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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Mid-Atlantic)

MUMMICHOG AND STRIPED KILLIFISH

Fish and Wildlife Service
U.S. Department of the Interior

Coastal Ecology Group
Waterways Experiment Station
U.S. Army Corps of Engineers

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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Mid-Atlantic)

MUMMICHOG AND STRIPED KILLIFISH

by

Barbara J. Abraham
Department of Biological Sciences
P.O. Box 6565
Hampton University
Hampton, VA 23668

Project Manager
Carroll L. Cordes
Project Officer
Pepsi Nunes
National Coastal Ecosystems Team
U.S. Fish and Wildlife Service
1010 Gause Boulevard
Slidell, LA 70458

Performed for
Coastal Ecology Group
Waterways Experiment Station
U.S. Army Corps of Engineers
Vicksburg, MS 39180

and

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PREFACE

This species profile is one of a series on coastal aquatic organisms, principally fish, of sport, commercial, or ecological importance. The profiles are designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the species and to describe how populations of the species may be expected to react to environmental changes caused by coastal development. Each profile has sections on taxonomy, life history, ecological role, environmental requirements, and economic importance, if applicable. A three-ring binder is used for this series so that new profiles can be added as they are prepared. This project is jointly planned and financed by the U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service.

Suggestions or questions regarding this report should be directed to one of the following addresses.

Information Transfer Specialist
National Coastal Ecosystems Team
U.S. Fish and Wildlife Service
NASA-Slidell Computer Complex
1010 Gause Boulevard
Slidell, LA 70458

or

U.S. Army Engineer Waterways Experiment Station
Attention: WESER-C
Post Office Box 631
Vicksburg, MS 39180

CONVERSION TABLES

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
kilometers (km)	0.6214	miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees	1.8(°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

Multiply	By	To Obtain
inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
acres	0.4047	hectares
square miles (mi^2)	2.590	square kilometers
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees	0.5556(°F - 32)	Celsius degrees

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I am grateful to M.H. Taylor, University of Delaware, and two anonymous reviewers who commented on an early draft of the manuscript.

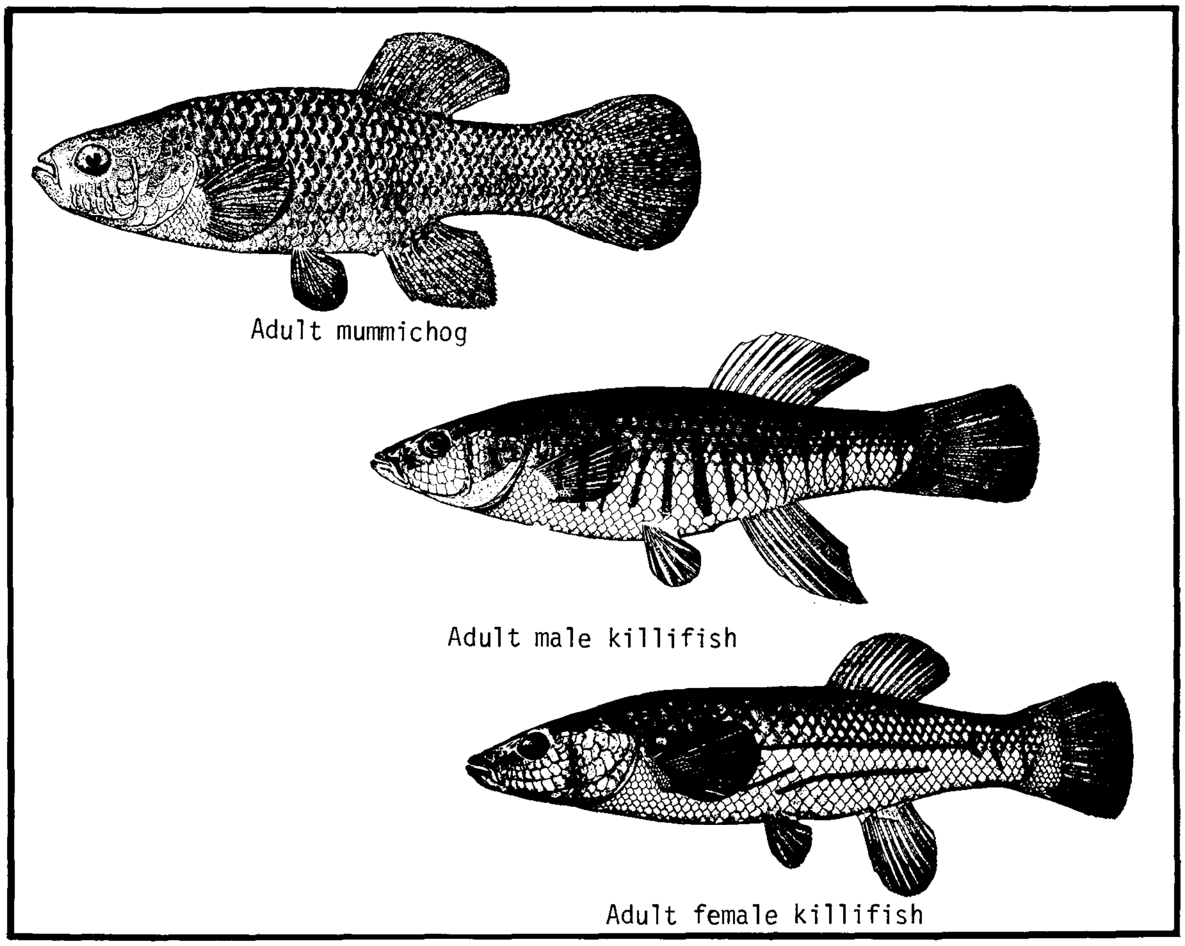

Figure 1. Mummichog and striped killifish.

MUMMICHOG AND STRIPED KILLIFISH

NOMENCLATURE/TAXONOMY/RANGE

Scientific name ... Fundulus heteroclitus (Linnaeus) (Robins et al. 1980)
Preferred common name .... mummichog (Figure 1, top)
Other common names .... mud minnow, pike minnow, mud dabbler, gudgeon (Hildebrand and Schroeder 1928); saltwater minnow, killie, mummie (Ursin 1977); marsh minnow (Teal and Burns 1979); common killifish, brackish water chub (Northcutt and Davis 1983)

Class .... Osteichthyes
Order .... Atheriniformes
Family .... Cyprinodontidae

Geographic range .... Gulf of St. Lawrence south to northeastern Florida (Figure 2). (F. grandis, previously F. h. grandis, includes populations which range from peninsular Florida to Tampico, Mexico.) Also found on Sable Island, Nova Scotia (Garside 1969) and Bermuda (Rosen 1973). Salt, brackish, and freshwater (Rosen 1973); characteristically close to shore (Daiber 1982).

