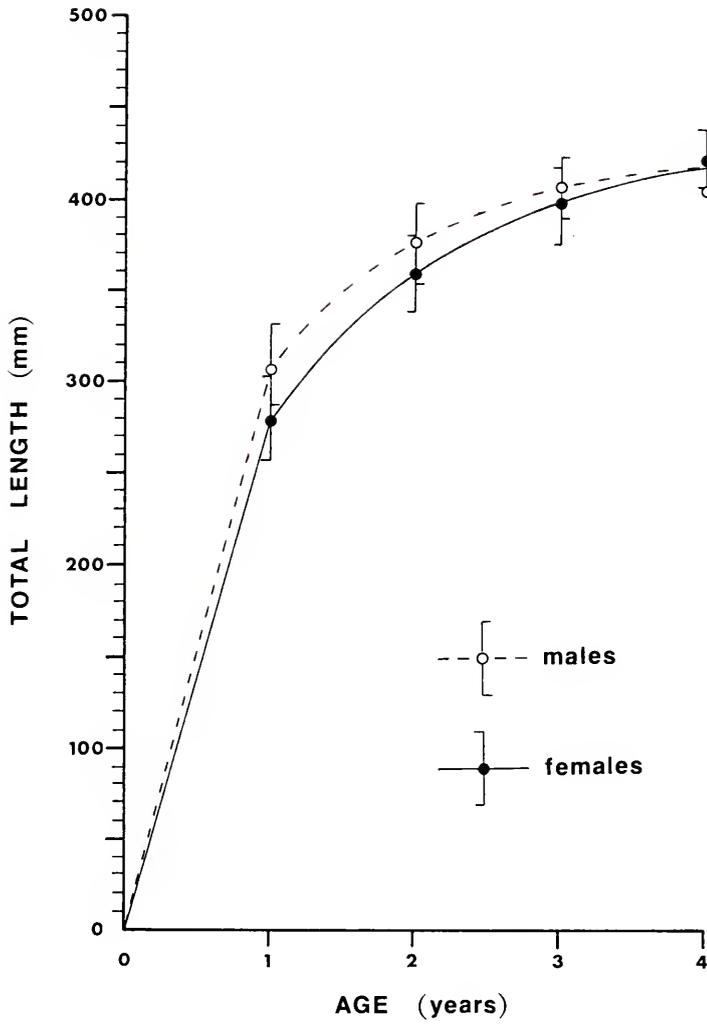


Fig. 38. Length-frequency distributions (5 mm intervals) of female and male blue tilapia plotted against scale-ring counts. All fish collected in Silver Glen Springs Run. Samples collected November to February 1981-82 and 1982-83 pooled for this representation.



partners by females. Accordingly, reproductive success of small males is probably low. Many age I males may forego attempts at spawning and thereby fail to develop scale rings.

Scale rings of females appeared to be formed annually at all ages, and were therefore considered to be valid annuli for the following growth analyses. However, conclusive demonstration of their validity (via mark-recapture) was lacking; the results should therefore be considered tentative. Results of growth analyses for males are also presented, but should be considered erroneous; they are included to emphasize the fallaciousness of using scale rings to age males.

Age and Growth

Maximum estimated age of female blue tilapia from the SGSR/LG system was 4+ years. Maximum total length at capture was 457 mm. First year growth of female blue tilapia was rapid; estimated mean back-calculated length at age I was 280 mm (Table 17). Estimated mean total lengths at ages II, III, and IV were 359, 397, and 423 mm, respectively. These lengths are considerably greater than age-specific lengths previously reported for this species (Ben-Tuvia 1959; El Bolock and Koura 1961; Gleastine 1974; Foote 1977; Shafland et al. 1980; Payne and Collinson 1983). Appreciable variability in back-calculated lengths at age (Table 17) was probably due in part to protracted spawning, but may also have been an artifact of missing annuli in a relatively low number of females (Fig. 38).

The von Bertalanffy growth equation (Table 18) for female blue tilapia was $L_t = 439.1(1 - \exp[-0.683(t + 0.485)])$. The relatively high Brody growth coefficient ($k = 0.683$) reflects rapid attainment of

Table 17. Mean back-calculated total lengths (mm) at age for blue tilapia from Silver Glen Springs Run / Lake George, Florida.

