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Smallmouth Bass

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When the egg of a smallmouth bass (*Micropterus dolomieu*) is about to hatch, it is only 1/10 inch in diameter (Tester 1930). But given the right conditions and some luck, it will hatch, and the tiny fish will grow to be one of the most sought after game fish in North America. Henshall (1889) was referring to the smallmouth bass when he stated perhaps the most frequently quoted words of praise for a fish, "inch for inch and pound for pound, the gamest fish that swims." The species has been studied by many competent scientists and the humorist, Stephen Leacock, and the serious bass angler would do well to read his treatises, "Personal experiments with the black bass" (1930) and "Bass fishing on Lake Simcoe with Jack Gaudaur" (1941). It was Leacock who discovered the ability of bass to take a hook and after fighting for awhile, go to the bottom, remove the hook, and either fasten it in a log or replace itself with a 6-inch perch.

Smallmouth differ from the other basses in having all of the following characteristics: (1) there is no dark horizontal band along the side, (2) the upper jaw never extends beyond the eye, and (3) there are 13-15 soft rays in the fin on the back.

Smallmouth bass have been divided into two subspecies: the northern smallmouth, *Micropterus d. dolomieu*, and the Neosho smallmouth, *Micropterus d. velox*, (Hubbs and Bailey 1940). The subspecies differ in body shape and morphological characters, growth rate and efficiency of food utilization, and vulnerability to angling (Hubbs and Bailey 1940, Mohler 1966, Divine 1968).

Smallmouth originally ranged from the Great Lakes and St. Lawrence River drainages in Canada south to northern Georgia, west to eastern Oklahoma, and north into Minnesota (Schneberger 1972, Scott and Crossman 1973, Robbins and MacCrimmon 1974). The species has been introduced, and self-sustaining populations established, across the continental United States and Canada, and in Hawaii, Asia, and Africa. The smallmouth bass also has been intro-

duced to Europe and South America, but its present status there seems questionable (Robbins and MacCrimmon 1974).

Habitat

Smallmouth bass occur naturally in large, clear-water lakes and cool, clear streams having moderate current and a substrate of rock and gravel. They also live in small ponds (Bennett and Childers 1957, Coble 1971) and turbid streams (Cleary 1956). In a typical stream that one might picture, trout would inhabit the upper, cold-water section; smallmouth bass, the middle section with cool water, rocky bottom, and good gradient with large pools between riffles; and largemouth bass (*Micropterus salmoides*), the lowland section with sluggish current, silt and mud bottom, and aquatic vegetation. The importance of rubble, gravel, and current to smallmouth bass was especially apparent in the study of Reynolds (1965). He found only sparsely scattered clumps of rocks in the Des Moines River, Iowa, a stream with predominantly sand bottom, turbid water, and sluggish current. Smallmouth bass were almost always found over such rocky clumps below a riffle.

According to Hubbs and Bailey (1938) the best smallmouth bass lakes are over 100 acres, more than 30 feet deep with thermal stratification, and have clear water with scanty vegetation and large shoals of rock and gravel. Smallmouth usually inhabit water less than 40 feet deep in lakes but have occasionally been found at greater depths (Hile and Juday 1941, Webster 1954). Often they are found over rocky bars and ledges in water 5 to 20 feet deep.

In streams, smallmouth bass are not found in an area of strong current, but instead in the lee of objects near the edge of the current (Hubbs and Bailey 1938, Harlan and Speaker 1956, Munther 1970). Characteristics of cover that seem to be attractive are darkness and quiet water (Haines and Butler 1969). Paragamian (1973) frequently found adults in pools having moderate surface current and

rock and rubble substrate, whereas fingerlings were in calm marginal regions containing rocks and vegetation. Smallmouth have been observed near the surface seemingly sunning themselves (Webster 1954, Munther 1970). At night the fish lie on the bottom or actually enter the substrate (Hubbs and Bailey 1938, Munther 1970).

In summer smallmouth bass have been found occupying water with temperatures of 67 to 71°F (Hile and Juday 1941, Westman and Westman 1949, Hallman 1959). The temperature selected when smallmouth were offered a choice in laboratory experiments was about 82°F (Ferguson 1958, Peek 1965, Robbins and MacCrimmon 1974). Although selected temperatures in laboratory studies may typically exceed those indicated by field observations for warmwater fish (Ferguson 1958), occasionally smallmouth have been observed in the field occupying waters of 79 or 80°F (Munther 1970, White 1970).