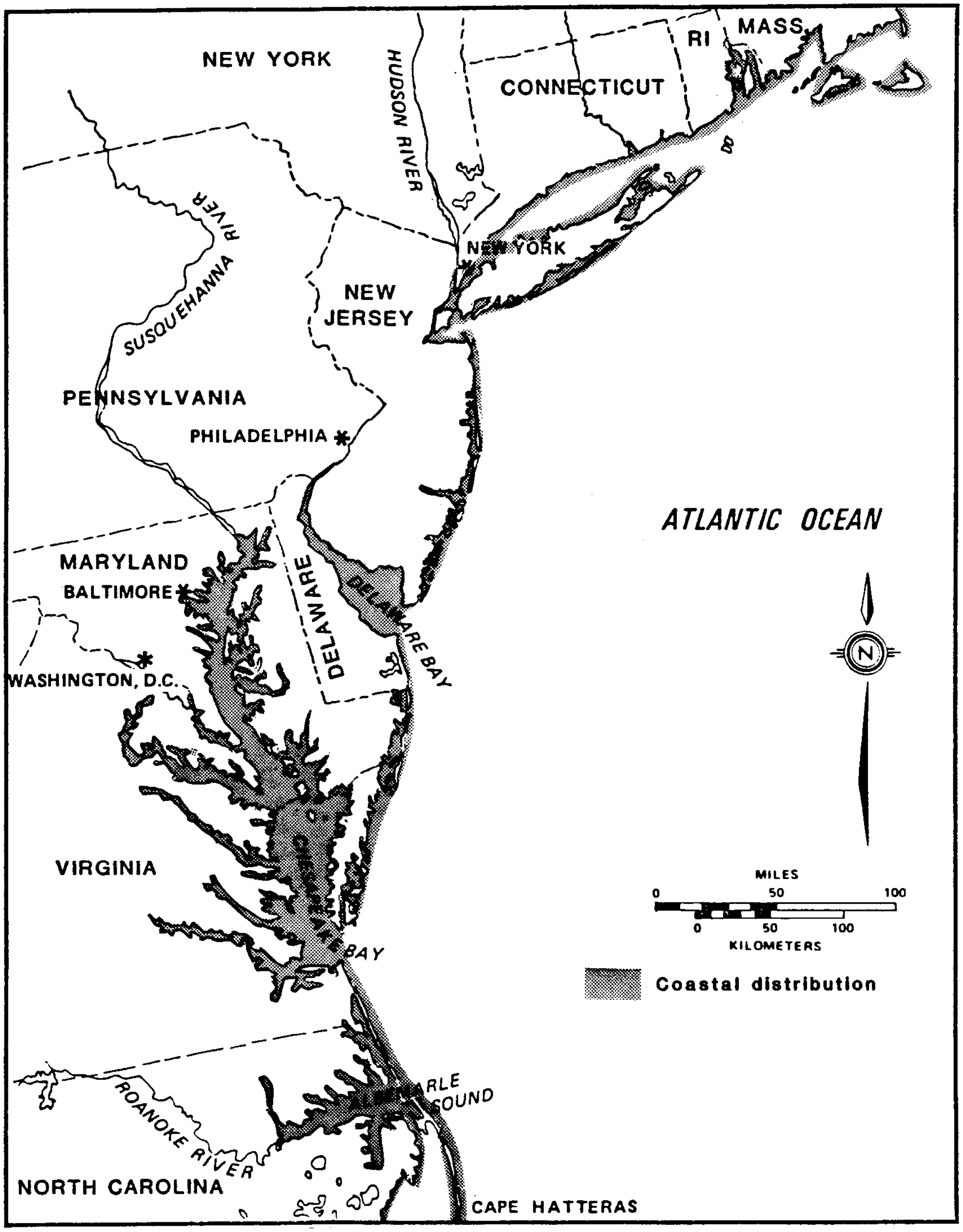

Figure 2. Mid-Atlantic coast distribution of mummichog and striped killifish. Both are found the entire length of the Mid-Atlantic region close to shore (within 110 m for mummichogs: Armstrong and Child 1965) and in bays, estuaries and tidal creeks (Hardy 1978). Striped killifish penetrate tidal rivers only as far as the mean boundary between fresh and brackish water; mummichogs penetrate as far as 75 km beyond this boundary (Massman 1954).

Recent systematic studies ..... On the basis of differences in egg morphology, gene frequencies, and spawning sites between populations north and south of northern New Jersey, Morin and Able (1983) proposed retaining the subspecies names F. h. heteroclitus for the southern population and F. h. macrolepidotus for the northern. Populations in the upper Delaware and Chesapeake Bays seem to be relicts of the northern subspecies. (These distributions do not match those of the subspecies as originally named.)

Scientific name ..... Fundulus majalis (Walbaum) (Robins et al. 1980)
Preferred common name .... striped killifish (Figure 1, bottom)
Other common names ...... bull minnow, gudgeon (Hildebrand and Schroeder 1928); striped mummichog, banded killifish, killie, mummie (Ursin 1977)
Class .... Osteichthyes
Order .... Atheriniformes
Family .... Cyprinodontidae

Geographic range .... New Hampshire south to northeastern Florida (Figure 2). Mainly in saltwater, less often in brackish (Rosen 1973). Most authors do not record it from freshwater (but see Hardy 1978). (See also "Salinity.")

MORPHOLOGY/IDENTIFICATION AIDS

The name "killifish" may be applied to members of three families: Cyprinodontidae, Anablepidae, and Poecilidae (Rosen 1973). Killifishes are soft-rayed, with no dorsal spine or spine preceding the anal fin. Most species are sexually dimorphic. Sexes are polymorphic with respect to pigment patterns and body and fin shape and size. Rosen (1973) suggested fin-ray and scale counts to identify correctly males and females within species. His paper contains a key to species of these three families.

In the Cyprinodontidae there is no lateral line and the upper surface of the head is conspicuously flattened (Hardy 1978). The anal fin in the male is not modified as an intromittent organ, and the third anal ray is branched. In the Fundulinae the jaw teeth are conical without cusps. Among members of the genus Fundulus, the body is not sharply angular or trapezoidal, and there is more than one series of jaw teeth (Rosen 1973). The mouth is terminal or the lower jaw projects slightly (Hildebrand and Schroeder 1928).

In both mummichogs and striped killifish, males are smaller than females after the first year. The origin of the dorsal fin in the male is directly above or in advance of the origin of the anal fin (Rosen 1973). The caudal fin is rounded in both species (Hardy 1978).

Fundulus heteroclitus: The snout is short, rounded, a little longer than diameter of eye in side view, with 8 mandibular pores. A well-developed fleshy pouch is found at the anterior base of the anal fin. Scales along the lateral line number 31-35 (Rosen 1973, but Hardy 1978 gives 31-39). There are 11-12 dorsal fin rays (Hildebrand and Schroeder 1928). There is no conspicuous silvery sheen on the sides; adult females have no dark spot on dorsal fin (Rosen 1973), and are brownish-green above, paler below. Small females have 13-15 dark vertical bars (Hildebrand and Schroeder 1928); adult females may be confused with those of F. confluentis (Rosen 1973). Adult males are dark green or olive above, yellow beneath; have sides with about 15 narrow silvery vertical bars and numerous white or yellowish spots; and may have a dark spot on posterior 4-5 rays of dorsal fin. Sex-specific color patterns appear when fish are 38-44 mm long (Hildebrand and Schroeder 1928); until then, young may be confused with adult female F. luciae (Rosen 1973). Adults are commonly 51-102 mm long (Armstrong and Child 1965). The largest specimen reported from Chesapeake Bay was 125 mm (Hildebrand and Schroeder 1928). (Throughout this paper, length measurements are as noted by the original authors. Total length may be assumed where the authors did not specify standard length.)