Age group	N	Length at capture		Back-calculated total lengths \pm SD (range)			
		Mean \pm SD	Range	1	2	3	4
<i>Females</i>							
I	264	352 \pm 23	272-411	277 \pm 21 (211-364)			
II	130	389 \pm 17	311-422	278 \pm 22 (146-320)	358 \pm 18 (241-395)		
III	47	412 \pm 19	368-457	293 \pm 33 (171-352)	360 \pm 28 (276-408)	394 \pm 22 (336-438)	
IV	13	434 \pm 15	414-453	303 \pm 20 (279-340)	371 \pm 16 (349-401)	407 \pm 18 (376-434)	423 \pm 16 (400-444)
Weighted mean				280 \pm 24 (146-364)	359 \pm 21 (241-408)	397 \pm 22 (336-438)	423 \pm 16 (400-444)
N				454	190	60	13
Annual increment				280	79	38	26
<i>Males</i>							
I	471	373 \pm 18	291-432	306 \pm 21 (193-406)			
II	124	395 \pm 20	327-444	311 \pm 25 (220-350)	375 \pm 23 (286-417)		
III	28	418 \pm 17	373-449	329 \pm 22 (273-370)	386 \pm 19 (335-413)	408 \pm 17 (360-435)	
IV	1	413		321	300	392	405
Weighted mean				308 \pm 22 (193-406)	377 \pm 22 (286-417)	407 \pm 17 (360-435)	405
N				624	153	29	1
Annual increment				308	69	30	-2

Table 18. Fitted parameter values, standard errors, 95 % confidence intervals, and error correlations for von Bertalanffy growth equations describing growth of blue tilapia from Silver Glen Springs Run / Lake George, Florida.

Sex	Fitted values			Error correlations		
	TL _∞ (mm)	k, per year	t ₀ (years)	TL _∞ -k	TL _∞ -t ₀	k - t ₀
Females n=717	439.1	0.683	-0.485	-0.968	-0.910	0.983
Standard error	9.919	0.073	0.106			
95 % confidence interval	419.6 to 458.6	0.539 to 0.826	-0.694 to -0.276			
Males n=807	426.7	0.874	-0.464	-0.976	-0.946	0.993
Standard error	12.157	0.159	0.186			
95 % confidence interval	402.9 to 450.6	0.562 to 1.188	-0.829 to -0.098			

asymptotic size (i.e. rapid early growth and a short life span). Predicted lengths at age (Fig. 39) corresponded closely to back-calculated lengths. The estimate of asymptotic length ($L_{\infty} = 439.1$ mm) is similar to the mean total length at capture of age IV females (434 mm).

Only one male with 4 scale rings was captured. Estimated back-calculated total lengths at age of males exceeded those of females, and incremental growth of males after age I was less than calculated for females (Table 17). Standard errors of the von Bertalanffy parameter estimates for males exceeded those for females and the Brody growth coefficient for males ($k = 0.874$) was much higher than for females (Table 18). These differences resulted from missing first annuli in many males; males lacking the first annulus were erroneously considered one year younger than their true age and thereby inflated age-specific length estimates and compounded heterogeneity.

The inability to accurately age males would appear to severely limit the utility of the findings presented here. However, the following findings suggest that the growth relationships discerned for females may also be applicable to the male component of the population. First, maximum total lengths at capture for the sexes were similar (457 and 449 mm for females and males, respectively). Second, maximum ages of both sexes were 4+ years (note that many of the 'age III' males were probably 4+ years old). Third, total lengths of young-of-the-year (YOY) males and females captured simultaneously were similar. Figures 40 and 41 show monthly length-frequency distributions of females and males, respectively, captured during this study. YOY can be discerned readily during the winter months. Comparing total lengths of male and female

Fig. 39. Mean back-calculated total lengths (mm) at age and fitted von Bertalanffy growth curves for male (open circles) and female (solid circles) blue tilapia captured October 1981 to July 1983 in Silver Glen Springs Run and Lake George, Florida. Brackets represent ± 1 SD.