In winter smallmouth bass move to deeper water and seek places that are dark and devoid of current — crevices between rocks, holes, submarine caves, and hollow logs (Henshall 1889, Beeman 1924, Webster 1954, Munther 1970). This migration begins when water temperature is falling, and though it may begin when temperature is as high as 60°F (Munther 1970), the behavioral pattern becomes more pronounced at 50°F and lower (Beeman 1924, Hubbs and Bailey 1938, Webster 1954). The fish become torpid when water temperature reaches the lower 40°F range and less, and rarely feed. In streams, rough substrate to brace against or protect from the current is necessary to prevent downstream displacement of the inactive fish (Klauda 1968). In laboratory studies, it has been observed that the amount of voluntary movement decreases as water temperature decreases below 59°F (Klauda 1968), and that swimming ability (maximum swimming speed) of fingerlings is reduced substantially at temperatures below 68°F (Kerr 1966). Munther (1970) observed that as temperature fell below 50°F in a tank smallmouth bass became less active and moved closer to the bottom, and at 44-46°F most fish entered the substrate. I once found fingerling smallmouth bass in a tank congregating in a hose at a temperature of 50°F and less.

In the northern part of the range, the fish

return to shallower water in spring and resume feeding about the time ice disappears. Occasionally, one may be caught through the ice in early spring (Beeman 1924, Anderson 1947, Webster 1954). Keast (1968) found fresh food in the stomach of one of three smallmouth bass in an Ontario stream on April 19 when water temperature was 47°F.

The temperature that is lethal for a fish varies and depends greatly on the temperature previously experienced — the acclimation temperature. Lethal temperatures also vary somewhat according to the amount of time a fish is exposed to a certain temperature, to its age, and sometimes to the season when it is tested, or to its acclimatization.

Working with smallmouth bass acclimated to 68°F, Kerr (1966) found the 1-hour upper TL 50 temperature (upper temperature that would kill half a batch of test fish in 1 hour) to be 95°F for larvae 2 days after hatching. The upper TL 50 temperature was about 91°F for older larvae in the yolk sac absorption stage and fingerlings 2½ months old. When Kerr (1966) exposed groups of 2-month old fingerlings about 2 inches long, acclimated to 68°F, for 1 hour to 50° and 41°F, the fish held at 50°F changed color and became immobile but did not die, but 95 percent of those exposed to 41°F died. Horning and Pearson (1973) found that the 96 hour lower TL 50 temperature for juvenile smallmouth bass declined from about 50°F for those acclimated to 79°F to about 35°F for fish acclimated to 59°F.

Many species of fish have been found associated with smallmouth bass, a circumstance to be expected for a species that is distributed over such a large area of North America in water ranging from small Ozark streams to the Great Lakes. Two species that occur with smallmouth bass throughout most of its original range are rock bass (*Ambloplites rupestris*) and white sucker (*Catostomus commersoni*).

Most smallmouth bass do not move even modest distances and have restricted home ranges in both lakes and streams (Gerking 1953, Fraser 1955, Funk 1957, Latta 1963, White 1970). In large lakes, the species often occurs as several discrete populations (Stone et al. 1954, Webster 1954, Forney 1961). In streams, fish may occupy a single pool throughout an entire season (Larimore 1952,

Munther 1970).

Feeding

From the time they begin feeding, the diet of smallmouth bass changes from small to large food items as the fish grows. The times that changes occur depend on size of bass, size of prey, and kind of prey available. If zooplankton is present, as in lakes, young bass begin feeding on such zooplankton as Copepods and Cladocera; then insects become progressively more important in the diet, and finally fish and crayfish (Wickliff 1920, Tester 1932, Doan 1940 in Cache Lake).

Insects, for example immature midges and mayflies, may enter the diet when bass are 0.3 to 0.8 inch long (Wickliff 1920, Tester 1932, Webster 1954, Pflieger 1966a), and may remain the staple of the diet throughout the first summer (Surber 1941, Webster 1954, Paragamian 1973). On the other hand, fish may become an important part of the diet when bass are as small as 0.6 inch (Wickliff 1920, Pflieger 1966a); or the bass may not start eating fish until they reach lengths of 1.6 to 2.7 inches (Tester 1932, Lachner 1950, Webster 1954). When zooplankton is scarce, as in streams, small insects make up a large part of the diet from the beginning (Surber 1941, Lachner 1950, Pflieger 1966a, Paragamian 1973).