Fundulus majalis: The snout is long, pointed, and a little less than two eye diameters in profile (Rosen 1973). Overall body shape is slimmer than that of F. heteroclitus (Ursin 1977). There are 13-15 dorsal fin rays (Hildebrand and Schroeder 1928); and 32-37 scales in lateral series (Hardy 1978). A conspicuous silvery sheen appears on the sides of young and adults of both sexes (Rosen 1973); adults of both sexes have a black spot on the last rays of the dorsal fin. Adult females have one to several dark longitudinal lines and one or more disrupted vertical bars near the base of the tail; adult females are olive above, white below. Adult males are dark olive on back, and their sides and belly are salmon yellow, with 15-20 vertical black stripes (Hildebrand and Schroeder 1928; Hardy 1978 gives 11-20 stripes). Sex-specific color patterns appear when fish reach 38-51 mm (Hildebrand and Schroeder 1928); the young have bars similar to those of males (Rosen 1973). This species is the largest member of the genus in the study area; it frequently reaches 152-178 mm. The record is 203 mm long (Ursin 1977).

REASON FOR INCLUSION IN SERIES

Although not valued as commercial or sport fishes, both killifishes are important in food chains because of their distribution and abundance. (See also "Predators.") Because of their importance in marsh food chains, mummichogs may be instrumental in movement of organic material within and out of salt marsh ecosystems (Kneib et al. 1980). (See also "Movement Patterns" and "Food Habits.")

Mummichogs are sold as bait in sport fisheries for summer founder or fluke (Paralichthys dentatus) and young bluefish or snappers (Pomatomus saltatrix) in New York and New Jersey (Perlmutter 1961), and for flounder in Delaware (M.H. Taylor, University of Delaware, Newark, pers. comm.).

Mummichogs are the primary predators in the Open Marsh Water Management mosquito control program currently being tested in New Jersey, Delaware, and Maryland (Winner et al. in press). Although Gambusia (mosquitofish, Family Poeciliidae) is more often used as a biological control agent, the portion of the diet consisting of mosquito larvae is higher in studied species of Fundulus (grandis and confluentis). According to Harrington and Harrington (1961), the role of Gambusia affinis against Aedes mosquitoes has been overvalued because of its reputation as a predator on freshwater anophelines; in the control of saltmarsh mosquitoes, primary consideration should be given to the local endemic cyprinodontiform fishes rather than any single species.

As a group, killifishes are used in research in experimental studies of embryology, genetics, physiology, endocrinology, cytology, and behavior. Some of this research has important medical implications, such as the action of steroids in the regulation and reversal of sexual development, inheritance and development of cancerous tissues, and the genetics of histocompatability in tissue and organ transplants (Rosen 1973).

Mummichogs are the nondomesticated fish most frequently used in research (Rosen 1973), including such disparate studies as bioassay for water pollution (Isai et al. 1979), effects of weightlessness in outer space (Hoffman et al. 1978), ion transport in tissues (Evans

1980), and cycling and biological magnification of radioisotopes (Huver 1973).

LIFE HISTORY

Reproductive Physiology

During the breeding season, males of mummichogs and striped killifish assume a brighter coloration (Ursin 1977) and grow contact organs (Hardy 1978).

Fundulus spp. are oviparous. The ovary is single, and the number of ova produced depends upon the size of the fish. The largest number of ripe ova in a mummichog from Chesapeake Bay counted by Hildebrand and Schroeder (1928) was 460, in a female 98 mm long; the maximum for a striped killifish was 540 (length not given). Hardy (1978) gave a range of 200-800 ova for mummichogs and 460-800 for striped killifish in the Mid-Atlantic region. According to Taylor (in press), production of 100-300 eggs per day for 3-5 days is not unusual for Delaware mummichogs early in the spawning season. However, even early in the spawning season in North Carolina, up to 50% of the ova may be reabsorbed (Kneib and Stiven 1978).

In male and female mummichogs, the gonadosomatic index (GSI = gonad wt/body wt x 100) rises steeply in the spring and declines steeply in the autumn (Kneib and Stiven 1978). GSI fluctuates in both sexes during the spawning season; mean GSI gradually declines as the season progresses (Taylor, in press). Although ripe ova may be constantly available early in the season (Wallace and Selman 1981), the number of eggs laid is always greater during spring tides (Taylor et al. 1979). This semilunar cycle is most pronounced late in the spawning season in southern populations (Taylor, in press).

Food availability may be the ultimate control for egg production in mummichogs. If feeding ceases, vitellogenesis (yolk formation) ceases and maturational stages are flushed from the reproductive tract; renewed feeding causes reappearance of maturational stages (Wallace and Selman 1980). Fritz and Garside (1975) reported that in an estuarine population, spawning mummichog females averaged 65 mm long and 243 ova; in a population in less brackish water (0.6-15.5 ppt), averages were 60 mm and 161 ova. The difference was attributed to lower food density in the less brackish area. Weisberg (1981) also attributed the reduced female GSI observed in crowded experimental populations to insufficient food availability. Taylor (in press), however, cautioned that additional sources of stress may contribute to reduced fecundity in fish populations in nature.

Spawning Season and Periodicity

The spawning seasons of mummichogs and striped killifish vary with latitude. In Chesapeake Bay striped killifish spawn from April through September; from New Jersey northward, the season lasts from June through August (Hardy 1978). Spawning of mummichogs usually begins in spring (March to May) and ends in later summer or early autumn (July to September) (Hardy 1978; Kneib, in press). Although timing and duration of spawning seasons differ, the water temperature range over which spawning occurs is similar (Taylor, in press).

Mummichogs may spawn eight or more times in a season. Each spawning peak may last five or more days and coincides with a high spring tide of the full or new moon (semilunar periodicity: Taylor and DiMichele 1980). A circadian periodicity may be superimposed on the semilunar rhythm in some populations; maximal spawning then occurs when high spring tides are at night (Taylor et al. 1979). Spawning also occurs during the day (Hardy 1978).