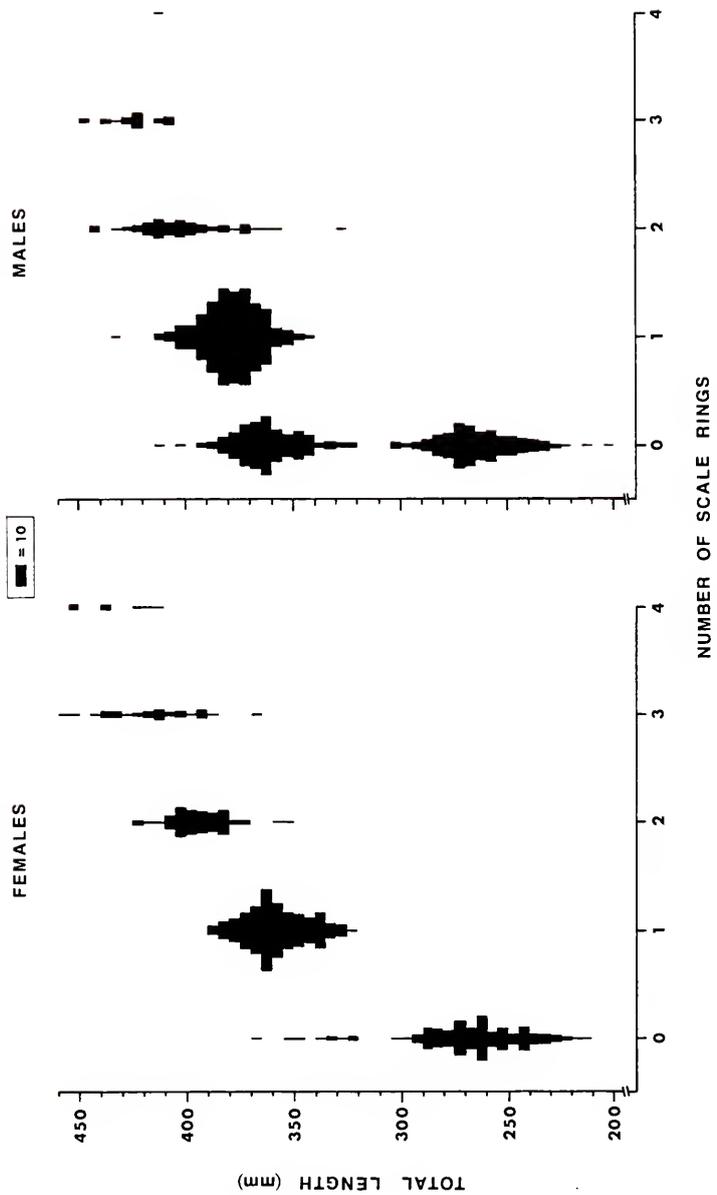
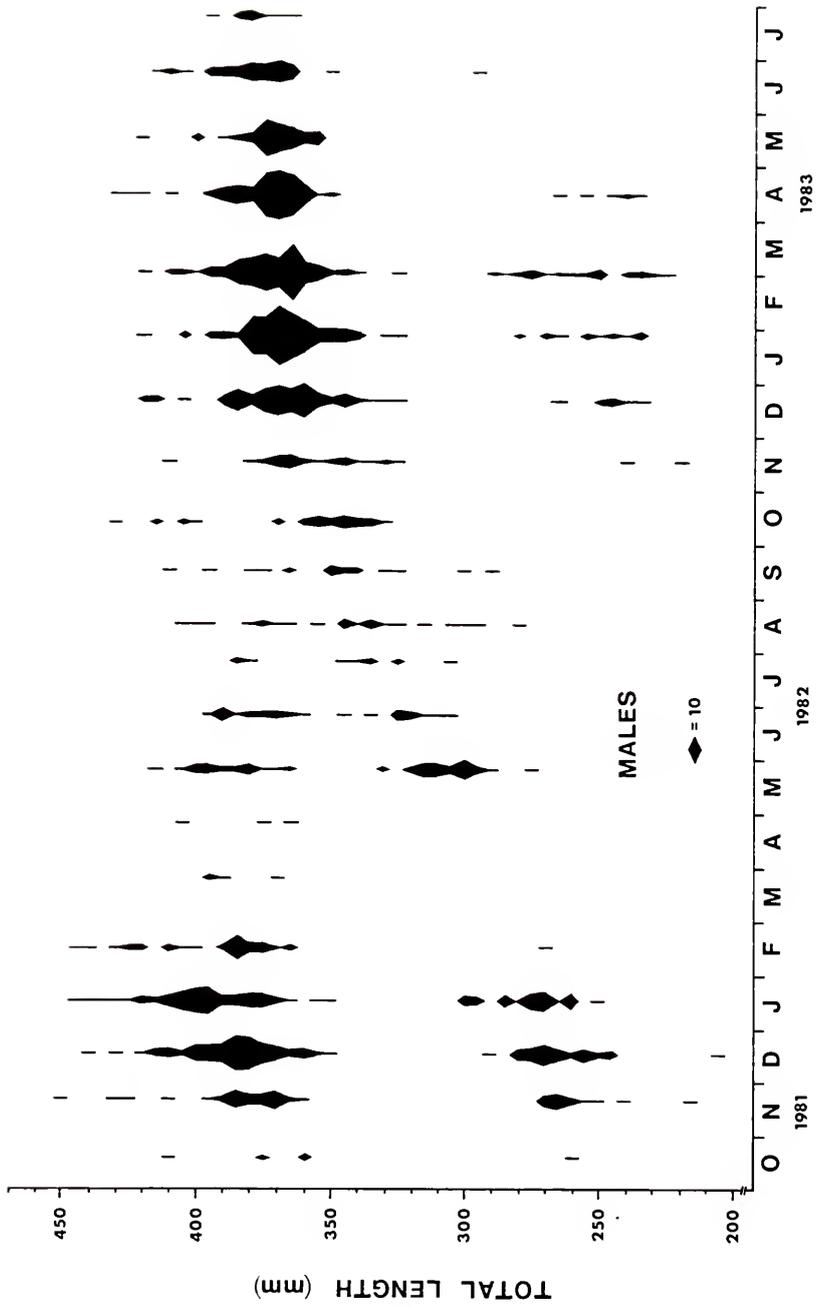