Older smallmouth bass feed mainly on fish, crayfish, and insects (Adams and Hankinson 1928, Tester 1932, Doan 1940 in Lakes Erie, Huron and Opeongo, Tate 1949, Webster 1954, Watt 1959, Reynolds 1965, Keating 1970, Paragamian 1973). Members of the minnow family are important food items (Wickliff 1920, Tate 1949, Reynolds 1965), especially shiners of the genus *Notropis* (Wickliff 1920, Doan 1940, Surber 1941, Paragamian 1973). Other fish, important in the diet are darters and the alewife (*Alosa pseudoharengus*), if present (Wickliff 1920, Lachner 1950, Webster 1954).

Diet is influenced greatly by abundance and availability of prey. As an example, Paragamian (1973) found caddis flies in stomachs of adult smallmouth bass captured in a plunge pool below a large rapids in which caddis flies were drifting, but did not find the insects in bass caught downstream. Diet also is affected by differences among prey in vulnerability to predation by smallmouth bass. In controlled experiments, Lewis and Helms (1964) found crayfish and tadpoles to be more vulnerable than bluegill (*Lepomis macrochirus*) to smallmouth bass, and Paragamian (1973) found the common shiner (*Notropis cornutus*) to be more vulnerable than hornyhead chub (*Nocomus biguttatus*) and white sucker.

Age, Growth, Maturity

Smallmouth bass exhibit a wide range of growth rates throughout North America. In Table 1 the total lengths (maximum length from tip of snout to tip of tail) for ages I through IX may represent averages for the species on this continent.

I calculated these average lengths from growth data (extreme values omitted) for several populations listed by Doan (1940), Stroud (1948), Tate (1949), Stone et al. (1954), Sanderson (1958), Emig (1966), Keating (1970), and Paragamian (1973). Perhaps the slowest growing population studied was in Fall Creek, New York. Total length of fish at ages II, III and IV was about 5.5, 7, and 8.5 inches (Suttkus 1955). Other slow-growing populations have been found in Georgian Bay and eastern Lake Ontario-St. Lawrence River (Doan 1940, Stone et al. 1954). The fastest growing population studied probably was that in Norris Reservoir, Tennessee, where total length at ages II, III and IV was about 10, 14 and 16 inches (Stroud 1948).

Growth rate is influenced greatly by temperature and food supply. In wild populations higher growth rates generally are

Table 1. Average total lengths of smallmouth bass for ages I through IX

Age (years)	I	II	III	IV	V	VI	VII	VIII	IX
Length (inches)	3.7	6.7	9.2	11.0	12.7	14.1	15.0	15.9	16.9
Number of observations	35	39	42	44	39	36	30	27	11

associated with warmer summer temperatures, but the effect of temperature may be hidden by other factors, such as shortage of food (Brown 1960, Coble 1967, Keating 1970, Forney 1972). Laboratory experiments indicate that temperatures of about 79 to 84°F are optimal, with lower growth rates occurring at both lower and higher temperatures (Rowan 1962, Peek 1965, Horning and Pearson 1973). Smallmouth bass may lose weight at 95°F even with an unlimited food supply (Horning and Pearson 1973). Growth rate has been shown to be related to supply of forage fish, but this relation may not be apparent when food is abundant (Coble 1971, Forney 1972). Adverse conditions such as infestation with parasites may restrict growth (Hunter and Hunter 1938).

Males and females grow at the same rate (Bennett 1938, Doan 1940, Stroud 1948, Westman and Westman 1949, Tate 1949, Webster 1954, Stone et al. 1954, Latta 1963). As with most fishes, weight of smallmouth bass increases approximately as the cube of the length. The maximum age attained by the species probably is about 15 years (Stone et al. 1954, Keating 1970, Scott and Crossman 1973). Generally, maturity begins at ages II-IV for males and III-V for females. The smallest ripe male found by Stone et al. (1954) was 7¾ inches long and the smallest ripe female, about 10 inches. Most spawning fish are larger. Mature females can be expected to contain from 2,000 to 15,000 eggs or more depending on size and age (Bower 1897, Reighard 1905, Carlander 1953, Reynolds 1965).