Spawning in separate genetic populations of mummichogs may be timed by different environmental stimuli (Wallace and Selman 1981). Spawning rhythms may be timed by temperature (Brummett 1966), tides, moonlight, and salinity (Taylor et al. 1979). Early and late season peaks in spawning, such as Kneib and Stiven (1978) observed in mummichogs, may be caused by a combination of moderate temperatures and shorter daylengths (Harrington 1959). Day and Taylor (1983) found that a photoreceptor other than the pineal gland or retina of the eye influences seasonal reproduction in mummichogs. Female mummichogs respond to photoperiod, but its effectiveness has not been rigorously tested in males (Taylor, in press). In both sexes, low temperature prevents and high temperature permits gonadal development (Taylor, in press). The semilunar cycle of oogenesis persists in the absence of lunar or tidal stimuli (Taylor and Dimichele 1980). Schwassmann (1980) argued that we have no idea of the actual timing mechanism that entrains semilunar spawning in mummichogs.

Spawning Behavior

Rivalry is intense among breeding male mummichogs, and size seems to be less important than nuptial coloration in defense of territories. Females with very ripe ova may solicit males by turning on their sides to display their white bellies (Newman 1907). Adults gather in shallow weedy areas, and one or more males chase a female until she stops, at which time one male moves beside her and pushes her against the vegetation (Keenleyside 1979). Newman (1907) noted that courtship, consisting of tandem swimming, merges gradually into spawning as the male's movements become progressively more excited. Eventually the male clasps the female; their bodies form a shallow S-curve. The pair quiver vigorously and shed their gametes several times in rapid succession (Keenleyside 1979).

Spawning Site

Mummichogs spawn in fresh, brackish, and saltwater (Hardy 1978). In a Delaware marsh, eggs were laid in clutches of 10-300, at levels only reached by high spring tides (1.2-1.4 m above mean low water). Eggs are laid in empty shells of the ribbed mussel Geukensia demissa or inside the outer dead leaves of smooth cordgrass (Spartina alterniflora) (Taylor and DiMichele 1983). Egg deposition in shells has also been reported in Virginia (Able and Castagna 1975), North Carolina (Kneib and Stiven 1978), and Georgia (Taylor et al. 1981). Other reported spawning sites include algal mats in Massachusetts (Taylor et al. 1981) and Connecticut (Pearcy and Richards 1962), shallow pits covered by the female (Newman 1907), and scattered on the substrate (Keenleyside 1979). Selection of these different spawning sites may reflect an inherited preference or merely a response to substrate availability (Taylor, in press).

Striped killifish spawn in still, shallow water close to shore and, presumably, in small ponds. Active burying of eggs by females has been observed (Hardy 1978).

Eggs

A key to eggs of cyprinodontids of the Mid-Atlantic Bight appears in Hardy (1978). Fertilized eggs of striped killifish are spherical, 2.0-3.0 mm in diameter, translucent yellow to amber, and slightly adhesive (Hardy 1978).

Fertilized eggs of mummichogs are spherical, about 2 mm in diameter (range: 1.5-2.5 mm), and transparent yellow to amber (Hardy 1978); dead or infertile eggs are opaque (Taylor, in press). Adhesive chorionic fibrils on eggs may be long and dense, short and sparse, or absent in various populations (Hardy 1978; Morin and Able 1983). These fibrils may anchor eggs to the substrate and/or retain moisture when eggs are stranded (Brummett and DuMont 1981).

Mummichog eggs normally incubate in air and are not submerged until the next spring tide after they are laid (Taylor and DiMichele 1980). Eggs fail to develop if immersed for extended periods in water with less than 1 ml/l dissolved oxygen (DO) (Taylor, in press). Incubation of mummichog eggs in the field takes 7-8 days at 22-34 °C (Taylor et al. 1977); in the laboratory at 20 °C, hatching occurs in 10.5 days (Armstrong and Child 1965). In striped killifish 50% of the eggs hatch by 41 days at 16-20 °C, by 17 days at 22-26 °C, and by 12 days at 28-32 °C (Hardy 1978).

In mummichogs, hatching is controlled by oxygen concentration of the environment and hydration of the egg (DiMichele and Taylor 1980); it can be delayed 2 weeks or more if eggs are not immersed. Within seconds after immersion of fully developed eggs, hatching begins. The egg swells, the embryo's mouth opens, and heartbeat and respiration increase. Chorionase (hatching enzyme) is released from glands in the oral cavity and gills of the embryo in response to hypoxia ("respiratory distress syndrome" of DiMichele and Taylor 1981). This enzyme weakens the chorion so that body movements of the embryo can break it. Five minutes after immersion, the embryo begins to turn in the egg; the egg ruptures in 15-20 min (Taylor et al. 1977).

Yolk-Sac Larvae

The yolk-sac larval stage lasts from hatching until all yolk is absorbed, and may also be called the prolarva, free embryo (Chuganova 1963), or alevin (Tay and Garside 1978). A key to yolk-sac larvae of fishes of the Mid-Atlantic Bight appears in Hardy (1978). Larvae of mummichogs may hatch with the yolk already absorbed, if immersion of developed eggs has been delayed (Taylor et al. 1977). At hatching mummichog embryos are 4.0-7.7 mm (mean 5.0 mm) long; striped killifish are 7.0-11.00 mm long (Hardy 1978). In the laboratory at 20 °C, newly hatched mummichogs require 5.5 days to absorb the yolk. As the yolk disappears, dorsal and ventral fins form, and the coordination of the lower jaw and operculum, undulating swimming, and pectoral fin movements are perfected (Armstrong and Child 1965).

Larvae

The larval stage lasts from yolk-sac absorption until the fish attains the characteristic shape of the species. During this stage the fin rays and scales develop (Chuganova 1963). Striped killifish larvae are 11.8-23.8 mm long. In mummichogs scales first appear above the pectoral fin at about 12.5 mm, and are well developed at 20.0 mm (Hardy 1978).

Juveniles

Juveniles are also called fry or young-of-the-year, and have fully developed fins and a more or less distinct scale covering (Chuganova 1963). The minimum described length of this stage in mummichogs is 25.0 mm; in striped killifish it is 26.0 mm (Hardy 1978). For a detailed description of this stage for both species, see Hardy (1978).

Adults

Female mummichogs are sexually mature at 38 mm and males at 32 mm; striped killifish females mature at 76 mm and males at 64 mm (Hildebrand and Schroeder 1928). Most members of both species attain maturity during their second year, although some mummichogs may mature and spawn during their first year (Hardy 1978; Kneib and Stiven 1978). (See also

"MORPHOLOGY/IDENTIFICATION AIDS" and "Population Size and Structure.")

Movement Patterns and Seasonal Use of Habitats

The mummichog is "one of the most stationary of fishes," according to Bigelow and Schroeder (1953). Breeding migrations do not occur (Rosen 1973). Fish over 60 mm long maintain a summer home range of 36-38 m along one bank of tidal creeks; however, some may move as much as 375 m (Lotrich 1975).

In winter, mummichogs in pools burrow 150-200 mm into the mud (Chidester 1920; Hardy 1978). Others migrate to the mouth of the tidal channel where they have been living; in the subsequent spring they usually return up the same channel (Butner and Brattstrom 1960). Spring migration begins when the water reaches 15 °C (Hardy 1978); feeding begins in New England marshes during the first week in April (Valiela et al. 1977).