Fig. 40. Monthly length-frequency distributions (5 mm intervals) of female blue tilapia collected October 1981 to July 1983, Silver Glen Springs Run and Lake George, Florida.

Fig. 41. Monthly length-frequency distributions (5 mm intervals) of male blue tilapia collected October 1981 to July 1983, Silver Glen Springs Run and Lake George, Florida.



YOY collected from November 1981 to January 1982 and December 1982 to February 1983 by month, no significant differences were found ($P = 0.0749$, analysis of variance). There were highly significant differences ($P < 0.0001$) in lengths of fish between months (due to growth), indicating that the equivalent lengths of the sexes were not simply artifacts of gear selectivity. Shafland et al. (1980) and Payne and Collinson (1983) also found no significant differences in growth rates of male and female blue tilapia.

In Florida, blue tilapia have exhibited a potential for relatively high recruitment and an ability to attain high biomasses (see Chapter IV). These attributes, in conjunction with the rapid growth rate and relatively short life span of the species, suggest that stocks of blue tilapia in Florida may be able to support intense and sustained exploitation.

CHAPTER X OVERVIEW AND CONCLUSIONS

Objectives

My primary objective, in conducting this research, was to augment understanding of the ecology of the blue tilapia on issues relevant to the effective management of the species in U.S. waters. Development of a sound management protocol for the species requires thorough knowledge of its life history, environmental physiology, and ecology. Only when we understand how an introduced organism interacts with its physical and biotic environment can we begin to determine what management actions, if any, its presence warrants. Accordingly, my objectives were 1) to characterize the cold tolerance of blue tilapia; 2) to evaluate the behavioral thermoregulatory capacity of blue tilapia during winter; 3) to quantify the relative foraging abilities of young blue tilapia; 4) to characterize and compare food selection of early life history stages of blue tilapia and sympatric native species under natural conditions; 5) to determine the relative preference of largemouth bass for blue tilapia and bluegill as forage; 6) to examine competition for nest sites between blue tilapia and largemouth bass in a spring run; 7) to characterize the reproductive biology of blue tilapia; and 8) to determine age, growth, and morphometric relationships of blue tilapia.

In the following sections, I present the findings of my research together with specific ecological and management implications,

recommendations for further research suggested by my studies, some additional comments and management recommendations, and a summary.

Results and Implications

An important consideration in managing an exotic species concerns assessment of its ability to survive in a candidate habitat. The sensitivity of blue tilapia to low temperatures is apparently the most important factor affecting the potential range of the species in North America. I therefore investigated several aspects of low temperature tolerance of the species. I found that salinity has a slight but significant effect on the cold tolerance of blue tilapia, suggesting that the species may be expected to extend its range furthest north along the coast and that populations in estuarine systems may be able to withstand exceptionally cold weather better than inland populations. Furthermore, I determined that temperature and exposure time interact to elicit cold death in blue tilapia, and by quantifying this relationship, was able to develop a preliminary predictive model potentially useful in evaluating the suitability of an environment for overwintering blue tilapia. I believe this approach has tangible advantages over methods used in the past because it employs environmentally-realistic temperature schedules and allows continuous acclimation to changing temperatures, and can be applied readily to other species. A consequential finding of my research on the thermal biology of the species was demonstration of considerable heterogeneity in thermal tolerance among individual blue tilapia. Selection for enhanced cold tolerance in this species may be possible. The tolerances

I documented eventually may be rendered obsolete, or may already be exceeded in some populations; caution in their use may be advisable.

A further caveat regarding the thermal biology of the blue tilapia pertains to its decidedly thermophilic tendencies in habitat selection. Blue tilapia moved in and out of Silver Glen Springs Run in direct response to changing surface-water temperatures. Although surface-water temperatures were not immediately injurious to the fish during my investigation, such behavior could result in aversion of cold death during exceptionally cold winters or at higher latitudes. Locations of potential thermal refugia must be considered when assessing habitat suitability on thermal criteria. Heated water discharges of human origin (e.g. power plants) may allow considerable range expansion beyond climatically-dictated limits. However, the thermophilic behavior of the species can also work to its detriment; when concentrated in warm-water discharges the fish are highly vulnerable to exploitation and provide fishery managers an opportunity to exercise population-control measures. Best results could be expected during, and immediately following, periods when ambient water temperatures are lowest.