Reproduction

Smallmouth bass spawn in the spring. They may spawn in a lake or river, or ascend tributaries to spawn (Webster 1954, Harlan and Speaker 1956, Cleary 1956, Sanderson 1958). Male bass move into spawning areas when water temperature approaches 60°F. The male selects a nest site, usually near an object such as a boulder or stump away from strong current or wave action, and frequently in water 1 to 3 feet deep, although smallmouth bass nests have been found in water as deep as 20 feet (Mraz 1964). Substrate is usually sand, gravel, or rubble (Latta 1963, Mraz 1964, Hubbs and Bailey 1938), but areas of woody debris and broken clam shells

have been used when gravel was not available (Turner and MacCrimmon 1970). Although Bennett and Childers (1957) reported smallmouth bass nesting in silt and clay ponds in Illinois, I have observed that adult smallmouth in turbid, mud-bottomed ponds in Missouri failed to spawn year after year. When a box of gravel was placed in the ponds, the bass spawned.

The male smallmouth bass may prepare several preliminary nests before it constructs the one in which the eggs are deposited (Cleary 1956, Mraz 1964). He digs the nest with vigorous sweeping motions of the tail (Beeman 1924, Hubbs and Bailey 1938, Pflieger 1966a). The nest is a circular, saucer-shaped depression, 2 to 4 inches deep and usually 2 feet in diameter, although it may be 1 to 4 feet across (Doan 1940, Pflieger 1966a). The displaced sand and small stones are deposited in a ridge around the edge of the nest, and stems and roots of plants and larger stones may remain on the bottom. Nests are conspicuous when new because silt and plant material are swept away during construction.

Nests may be constructed within 4 feet of each other although usually they are farther apart (Mraz 1964, Pflieger 1966a). Doan (1940) found densities of one nest per 20 to 75 square yards in Lake St. Clair and Georgian Bay, and Surber (1943), Cleary (1956), and Brown (1960) reported 5 to 414 nests per mile in rivers and streams.

Spawning may occur as soon as the nest is constructed, but it may be delayed a week or more depending on temperature and availability of a ripe female. Before spawning the male does not necessarily stay close to the nest, and other fish, including bass, may come near it without disturbing the male (Pflieger 1966a).

Females approach spawning areas from deeper water. When a male sees a female, he rushes toward her and attempts to drive her to the nest. At first she swims rapidly away only to return later, and the process is repeated. As time passes, the pair remains together progressively longer and approaches closer to the nest. When both fish are finally over the nest, the background color of the female seems to become lighter, and the dark blotchings darken, so that she has a pronounced mottled appearance. As the pair

moves slowly over the nest, the male may gently nudge and bite the female (Bower 1897, Reighard 1905, James 1930). Immediately before spawning the pair settle down over the nest, side by side usually facing the same direction. Then the female turns partly on her side and discharges eggs next to the vent of the male. The male emits milt simultaneously or within a few seconds.

James (1930) thought that 20 to 50 eggs were discharged at each emission, which lasts 4 to 10 seconds. Intervals between such emissions have been reported to be 22 to 45 seconds (Reighard 1905), 3 minutes (James 1930), and 5 to 15 minutes (Latta 1963). Beeman (1924) reported that spawning continues until a female has spawned all of her ripe eggs, but it has also been reported that a female may leave the nest of one male and go to nests of others within an hour. After spawning, the female loses the spawning color pattern and leaves the nest.

After the eggs are deposited, the male guards the nest vigorously, driving away other fish. A male may spawn with several females successively in the same nest. The interval between successive spawnings has been reported to be as short as 1 hour (Langlois 1932) and as long as 36 hours (Beeman 1924, Hubbs and Bailey 1938). Spawning of one male simultaneously with two females has been observed (Beeman 1924, Webster 1954).

A second nesting and spawning period may take place after a period of adverse weather conditions, such as floods or drops in water temperature, has caused the first spawning efforts to fail (Surber 1943, Cleary 1956, Henderson and Foster 1957, Brown 1960, Latta 1963, Mraz 1964). Renesting may occur also without an intervening period of adverse weather and nest failure (Pflieger 1966a). There is some contradiction as to whether the same females participate in a second spawning that takes place several days or more after the first. Beeman (1924) stated that a female may spawn three times in a season, whereas Surber (1943) stated that a female spawns out completely and does not produce eggs at intervals. Cleary (1956) found that the average size of renesting bass was smaller than that of first nesting bass, which indicates that some different fish were involved. Also, Sanderson (1958) found different degrees of ovarian development

among smallmouth bass taken from the same pool on the same day, which he thought indicated that they would spawn at different times.