During the growing season, young mummichogs remain in the intertidal zone for 6-8 weeks, inhabiting shallow pools on the marsh surface at low tide (Taylor et al. 1979). Juveniles of 15-20 mm Standard Length (SL) begin to move with the adults onto the marsh surface to feed (Kneib in press). To grow at a normal rate, mummichogs may need food from the marsh surface for at least part of their diet. Despite abundant food resources on the marsh surface, mummichogs may be food limited because tides limit foraging time there (Weisberg and Lotrich 1980).

Mummichogs maintain an endogeneous circadian feeding pattern which, superimposed upon the tidal rhythm, allows maximal use of food resources available only at high tide (Weisberg et al. 1981). They feed primarily at high tide during daylight (Weisberg and Lotrich 1980; Reis and Dean 1981), but also opportunistically (Weisberg et al. 1981).

GROWTH CHARACTERISTICS

Length-Weight Relationship

Length-weight equations have been calculated for mummichogs:

(1) $\log W = -5.232 + 3.172 \log L$
where W = wt and L = Total Length (Fritz and Garside 1975)

(2) $\log Y = -2.06 + 3.27 \log X$
X = Total Length (cm) and Y = wet wt (g)
(Meredith and Lotrich 1979)

In some populations of mummichogs, the relation of weight to length may vary significantly through the year (Kneib and Stiven 1978). Females are larger than males of the same age, but males are heavier than females of the same length (except during the spring spawning peak). In the North Carolina population studied, males averaged 251 mg and females 245 mg.

Seasonal and Annual Growth and Production

Growth of first-season mummichogs in mid-summer may average 5% of their total weight per day. In North Carolina the major growing season is April to September. Both sexes grow fastest during their first two growing seasons. Females mature sexually at 30-35 mm SL in 5-6 months (Kneib and Stiven 1978).

The age of mummichogs can be determined by observing growth marks on the otoliths after a fish has overwintered once. For a field population in Nova Scotia, Fritz and Garside (1975) observed the following age-length correlations:

AGE (yr):	1	2	3	4
LENGTH(mm):	35-50	51-74	68-83	78-95

Mummichogs reared in the laboratory at 13 °C have a maximum daily growth of 0.5% of their dry weight at a feeding level of 6.0% of their body weight (Prinslow et al. 1974). There is no stomach in mummichogs (i.e, no region of the gut secretes pepsin and hydrochloric acid); digestion occurs under alkaline conditions (Targett 1979). Nevertheless, mummichogs have a higher than average assimilation (digestion) efficiency (87% on three laboratory diets) compared to other fishes (Weisberg and Lotrich 1982). Metabolic costs account for 69% of ingested energy. Excretion exceeds egested energy on some diets.

Gross growth efficiency (proportion of calories ingested that is incorporated into biomass x 100) has been calculated by several authors. Larval mummichogs fed brine shrimp nauplii were thought to be inefficient converters of food to biomass by Radtke and Dean (1979), but Kneib (1981), using their data, calculated that gross growth efficiency might be as high as 25%-41%. Efficiency of adults was determined to be 12% (Weisberg and Lotrich 1982); this is at the low end of the normal range for carnivorous fishes.

Total production of mummichogs in salt marshes is among the highest calculated for natural populations of fishes: 160 kg dry wt/ha in New England (Valiela et al. 1977). Meredith and Lotrich (1979) also calculated a high production (40.7 $g/m^2/yr$) and believed that local conditions were the main reason that their figure varied from that of Valiela et al. (1977).

POPULATION DYNAMICS

Population Size and Structure

Mummichogs are the most abundant member of their genus in some areas (e.g., Beaufort, North Carolina: Huver 1973). Their name, in fact, is related to their abundance: "mummichog" is an Indian word meaning "going in crowds" (Nichols and Breder 1927). Schools may number from a few fish to several hundred or more (Hildebrand and Schroeder 1928). The density in summer of mummichogs longer than 40 mm may range from 0.35 to $6.04/m^2$ in certain estuarine habitats (Kelso 1979). From 130,000 to 136,000 mummichogs longer than 30 mm have been reported along 3 km of a tidal creek in July, and from 63,000 to 81,000 individuals in September (Meredith and Lotrich 1979).

Autumn, winter, and spring populations of mummichogs are dominated by survivors of one growing season (Kneib and Stiven 1978). During the spawning season, synchronization of spawning and hatching with spring tides results in pulses of larval and juvenile abundance on the marsh (Kneib 1984). Later in the summer, the population is overwhelmingly dominated by young-of-the-year. In August, when all age classes are present, nearly 60% of the population has not yet overwintered and less than 8% has completed two growing seasons (Kneib and Stiven 1978). The number of fish in the largest size class (longer than 70 mm) peaks in August and declines drastically by October (Meredith and Lotrich 1979). Migration, however, as well as mortality, may contribute to this decline. In October and November, there are very few 3-year-olds (Valiela et al. 1977). There is no evidence that any members of this species survive beyond their fourth growing season (Kneib and Stiven 1978).

Mortality

Most mummichog eggs are fertile and survive to hatching; loss due to infertility, mortality, and predation is about 10% (Taylor, in press). Young-of-the-year may have an annual mortality of up to 99.5% and adults, 54% (Meredith and Lotrich 1979). Female mortality increases dramatically after first reproduction (Kneib and Stiven 1978), perhaps because of detrimental after-effects of spawning (Meredith and Lotrich 1979). The decline in the survivorship curve with age is not as marked as expected if senescence were wholly responsible;

predation may be an important source of mortality (Kneib and Stiven 1978). During winter on the marsh, predation is low (Valiela et al. 1977); less than half as many large fish are lost between October and April as between August and October (Meredith and Lotrich 1979).

ECOLOGICAL ROLE

Feeding Behavior/Food Habits

The protruding lower jaw and tilted mouth of cyprinodontids are well-adapted to surface feeding (Eddy 1957). Fundulus, however, does not hesitate to feed in mid-water or on the bottom (Huver 1973). Grass shrimp (Palaemonetes pugio) swimming near the surface are often consumed, perhaps because they are silhouetted against the light (Heck and Thoman 1981). Vision plays an important role in feeding of mummichogs, but swallowing depends upon another sense, probably olfactory (Hara 1971). Mummichogs are attracted to the amino acid gamma-aminobutyric acid (GABA), but will not swallow substrate containing GABA (Jonsson 1980).

Mummichogs use all potential food sources: organisms in the water column, subtidal benthos, and intertidal benthos (Weisberg and Lotrich 1982). Recent radioisotope tracer studies have shown that 56% of mummichogs' body carbon is derived from algal (benthic and planktonic) food chains and 44% from the Spartina food chain (Hughes and Sherr 1983).