Control of blue tilapia populations might be considered if the species is deemed undesirable. Soon after the blue tilapia became established in open waters it became apparent that the desirable qualities attributed to the species (e.g. weed control, sport fishing) were not realized, but demonstration of clearly detrimental impacts on aquatic ecosystems in North America promulgated by the species has been equivocal. In an attempt to evaluate the potential of the blue tilapia to impart negative ecological impacts, I conducted several studies

designed to examine interactions between this exotic and native fish species.

Perhaps the most notorious impact attributed to the blue tilapia relates to its alleged capacity to disrupt spawning by centrarchids, most notably the largemouth bass, a species of considerable socio-economic importance. Aided by a pre-tilapia study of largemouth bass nesting in Silver Glen Springs Run, I was able to document a severe decrease in the number of bass nests in the run, possibly attributable to the presence of nesting tilapia. Spawning by largemouth bass is behaviorally suppressed in crowded environments. Aggregations of nesting blue tilapia, in habitats suitable for nesting by largemouth bass, would be expected therefore to inhibit nesting by bass; densities of tilapia nests in the run were high in microhabitats formerly used by bass. However, Silver Glen Springs Run is an atypical habitat in that it is stenothermal. In most habitats, seasonal changes in water temperatures would lessen the degree of temporal overlap in nesting between the two species. Nevertheless, this impact may be substantial because spring runs are common in Florida and appear to be excellent spawning habitats for largemouth bass.

Another potential impact, heretofore not considered, concerns exploitative competition between early life history stages of blue tilapia and native species for trophic resources. In a series of laboratory experiments, I found that young tilapia, because of their large size, are extremely capable zooplanktivores. Because acquisition of sufficient food is a major determinant of early life history survivorship in fishes, the success of the blue tilapia in colonizing systems and rapidly achieving high abundances may be a result of their

considerable predatory prowess during early life stages. Addition of such an effective zooplanktivore may increase demand upon the zooplanktonic resource of a system and thereby directly affect survival of larvae of native fishes. I found a high degree of trophic overlap between young tilapia and larval shad in Lake George; perhaps the declines in shad abundances documented following introductions of blue tilapia have resulted from exploitative competition for zooplankton during early life stages. This would appear to be a more realistic explanation than the "competition for algae and detritus among adults" theory usually invoked.

Because blue tilapia have become a dominant component of fish assemblages in many systems and may be displacing native forage fishes, concern has developed regarding the effects of the species on predator-prey interactions. I therefore conducted laboratory electivity experiments to determine the relative preference of largemouth bass for juvenile blue tilapia and bluegill as forage. The bass exhibited a strong tendency to consume tilapia in preference to bluegill. Because bluegill are often prominent in the diets of largemouth bass, the preference for tilapia suggests that tilapia may enhance the forage base available to bass. However, this preference could also decrease predation pressures on bluegill populations, thereby promoting stunting. Such subtle, but potentially significant effects, require further examination.

Knowledge of the life history characteristics of a species is essential for its effective management. Because the life history of the blue tilapia in open waters in the U.S. is poorly known, I described the reproductive biology and age and growth relationships of the Silver

Glen Springs Run / Lake George blue tilapia population. Several significant findings were elucidated through these investigations.

Spawning in this population was restricted to spring and early summer and gonadal recrudescence was correlated with increasing photoperiod; other populations have shown a capacity for spawning from spring through fall, for as long as temperatures were favorable. Periodicity of spawning can have important implications regarding recruitment, trophic overlap with larvae of native fishes, and availability of juvenile blue tilapia as forage for piscivores.

Fecundities of blue tilapia in the Silver Glen Springs Run / Lake George system greatly exceeded previously-reported values. Because survivorship of young tilapia is relatively high, fecundity may directly affect stock-recruitment relationships in this species. Therefore, estimates of fecundity / body size relationships may have utility in management of exploited stocks.

Growth of blue tilapia in the Silver Glen Springs Run / Lake George system was rapid and lengths-at-age exceeded values reported in the literature by considerable margins. Because this system is highly productive, the growth parameters ascertained may approximate maximum values attainable in open waters, and may be useful for comparative purposes. Also, the rapid growth rates suggest that juvenile blue tilapia may be vulnerable to predation for a relatively short period.