When first spawned, eggs are grayish white to pale yellow, highly visible, and so sticky that they adhere to each other and to stones and other objects in the nest. As the embryo develops, the eggs lose adhesiveness, settle into any available space between stones, and become difficult to see. The number of eggs deposited in nests varies greatly; counts have ranged from 1,092 to 9,593 per nest (Latta 1963, Pflieger 1966a). The incubation period is controlled by temperature. Eggs hatch in about 10 days at 54°F and 2 days at 77°F (Webster 1948, Kerr 1966).

The newly hatched fry, which are about 1/5 inch long and nearly transparent, are extremely difficult to see (Reighard 1905, Beeman 1924, Mraz 1964). They remain in crevices for several days depending on temperature, living off the attached yolk and growing in length. About the time the yolk is completely absorbed, they begin to feed and become increasingly conspicuous as they become progressively darker, finally black. They then rise and swim over the nest. It is from this stage that the species came to be called black bass. The black-fry stage lasts from days (Mraz 1964, Pflieger 1966a) to weeks (Beeman 1924, Doan 1940). During this period, the school, which is dense at first, becomes more diffuse and gradually ranges farther from the nest (Turner and MacCrimmon 1970). The fry have been described as essentially helpless in this period. Beeman (1924) wrote that they swim aimlessly at a 45° angle with the mouth open. According to Doan (1940), they basked or feebly swam short distances with no apparent sense of self-protection. As the fry approach a length of about 1/3 inch or more, their color changes from black to the green of the adult, and they disperse from the nest for good.

The adult male guards the nest and the offspring from egg deposition to fry dispersal—often a period of a month or more. Common hazards to eggs and fry include temperature fluctuation, floods and water level recessions, predation, nest destruction by humans, and fungus. Predation is the only one of these that can be prevented by the male, and such prevention seems to be the sole benefit of his

guarding. Unattended eggs are likely to be eaten by predators (Surber 1943, Latta 1963, Pflieger 1966a). A guarding male is effective against a single intruder but not against a school of determined predators. When he leaves the nest to chase one fish, others dart in and feed. When he returns, they leave the nest; he chases another one, and the rest dart in again.

Contrary to Emig (1966) and Schneberger (1972), the male does not fan the nest to provide oxygen or prevent silt deposition (Reighard 1905, Hubbs and Bailey 1938, Webster 1954, Cleary 1956, Latta 1963, Pflieger 1966a). Langlois (1932) and Mraz (1964) obtained successful hatches in hatchery ponds from nests that had been screened to keep the male away, or from which the guarding male was removed.

When water temperature falls from the 60°F range into the 50° or 40°F range, guarding bass desert nests (Henderson and Foster 1957, Latta 1963, Mraz 1964). If a temperature change is rapid and of sufficient magnitude, eggs and fry may be lost from temperature shock as well as from predation. Kerr (1966) found that smallmouth bass eggs developed normally between temperatures of 59° to 77°F, and that survival was reduced at lower and higher temperatures. The embryos were most sensitive to temperature stress early in the incubation period and again just before hatching.

Anglers can destroy nests by stepping in them, or probably more often, by catching the guarding male. Fungus, which has been observed on eggs in nests, starts on dead eggs but can spread to live ones. Dead eggs may be present for several reasons, including adverse temperature changes or nonfertilization of some eggs at the time of spawning. Pflieger (1966a) found that 6 percent of the eggs were dead in 17 nests that had not been exposed to adverse temperature changes.

Counts of smallmouth bass fry in nests have usually ranged from about 1,000 to 5,000 (Doan 1940, Surber 1943, Sanderson 1958, Latta 1963, Pflieger 1966a) although Langlois (1932) reported extremes of 92 to 11,329. The accuracy and usefulness of such counts may be limited because frequently it is not known how many eggs were deposited in the nests, how many fry died before counts

were made, and how many would have survived to dispersion or to older ages. Also, reports of nest success based on counts of successful and unsuccessful nests in an area are sometimes of limited value because it is difficult to avoid overlooking eggs and fry at some stages (Mraz 1964), and even entire nests when guarding males are absent (Reighard 1905, Webster 1954). For investigations in which the author specified that observations began with nests known to contain eggs, nest loss has been reported to be 17 percent (Pflieger 1966a), about 45 percent (Latta 1963), zero to 57 percent (Doan 1940, in Georgian Bay), and 50 to 100 percent (Brown 1960).