Baker-Dittus (1978) decided that Fundulus uses all available food items except detritus. She found small crustaceans and polychaetes to be the most frequent food of both mummichogs and striped killifish. Fritz (1974) ranked food items found in the guts of mummichogs 22-101 mm long. Copepods were the most common, followed in order by flies (mostly larvae and pupae), amphipods, polychaetes (mostly Nereis virens), isopods, ostracods, snails, insects, bivalves, algae, fishes, fish eggs, beetles and shrimps, and hymenopterans. In one North Carolina marsh, the major prey of mummichogs were fiddler crabs, polychaetes, tanaids, and other small crustaceans. Fish less than 30 mm SL primarily ate small crustaceans (amphipods, tanaids, copepods); larger fish consumed crabs, detritus, and algae more often (Kneib and Stiven 1978; Kneib et al. 1980). Although mummichogs may ingest large quantities of detritus while feeding on the surface of the substrate, detritus is not a significant energy source for them because it is not assimilated (Prinslow et al. 1974). Mummichogs cannot subsist on a diet of plant material or detritus (Katz 1975).

Mummichogs swallow their prey intact, so mouth gape limits prey size. Large mummichogs will also eat small prey, but larger prey are more important in their diet (Vince et al. 1976). The numerical response of most infaunal invertebrates to mummichog predation depends on fish size more than fish density. Kneib and Stiven (1982) attributed this to very small infauna (organisms in bottom sediments) not being readily available to larger fish.

Mummichog populations are large enough to influence their prey's distribution and abundance (Valiela et al. 1977), but few studies have convincingly demonstrated this result (Kneib 1984). Some prey species that may be regulated by mummichogs are the amphipod Gammarus palustris (Van Dolah 1978), the pulmonate snail Melampus bidentatus (Vince et al. 1976), and the soft-shelled clam Mya arenaria (Kelso 1979). Kneib (in press) points out that, by controlling smaller predators, mummichogs may indirectly increase densities of some infaunal marsh invertebrates. Also, predation by larval and juvenile mummichogs, which has previously been overlooked, may affect the patchy distribution patterns of some small invertebrates (e.g., harpacticoid copepods) in salt marshes.

Predators

Small tidal marsh fishes, such as killifishes, are the major prey for wading birds, aerial searching birds, piscivorous ducks, and many predatory fishes (Peterson and Peterson 1979). These predators include herons, egrets, terns, gulls, striped bass, and bluefish (Valiela et al. 1977). The diet of nestling herons and egrets may contain up to 95% killifishes (including Gambusia), and up to 30% Fundulus spp. (Jenni 1969). Least and common terns eat Fundulus spp. in pools when the tide goes out (Butner and Brattstrom 1960). Selective predation by visual predators is suggested by increased mortality in male mummichogs after they achieve sex-specific coloration (Kneib and Stiven 1978).

From late August to early September in Delaware, American eels (Anguilla rostrata) preyed heavily on mummichogs (Lotrich 1975). Other fish that prey on Fundulus spp. are white perch (Morone americana: Miller 1963), summer flounder (Paralichthys dentatus: Meredith and Lotrich 1979), and red drum (Sciaenops ocellata: Peterson and Peterson 1979). Fundulus spp. are also eaten by crabs (Libinia, Callinectes, Uca: Butner and Brattstrom 1960; Eurytium limosum: Kneib in press). Predation by blue crabs produces size-specific losses in experimental field populations of mummichogs (Kneib 1982). Another example of size-specific predation is cannibalism of their own eggs by spawning mummichogs (Able and Castagna 1975).

Competitors

Three species of killifishes (Figure 3)--mummichog, striped killifish, and sheepshead minnow (Cyprinodon variegatus)--may occur together in permanent ponds of the high marsh (Nixon 1982), tidal creeks, the low marsh surface (Daiber 1982), and unvegetated tidal flats (Peterson and Peterson 1979). All three species use the marsh surface at high tide, but only mummichogs and sheepshead minnows do most of their feeding at this time. These two species consume more epiphytic algae than do striped killifish, which eat more benthic invertebrates. Sheepshead minnows are herbivores, but mummichogs and striped killifish seek invertebrates in the algal mats (Werme 1981).

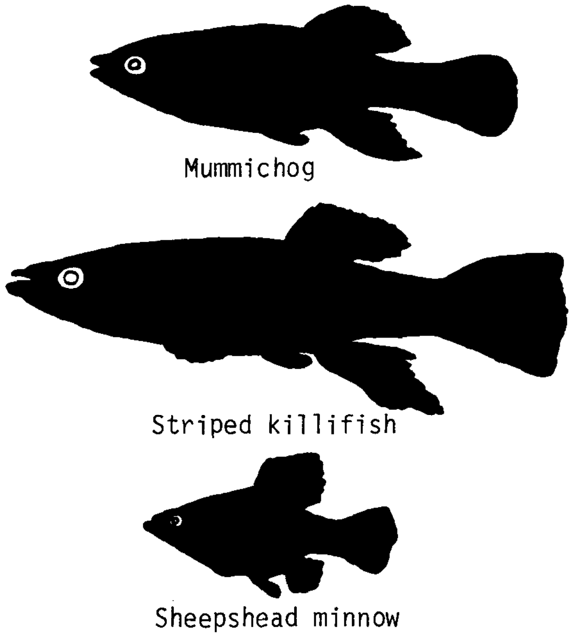

Figure 3. Silhouettes of the three most common killifishes on the Mid-Atlantic coast of the United States (from Rosen 1973).

In the laboratory, sheepshead minnows chase mummichogs from their territories more often than they chase rainwater killifish (Lucania parva) or mosquitofish (Gambusia affinis). This may be due to similar spawning behavior. All four of these species may occur together in nature, but in ponds in the field, mummichogs tend to remain in water deeper than 10 cm, and only briefly visit sheepshead minnow territories (Itzkowitz 1974).

Mummichogs, striped killifish, and Fundulus diaphanus were found in heterotypic schools in the intertidal region of a Maryland estuary by Baker-Dittus (1978). Mummichogs were by far the most abundant in May and June, but striped killifish slightly dominated in August and September. Diets of these two species differed in only one aspect: during July and August striped killifish continued to eat many polychaetes, while mummichogs ate more plant material. Greatest dietary overlap coincided with both the highest density of all three fish species and the highest food density.

Parasites

Parasites of Fundulus spp. are listed by Dillon (1966); Hoffman (1967) listed additional species and noted larval stages. Parasites of mummichogs and striped killifish include dinoflagellates, sporozoans, monogenetic flukes, digenetic flukes, tapeworms, roundworms, spiny-headed worms and copepods. Mummichogs are also susceptible to lymphocystis (caused by a virus) and Chondrococcus columnaris, a myxobacterium infecting the skin, gills, and fins (Sinderman 1970).

Since 1967 additional parasites have been recorded from mummichogs, including Eimeria funduli, a sporozoan unusual in that it requires grass shrimp (Palaemonetes pugio) as a second host (Upton and Duszynski 1982); Trypanoplasma bullocki, a flagellate vectored by a leech in Chesapeake Bay (Burreson and Zwerner 1980); and Dichelne bullocki, a roundworm whose larvae live in the anterior, and adults in the posterior, intestine (Kuzia 1978).