Recommendations for Further Research

My goal was to augment knowledge of the applied ecology of blue tilapia, but clearly additional research is needed before the species can be managed effectively and with confidence. The topics I have

investigated are but a few of the many commanding attention. In the following paragraphs I suggest avenues of research which, in my opinion, may provide additional information of potential utility.

Thermal Biology

Much work remains to be done on the thermal biology of the species, particularly with respect to the proposed temperature-tolerance model. The model has potential applications not only in predicting eventual ranges of tropical exotics in North America, but also for evaluating effects of heat stress on temperate species (e.g. Gulf-strain striped bass). Practical applications in aquaculture are also apparent. Furthermore, the general approach should also be applicable for determining tolerances to other environmental stresses that organisms may acclimate to (e.g. pH, dissolved oxygen, salinity).

The series of chronic-exposure experiments described in Chapter II should be repeated, albeit with adequate sample sizes and replication, to better ascertain the time vs. temperature relationship. The effects of different rates of temperature declination on cold tolerance in chronic-exposure experiments should also be evaluated. I used a 1 C/day declination rate under the assumption that it would allow full acclimation for cold tolerance. However, subsequent tests suggest that slower declination rates may enhance acclimation and extend survival times at comparable final temperatures. Additional refinements would be to vary the initial temperature and ascertain the effects of variable, and intermittantly negative, declination rates.

The chronic-exposure technique could also be used to better quantify the effect of salinity on cold death in tilapia. My salinity experiments showed that a significant effect exists, but quantified the extent of the effect under only one thermal regimen. Determination of time to cold death at a variety of final temperatures, using a range of declination rates, and in media of different salinities, would provide a more meaningful evaluation of the salinity/temperature interaction.

Similarly, the interaction between pH and temperature could be evaluated. In fact, pH alone may limit the distribution of blue tilapia (see comments by Lovshin in Chervinski 1982) and should be examined in this context. The possible inability of the species to survive and especially to reproduce in low pH waters may restrict its colonization of acidic habitats in north Florida and southern Georgia. Viabilities of sperm, eggs, and embryos in low pH media should be tested. Furthermore, the effects of pH on sex determination in tilapia require investigation. Tilapia lack heteromorphic sex chromosomes (Wohlfarth and Hulata 1981) and may therefore be susceptible to environmental sex determination (ESD). ESD may be relatively common in fishes (Conover 1984) and could be particularly useful in tilapia culture if present.

The expression of considerable heterogeneity in thermal tolerance among fish used in my experiments suggests a potential for selection for enhanced cold resistance may exist. Cold tolerance of fish collected along a latitudinal gradient in Florida could be determined, or selective-breeding experiments could be conducted to evaluate this possibility.

Sexual differences in temperature tolerance also require examination. The heterogeneity referred to above may have been an artifact of differential cold resistance by sex.

My studies at Silver Glen Springs Run demonstrated that blue tilapia inhabited the run in response to seasonal changes in surface-water temperatures. However, I was unable to estimate what proportion of the Lake George population exhibited this behavior. A substantial proportion of the population would have to congregate in the run for an eradication program there to be effective. I had planned to address this question via telemetry, but the physico-chemical properties of the system precluded use of either sonic or radio transmitters. Gill-netting in the lake during winter proved inconclusive. I caught no tilapia, but cold-induced lethargy may have reduced vulnerability of the fish to passive capture techniques. Primer-cord used in conjunction with block nets, or trawling gear, may be more effective in capturing tilapia in the lake during winter. However, I would recommend that a telemetry study be conducted in a freshwater system, where radio transmissions would not be impeded. Movements of individual fish could then be followed, and distances travelled to thermal refugia could be determined. To the best of my knowledge, tilapia have never been telemetrized; valuable information on their movements and habitat preferences could be collected through such an exercise. An alternative would be to mark large numbers of blue tilapia collected with gill-nets at standardized stations in Lake George (and in the St. Johns River above and below the lake) with color-coded tags. Fish entering the run could be 'recaptured' visually.

Early Life History

Potential effects of early life history stages of blue tilapia on larvae of native fishes deserve further attention. Because young tilapia are effective zooplanktivores, exploitative competition for zooplankton during the larval period could reduce survival and growth of native species. Competition experiments in small research ponds could be conducted to examine this interaction.

Further study of the ecology of young tilapia in open waters is also needed. The spatial and temporal occurrence and diets of young tilapia and sympatric native larvae need to be examined closely to identify overlap in resource use by potential competitors. These parameters could be compared in a system where the introduction of tilapia is recent; densities of their young would still be relatively low, and could be assumed to have not yet influenced diets, distributions, or abundances of native larvae.