Minnnows and darters have been found associated with smallmouth bass nests. Latta (1963) found common shiner over bass nests, but did find them to be harmful. Pflieger (1966b) believed that fry of the orangethroat darter (*Etheostoma spectabile*) occupied nests to take advantage of the protection of the guarding male.

Recruitment and Mortality

Fish that hatch and survive each year are members of the year class identified by the calendar year in which the eggs hatched. For example, eggs hatched in spring 1974 produced the 1974 year class. The strength of year classes (number of fish) has varied greatly in some populations (Doan 1940, Fraser 1955, Fry and Watt 1957, Brown 1960, Latta 1963, White 1970, Forney 1972, Funk and Fleener 1974). Some year classes may be 4 or 5 times larger than others (Fry and Watt 1957, Brown 1960). Moreover, these variations in strength seem to be synchronous among smallmouth populations in a region; that is, a strong or weak year class may be produced in all lakes or streams in an area in the same year.

Strong and weak year classes commonly are detected by the contribution they make to the anglers' harvest, which usually means at ages II and older. The relative strength of year classes, however, seems to be established much earlier, in the first summer of life (Brown 1960, Forney 1972, Funk and Fleener 1974). Causes of variation in year-class strength seem to be related to temperature experienced by the fish in their first summer.

Strongest year classes of some populations in Ontario were produced in years with the warmest late summer and fall, July through October (Fry and Watt 1957, Watt 1959). The strongest year classes in Oneida Lake, New York, developed in years with highest June temperatures (Forney 1972). The mechanism involved has not yet been found, but weather seems to be important and number of spawners does not (Watt 1959, Brown 1960, Forney 1972).

Estimates of densities or standing stocks of smallmouth bass populations vary tremendously—for example, from less than 1 fish per acre to more than 53 (Reynolds 1965, Paragamian 1973), and from 3 to 74 pounds per acre (Brown 1960, Brynildson and Truog 1965). Although some of the difference among populations is real, probably much of the variation in the estimates is caused by the sampling methods employed. In streams, for example, a fishery biologist usually studies one or more sections rather than the whole stream, and it may contain little or much smallmouth bass habitat. The amount of habitat, whatever it may be, determines the number of smallmouth bass present, often with no relation to the area of the section defined by the investigator. If all the study section happens to contain good smallmouth bass habitat, there should be twice as many bass present as if only half the section contains good habitat. Other variations in estimates of density occur when some investigators include yearlings and young-of-the-year, and some do not.

Many smallmouth bass populations consist mostly of young, and therefore small, fish, a characteristic of exploited populations. For example, few smallmouth older than age III could be found in some Iowa and Wisconsin streams (Tate 1949, Brynildson and Truog 1965, Paragamian 1973). And, if the population consists of mostly young, small fish, so do the anglers' catches. From 62 to 83 percent of the catch of bass consisted of fish age III or younger in the Niangua River and Huzzah and Courtois Creeks, Missouri, and the Red Cedar River, Wisconsin (Funk and Fleener 1966, Fajen 1972, Paragamian 1973). The average length of smallmouth harvested was 8.9 inches in Massie Creek, Ohio, and 8.2 inches (in 1973) in Nebish Lake, Wisconsin (Brown 1960, Kempinger 1973).

The age structure (relative abundance of various ages) of fish populations is determined by the mortality rate, as well as by variation in year-class strength. An individual does not have a mortality rate; it is either dead or alive. But a population does. It is characteristic of smallmouth bass that about half or more of the population dies each year. Annual mortality rates exceeded 50 percent for 11 of the 12 smallmouth bass populations listed in Table 2.

Rates shown were given by the authors for the first seven populations tabulated; rates shown for the remaining five were calculated from data given by authors.

Mortality of fish can be divided into two categories—fishing and natural. Each of these can be further divided. Natural causes of death of fish include environmental catastrophes such as pollution or winterkill (caused by lack of dissolved oxygen under the ice), predation, and diseases and parasites. Among the latter, smallmouth bass are