Additional parasites reported from both species of Fundulus are Swingelus sp., a monogenetic trematode (Billeter 1974), and Cryptobia bullocki, a biflagellate kinetoplastid found in the blood (Nigrelli et al. 1975).

Pathogenicity of parasites varies. Oodinium cyprinodontiform is believed to be a "symphoriont ectocommensal," deriving most of its energy from photosynthesis, but the other dinoflagellate recorded from Fundulus spp., Amylodinium, seriously disrupts gill epithelium (Lom and Lawler 1971). Although trematode metacercarial cysts in their brains must cause compression and tissue damage, the behavior of infected mummichogs remains normal (Abbott 1968). Because of its large size relative to the host, larval Eustronglides spp. are a substantial nutritional drain; they also reduce host gonadal weight (Hirschfield et al. 1983). Larvae of Eustrongylides ignotus, when eaten in infected mummichogs, may cause high mortality in nestling herons and egrets (Wiese et al. 1977).

ENVIRONMENTAL REQUIREMENTS/TOLERANCES

Temperature

Temperate marine fishes do not normally survive water temperatures greater than 34 °C (de Silva 1969). However, several species of Fundulus can recover from exposures to 40-42 °C water (Altman and Dittmer 1966). In laboratory experiments, mummichogs and striped killifish died of heat shock in 63 min at 34 °C, 28 min at 36 °C, 9 min at 37 °C, and 2 min at 42 °C (Orr 1955).

Mummichogs are eurythermal (de Silva 1969). In Delaware salt marshes, mummichogs experience a temperature fluctuation of 6-35 °C (Schmelz 1964). In Maine salt marshes, summer tidal cycles expose mummichogs to rapid temperature changes from 15 to 30 °C. Swimming ability is maintained in nature during temperature fluctuations which would substantially impair contractile function in other fishes. In the laboratory, low ATPase activity at very cold temperatures supports field observations of a relatively torpid state for overwintering mummichogs (Sidell et al. 1983).

Although assimilation (digestion) efficiency of mummichogs varies significantly with temperature in the laboratory, this is probably of little ecological significance. Maximum efficiency occured from 13 to 29 °C in the laboratory; at lower temperatures fish simply took longer to digest their food (Targett 1979). In the laboratory, rate of feeding of young mummichogs depended on temperature and increased rapidly above 24 °C (Radtke and Dean 1979).

Oxygen consumption is relatively independent of acclimation temperature from 15 to 25 °C (Moerland and Sidell 1981). Targett (1979) reported a similar relationship for the respiratory metabolic rate: temperature independence from 13 to 29 °C and temperature-sensitive reduction from 5 to 13 °C.

Mummichogs spawn in water from 16.5 to 25 °C (Hardy 1978). Eggs develop at temperatures of 12-27 °C with less than a 2% incidence of abnormality (Smith 1982). In the laboratory, mortality was low (7%) to moderate (29%) in striped killifish embryos transferred from an intermediate, fluctuating temperature regime (22-26 °C) to higher (28-32 °C) or lower (16-20 °C) fluctuating temperatures (Fahy 1976). The number of vertebrae and dorsal fin rays developed by embryos was inversely correlated with temperature, and was influenced more by cold water than by warm (Fahy 1979). Thermal effluents from electric power plants caused an elevated frequency of vertebral abnormalities in mummichog embryos (Mitton and Koehn 1976).

The median time to hatching is inversely related to water temperature (Tay and Garside 1975). Although hatching is not affected by the normally encountered range of temperatures, the hatching enzyme is unstable at 30 °C or above (DiMichele et al. 1981).

Salinity

Although mummichogs are physiologically euryhaline, Fritz and Garside (1974) considered salinity preference to be the most important environmental factor influencing their distribution in Nova Scotia. Laboratory studies supported this conclusion by showing that mummichogs strongly preferred salinity of 20 ppt over 8 ppt.

Striped killifish rarely if ever enter freshwater (Rosen 1973; Robins et al. 1980, but see Hardy 1978). In the Chesapeake Bay area mummichogs are rarely taken in full saltwater and are found more often in freshwater than are striped killifish, although the habitats of these species overlap (Hildebrand and Schroeder 1928). In North Carolina, striped killifish also tend to occur in higher salinities, while mummichogs tolerate lower salinities (Peterson and Peterson 1979). These studies support the long-held notion of the greater ability of mummichogs to live in a range of salinities, perhaps selected in a given area to avoid competition with congeners.

Mummichogs are especially tolerant of abrupt salinity changes. They adapt so quickly that prior salinity acclimation has no effect on laboratory testing of response to salinity (Garside and Chin-Yuen-Kee 1972).

The ability of ova from northern and southern populations of mummichogs to be fertilized at various salinities was examined by Bush and Weis (1983). There was no difference in the ability of sperm to fertilize ova at 30 ppt. However, at 15 ppt there was a difference, which may mean that egg response to salinity varies geographically.

Mummichog larvae survive in water between 0.39 ppt (fresh, by definition) and 100 ppt, although growth is retarded at salinities greater than that of seawater (32-33 ppt). Larvae are active and feed in water under 1 ppt, but do not survive more than 11 days in tap water (Joseph and Saksena 1966). When mummichog embryos are incubated in salinities of <0.5 ppt to 60 ppt, those in 20 ppt are always the longest and those in freshwater are always the shortest (Tay and Garside 1978).

Temperature-Salinity Interactions

Salinity affects response to water temperature in mummichogs. For example, the role of increased serum glucose in low temperature survival is affected by salinity (Leach and Taylor 1977). The upper lethal temperature is highest (34 °C) in an isosmotic (14 ppt) medium. The lethal temperature is depressed 6 °C in freshwater (0 ppt), but only 2.5 °C in seawater (32 ppt) (Garside and Chin-Yuen-Kee 1972). In the laboratory, mummichogs preferred 24 °C in seawater but 22 °C in freshwater. Stress imposed by unusual salinity does not allow complete expression of thermal acclimation (Garside and Morrison 1977).

Contaminants

Mummichogs are considered particularly stress- and pollution-tolerant (Huver 1973), although they are more susceptible to chlorine and chloramine than are winter flounder (*Pseudopleuronectes americanus*) and scup (*Stenotomus chrysops*) (Capuzzo et al. 1977). Response to pollutants may depend upon temperature, salinity, and presence or absence of certain chemicals in the water. The same concentration of a pollutant that is only mildly toxic to fish under optimal environmental conditions may be lethal to fish under thermal or osmotic stress. For example, under optimal conditions of temperature and salinity, a solution of 15% water soluble fraction (WSF) of No. 2 fuel oil, which contains 0.28 ppm naphthalenes, was only mildly toxic to mummichog embryos. Concentrations of 25% WSF (0.47 ppm naphthalenes) were required to attain >50% mortality. However, under suboptimal conditions, especially extreme temperatures, even the 15% exposure resulted in >50% mortality (Linden et al. 1979). Adult mummichogs under thermal or osmotic stress are also more sensitive to the lethal effect of emulsions of fuel oil (Butler et al. 1982).