Adult blue tilapia may also alter zooplankton abundances, either directly by ingestion or indirectly by competing for phytoplankton. The magnitude of these processes, and their effect on larvae of native fishes, need to be ascertained.

Predator-Prey Relationships

Because juvenile blue tilapia appear to be an acceptable forage of largemouth bass, their presence in a system may expand the forage base available to bass (and possibly other piscivores). However, if through rapid growth, juvenile tilapia quickly become invulnerable to predation, or if juvenile tilapia frequent habitats avoided by bass or where predation is impeded, the effect may be negligible. In fact, if

tilapia displace native forage species, their overall effect on piscivores may be detrimental. The distribution, accessibility to predators, size-distribution, relative abundance, and density of blue tilapia in a system relative to other forage will influence their relative value as forage to piscivorous species. Studies in natural systems are needed to determine if juvenile tilapia are spatially available to predators, how their rapid growth affects temporal availability, and to what extent they are consumed by predators relative to their abundance.

Suppression of Largemouth Bass Spawning

Suppression of largemouth bass spawning by blue tilapia has been inferred only in systems where water temperatures are constant or artificially elevated. Studies examining this interaction in natural waters not influenced by thermal discharges are needed in order to better appraise the actual scope of this impact in U.S. waters. Because largemouth bass begin spawning at lower temperatures than do tilapia, the severity of this impact may be less overt in systems where water temperatures fluctuate seasonally. Particularly informative would be an estimate of the proportion of spawning by bass completed at the time tilapia begin to nest.

Reproductive Biology and Age-Growth Relationships

Additional reproductive biology and age-growth studies of blue tilapia populations are needed if the species is to be managed coherently. Tilapia in Lake George exhibited life history parameters quite different from those previously reported. Research on populations

in a wide variety of habitats is needed to determine what factors influence the basic life history processes of this species.

Additional Comments and Recommendations

Although blue tilapia have been established in U.S. waters for over 20 years, conclusive evidence that the species has, or has not, imparted any ecological effects (either insidious or beneficial) on natural systems is still lacking. Even inferential evidence, derived by correlation of changes in ecological parameters with presence of tilapia, has been difficult to procure because adequate pre-tilapia data bases do not exist for systems now inhabited by the fish. Conclusive demonstration that the species is, or is not, capable of eliciting significant effects in natural waters can be accomplished only through a rigorous experimental program involving intentional introductions into selected waters.

Irrespective of whether the blue tilapia is eventually perceived to be detrimental, beneficial, or inconsequential in U.S. waters, it appears that the species at present is not managed in accordance with the utilitarian goals of applied fishery science. The fish is fine table fare, exhibits rapid growth, and is locally abundant. Therefore blue tilapia populations would appear to be capable of supporting productive commercial fisheries. However, its legal exploitation has been limited in Florida in an attempt to discourage further transplant by fishermen. While this strategy may have retarded the rate of range expansion, the blue tilapia has nevertheless colonized much of the state, both independently and with the aid of dilettante fishery

biologists. Deregulation may therefore now be appropriate in systems supporting fisheries for other species.

The recreational potential of the species is also underutilized. The general belief that the blue tilapia has little or no sporting value is erroneous. True, it is not vulnerable to angling in the traditional sense, but the species can provide excellent sport when taken by bow-fishing or snatch-hooking. Unfortunately, few anglers are aware of the legality, effectiveness, and recreational value of these methods, largely because these have been poorly publicized. This deficiency could be rectified easily through public-awareness programs.

The assumption that, once established, exotic fishes are permanent appears to be approaching dogmatic acceptance. However, I am optimistic that in the relatively near future, localized control, and possibly eradication, of some exotics may be feasible.

The blue tilapia may be especially susceptible to localized control. It congregates in thermal effluents during winter; large numbers of fish may be vulnerable therefore to control measures within a relatively small area. The species readily feeds on media into which control substances can be incorporated. Furthermore, the digestive physiology of tilapias is unique among vertebrates; gastric pH is much lower than in other genera, about 1.25 or even lower (Bowen 1982). Therefore, broad-spectrum control substances can be rendered tilapia-specific to protect non-target species. A possible control strategy could entail micro-encapsulation of a control substance in a coating degradable only at very low pH, mixing it into a palatable bait, and offering it to tilapia during winter in a stenothermal spring run or power-plant effluent.

Of course, a strictly tilapia-specific compound harmless to non-target species would be preferable. Fortunately, such a substance may exist. Henderson-Arzapalo et al. (1980) recovered a compound from mucus and culture water of T. mossambica which induced mortality and cutaneous anaphylactic reactions in T. mossambica, T. aurea, T. nilotica, and T. zillii but did not affect channel catfish (Ictalurus punctatus). If the compound can be recovered or synthesized in appreciable quantities it may be useful as a control agent. Much more research is needed before the feasibility of this method can be evaluated.