Table 2. Annual mortality rates in 12 smallmouth bass populations

Total Annual mortality rate percent	Locality	Source
43	Oneida Lake, New York	Forney 1972
51	South Bay, Lake Huron	Fry 1964
55	Red Cedar River, Wisconsin	Paragamian 1973
57	Potomac River, Maryland	Sanderson 1958
57	Baie du Doré, Lake Huron	White 1970
58	Waugoshance Point, Lake Michigan	Latta 1963
65	Plover River, Wisconsin	Paragamian 1973
53	Lake Opeongo, Ontario (1946-1949)	Christie 1957
55	Livingston Branch, Wisconsin	Brynildson and Truog 1965
57	Little Miami River and Massie Creek, Ohio	Brown 1960
65	Courtois Creek, Missouri	Fajen 1972
66	Huzzah Creek, Missouri	Fajen 1972

subject to fungal and bacterial diseases, and at least one viral disease, lymphocystis (Robbins and MacCrimmon 1974). At least 114 kinds of parasites attack the species including protozoa; flat, tape, round, and spiny-headed worms; leeches, mollusks, and crustaceans (Hoffman 1970). Many, perhaps most, bass carry some parasites, but there is little evidence that they kill the fish. One, the bass tapeworm, can be harmful to bass reproduction, but none of the parasites are harmful to humans (Watson 1965, Schnerberger 1972, Scott and Crossman 1973).

After smallmouth bass reach a length of about 6 inches, the angler probably is the greatest cause of mortality in many populations. Brown (1960) thought that anglers were the cause of much of the mortality evident in smallmouth populations in the Ohio streams that he studied, and Fajen (1972) found that almost all mortality of adult smallmouth bass in Huzzah and Courtois Creeks, Missouri, was fishing mortality. Fishing mortality also exceeded natural mortality in South Bay, Lake Huron and in three of five other populations for which data on the two sources of death were available, as shown in Table 3.

Sport Fisheries and Management

Angling pressure—the amount of sport fishing that occurs on a lake or stream—is influenced greatly by amount and ease of access to the waters, density of nearby human population, and fishing success. Intangible characteristics, such as reputation and scenic properties of a region, may be important too.

Table 3. Annual fishing and natural mortality rates (percent) of smallmouth bass in six northern populations

Fishing	Natural	Locality	Source
34	31	Red Cedar River, Wisconsin	Paragamian 1973
35	24	South Bay, Lake Huron	Fry 1964
35	12.5	Oneida Lake, New York	Forney 1972
38	25	Lake Opeongo, Ontario	Christie 1957
28	41	Waugoshance Point, Lake Michigan	Latta 1963
29	43	Baie du Dore, Lake Huron	White 1970

Angling pressure of about 1 to 193 fishing hours per acre have been reported for a number of smallmouth bass populations (White 1970, Paragamian and Coble 1975).

Fishery biologists measure fishing success by interviewing anglers in a creel census or survey. Since such surveys usually involve both poor and good anglers, the values of catch rate (number of fish caught per unit time) obtained are sometimes surprisingly low. A catch rate of one bass per hour is considered good, and it is seldom obtained for smallmouth bass. Rates for smallmouth frequently are less than 10 bass per 100 rod hours (Paragamian and Coble 1975). Higher values have been found for some fisheries, for example 25 bass per 100 hours at Waugoshance Point, Lake Michigan (Latta 1963) and even 111 and 112 smallmouth per 100 hours in Taderac Lake, Ontario and Lake Huron (Turner and MacCrimmon 1970, White 1970). High catch rates may occur in remote lakes and, of course, when many small fish are caught. A catch rate as high as 72 bass was reduced to 7 per 100 hours if sublegal-size fish were eliminated from the survey in the Shenandoah River (Surber 1969). Harvest, in terms of weight, of about 5 pounds per acre per year may be typical for smallmouth bass (Paragamian and Coble 1975).

Techniques to manage smallmouth bass include stocking, and imposition of creel limits, season limits, and length limits. Stocking smallmouth bass in waters not already containing the species is usually considered a sound procedure if biologists have determined that the waters have suitable smallmouth habitat, and if it appears that the bass would not be detrimental to other species present. Apparently, no attention has been given to the question of which subspecies to introduce, the northern or the Neosho smallmouth bass. Care should be taken with introductions so that the bass tapeworm and perhaps other parasites are not introduced along with the bass (Watson 1965).

Smallmouth usually are not stocked in waters where they already are present because of the high reproductive potential of the species. If successful nests produce only 1,000 fry each, the production of relatively few nests

would exceed that from hatcheries. On theoretical grounds, however, it seems that such stocking could be worthwhile in some years in waters where year-class strength varies widely. The stocked fish might form a substantial part of a year class in years when weak year classes were produced. Research on this question has been carried out in Oneida Lake, where about 0.2 fingerling smallmouth bass per acre were stocked in three successive years. They contributed substantially to 2 of the 3 year classes, but a connection with year-class strength was not clear (Forney 1972).