Teratogenicity (ability to cause birth defects) of a pollutant may also be higher under suboptimal salinities (Weis et al. 1979). For example, teratogenicity of methylmercury is higher at salinities of 10 ppt than at 30 ppt, and at temperatures of 16 °C than of 25 °C (Weis et al. 1979). Sensitivity to radiation also depends on temperature and salinity (Baptist et al. 1972). In both mummichogs and striped killifish, salinity plays an important role in copper uptake which differs for each species and life cycle stage (Bennett and Dooley 1982).

Other Environmental Factors

Low dissolved oxygen is a necessary hatching stimulus for mummichog eggs (DiMichele and Taylor 1980). Adult mummichogs survive overnight in anoxic tidal waters by gaping at the surface. Presumably splashing oxygenates the surface water that reaches the gills (M.H. Taylor, University of Delaware, Newark; pers. comm.).

Although found on many substrates, mummichogs prefer mud (Hildebrand and Schroeder 1928). Fritz (1973), however, was unable to detect a substrate preference. Mummichogs seem to prefer areas with grass (*Spartina patens*) over areas without (mud substrate), possibly because vegetation allows them to evade predators (confirmed in the laboratory by Ordzie

1978). Striped killifish tend to occur over sandy sediments more often than do mummichogs, and are by far the most important killifish on the unvegetated intertidal flats of North Carolina (Peterson and Peterson 1979). In the laboratory, both species respond more strongly to substrate and cover than to current (Rosen 1973).

The maximum depth at which mummichogs are found is seldom more than two fathoms (Bigelow and Schroeder 1953). Striped killifish may be found in water only a few centimeters in depth. This species is concentrated along the shoreline during flood tides, and, if washed ashore, can reenter the water (as can the mummichog) by a series of jumps (Hildebrand and Schroeder 1928; Rosen 1973). Mummichogs and striped killifish are positively rheotactic (face into a water current) (Rosen 1973).

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16. Abstract (Limit: 200 words)

Species profiles are literature summaries of the taxonomy, morphology, range, life history, and environmental requirements of coastal aquatic species. They are designed to assist in environmental impact assessment. Mummichogs and striped killifish are not commercial or sport fish; however, their distribution and abundance make them important in nearshore and estuarine food webs. These are two of the three most common killifishes on the Mid-Atlantic coast; summer density of mummichogs in estuaries may be as high as six per square meter. Most members of both species attain sexual maturity and spawn during their second year. Mummichogs have a semilunar spawning periodicity during the spawning season; eggs incubate in air and are not submerged until the next spring tide after they are laid. Young mummichogs remain on the marsh for 6-8 weeks, then begin to move off with the tides, with the adults. Mummichogs and striped killifish are euryphagous predators. Both species are tolerant of temperature and salinity fluctuations. Mummichogs are rarely taken in full seawater; striped killifish rarely, if ever, enter freshwater. Between these extremes, the habitats of the two species overlap.

17. Document Analysis a. Descriptors

Parasites
Fishes
Growth
Estuaries
Feeding
Salinity
Tidal marshes

b. Identifiers/Open-Ended Terms

Mummichog
Fundulus heteroclitus
Striped killifish
Fundulus majalis
Life history
Spawning
Temperature requirements
Salinity requirements
Predators
Competitors

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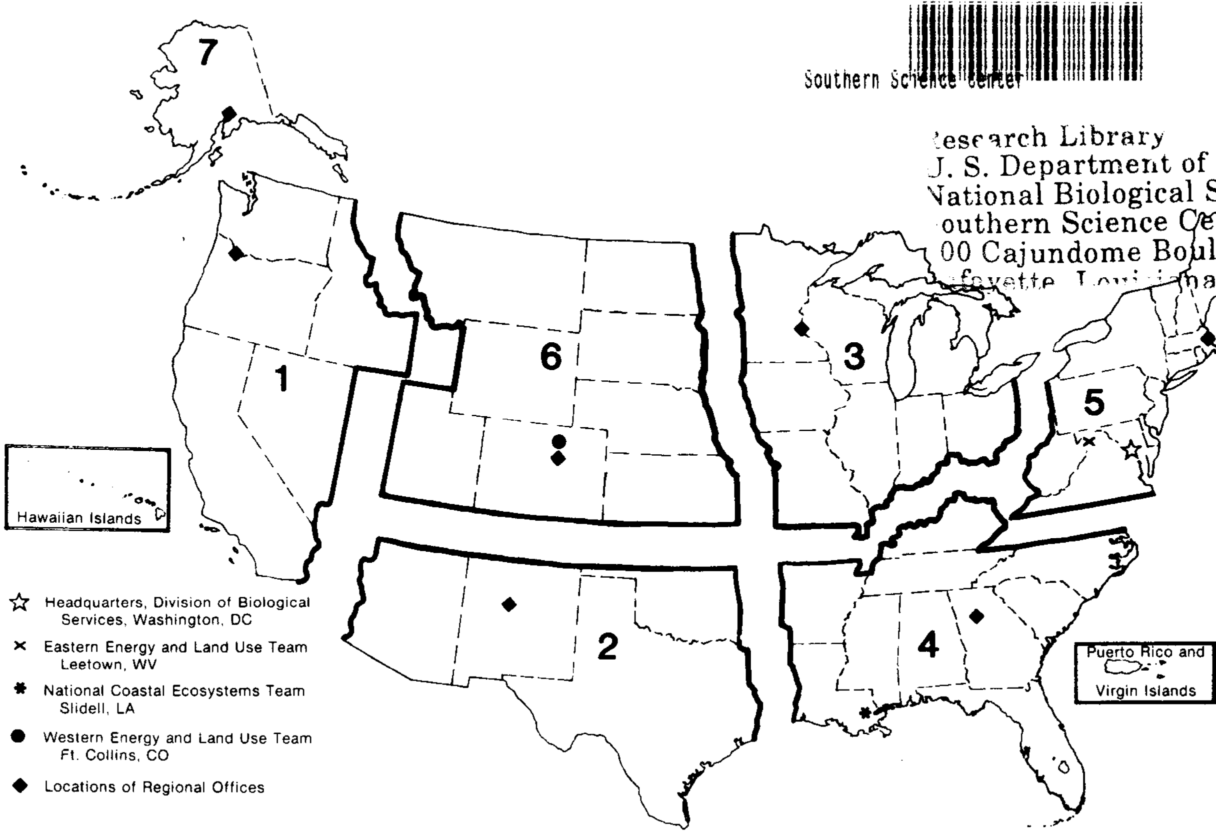

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Regional Director
U.S. Fish and Wildlife Service
Lloyd Five Hundred Building, Suite 1692
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Portland, Oregon 97232

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Regional Director
U.S. Fish and Wildlife Service
P.O. Box 1306
Albuquerque, New Mexico 87103

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