An alternative to population control by lethal substances is through sterilization. Chemosterilants have been used successfully on tilapia in the laboratory (Eckstein and Spira 1965; Al-Daham 1970; Dadzie 1974) and could be administered in the field using the methods described above. A promising technique for controlling reproduction in fishes is immunological luteinizing hormone-releasing hormone (LH-RH) neutralization (Carelli et al. 1982). LH-RH stimulates gonadal recrudescence, spermiation, and ovulation (Crim et al. 1983). The major advantage of the technique is that it uses no harmful substances. Basically, the technique involves vaccinating an organism against its own LH-RH by coupling synthetic LH-RH with a foreign carrier to produce an antigen that triggers production of antibodies specific for LH-RH. The technique has not been tried with fish, and use on wild fish may be logistically impossible. Nevertheless, it warrants examination. It could prove effective in controlling unwanted reproduction in aquacultural settings. Excessive recruitment of tilapias, which results in low yields of marketable-size fish, is a major problem in their

culture (Guerrero 1982; Shelton and Smitherman 1984). (An analogous technique, immunological neutralization of somatostatin, may enhance growth. Somatostatin inhibits release of growth-promoting hormones and thereby regulates growth rates and asymptotic size. Immunological demobilization of somatostatin may have significant aquacultural applications.)

Eventually, large-scale control or eradication of exotic fishes will be possible using species-specific pathogenic microorganisms (viruses, bacteria, fungi). Effective microbial insecticides are already in use (Miller et al. 1983). Genetic engineering using recombinant DNA technologies will render ichthyopathogens highly virulent, narrowly host-specific, and completely governable. Effective control of blue tilapia in U.S. waters is achievable, but development of appropriate techniques will require considerable research and expense.

Summary

The blue tilapia was selected for study because it may be a problem. The species is now firmly established throughout much of Florida. If the species is either a problem or a blessing, then its continued range expansion and ecological impacts, and the mechanisms which allow it to become established in exotic environments, are key informational needs for natural resource managers. Accordingly, I studied the cold tolerance, larval ecology, interspecific interactions, and life history of the species.

The cold tolerance of the blue tilapia is quantifiably affected by salinity and duration of exposure to each temperature. The suitability of a candidate habitat for overwintering blue tilapia can therefore be

evaluated. However, the fish is capable of finding thermal refuges during cold weather; the presence and location of these must be considered when assessing habitat suitability on thermal criteria. Young blue tilapia are extremely capable zooplanktivores and therefore exhibit relatively high survival and growth rates. Accordingly, the species has been highly successful in colonizing systems and rapidly achieving high abundances and probably competes with the young of native species for food. Furthermore, blue tilapia can inhibit reproduction of largemouth bass by competing for nest sites. However, juvenile blue tilapia can be suitable forage for native piscivores; largemouth bass tended to prefer blue tilapia to bluegill as forage. In north-central Florida, gonadal recrudescence of blue tilapia is correlated with increasing photoperiod and spawning occurs during spring and early summer. Fecundities exceed those of other mouthbrooding cichlids. Growth is rapid and the life span is relatively short (less than 5 years).

Considerable time and energy have been expended by fishery biologists fretting over the presence of blue tilapia in Florida waters. Conclusive demonstration that the blue tilapia does, or does not, appreciably impact native species in the U.S. is needed, but this can be accomplished only through a rigorous experimental program involving introductions into selected waters. Such studies should be initiated immediately. If the effects are negligible, commercial and recreational exploitation should be promoted. If the effects are appreciable and deleterious, the species should be controlled or eradicated. Control may be feasible, but virtually no research has been conducted to evaluate the possibilities.

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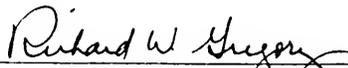
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BIOGRAPHICAL SKETCH

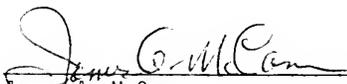
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



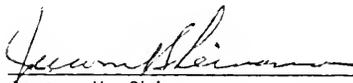
Richard W. Gregory, Chairman
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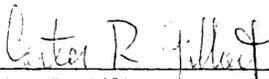
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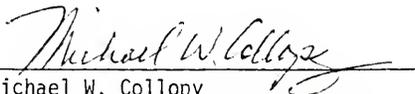
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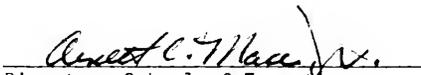
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This dissertation was submitted to the Graduate Faculty of the School of Forest Resources and Conservation in the College of Agriculture and to the Graduate School, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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