Creel limits often are considered unnecessary because few anglers catch the limit anyway. They may even tend to increase fishing pressure because some anglers consider the limit a goal to be attained. However, creel limits can help prevent adept anglers from making inroads on populations. Watson (1965) found one such angler in his creel survey; she caught 70 legal-size bass in 8 hours.

Season limits that close the season in winter are useless for smallmouth bass, at least in the northern part of its range. Few smallmouth are caught during this time of year when they are virtually dormant. Limits that close the season during the spawning period often are considered sound because of the vulnerability of a male guarding a nest. But inasmuch as the reproductive potential of smallmouth bass is high, a few successful nests produce more bass than a lake or stream can support. There are a number of thriving smallmouth bass populations that have no closed season to protect spawners, for example, in the Red Cedar River, Wisconsin (Paragamian 1973). Year-class production probably is influenced more by weather than by number of spawners (Brown 1960, Bennett 1965, Forney 1972).

One aspect of closed seasons is that they encourage angling at the opening of the season. Because of this psychological phenomenon, many fish are caught in the first 2 weeks of a season, regardless of when it opens (Forney 1972). Therefore, if spawning bass are to be protected, a season should not open until after the major part of the spawning period.

The purpose of minimum length limits is to protect the portion of a population that is

smaller than the limit. Because of the high reproductive potential of smallmouth bass, length limits probably are not necessary to protect fish until they have spawned. Length, limits, however, can change the size and age structure of exploited populations. Such a change may be desirable for reasons that have nothing to do with reproduction, a fact often not realized. It was mentioned previously that many smallmouth bass populations, as well as the catch obtained from them, consist mainly of young, small fish. A length limit set several inches above the average length of the bass caught in such populations would have the potential of increasing the average size and age of bass in the population and in the catch. Realization of that potential would depend not only on acceptance of the regulation by anglers and related law enforcement, but also on hooking mortality of released sublegal fish and on growth and natural mortality rates of the bass.

Studies of hooking mortality with trout indicate that substantial mortality occurs only among fish deeply hooked (Hunsacker et al. 1970), and that their rate of survival can exceed 50 percent if anglers cut the line and leave the hook in the fish (Mason and Hunt 1967). In one study of smallmouth bass, the number of sublegal bass caught increased after a 12-inch limit was imposed for the Shenandoah River, an indication that hooking mortality was not serious (Surber 1969).

Estimates of growth and mortality rates can be combined in mathematical computations to calculate the magnitude of the harvest from a population. The effect of various regulations on a fishery can be predicted if the calculations are carried out repeatedly with different values assigned to the rates used in the computations. For example, the effect of a 12-inch length limit on the harvest can be predicted if the fishing mortality rate is reduced to zero for fish smaller than 12 inches. Such calculations were carried out by Forney (1972) and Paragamian and Coble (1975). A length limit of 10 inches was in effect for smallmouth bass in Oneida Lake. Forney's calculations indicated that an 8-inch limit would reduce the harvest and a 12-inch limit would increase it. Paragamian and Coble's calculations indicated that length limits up to at least 13

inches would increase the harvest in the Red Cedar River where no length limit was in force. In both waters the length limit would have increased the average size and age of bass in the populations as well as in the catch, provided estimates of growth and mortality rates were reasonably accurate, hooking mortality was not substantial, and anglers abided by the regulation.

It may seem paradoxical that the weight harvested could be increased when the part of a population caught, that is smaller than a length limit, cannot be kept. It happens only if the weight of fish in the protected segment of the population increases through growth faster than it decreases from natural mortality. The studies of Fajen (1972), Forney (1972), Paragamian and Coble (1975), and others indicated that length limits should be established for some smallmouth bass fisheries. Then research should be continued to determine whether the predicted effects are realized and, if not, why not.

It has become more and more apparent over the past few decades that sport fisheries are extremely valuable. Smallmouth bass fisheries probably rank among the highest. Both monetary and esthetic values of fisheries vary from place to place, and the monetary values surely will increase with time. Watson (1965) estimated the value of smallmouth bass fisheries in the region of Big Lake, Maine, to be \$240,000 for a 3-month period. His estimate was based on tangible costs to anglers. Who knows what fraction it was of such intangible values as a parent taking a child fishing?

Summary

Smallmouth bass originally occurred in eastern North America, in the area between the Great Lakes drainages and Georgia east from Minnesota and Oklahoma. They have been introduced around the world and now occur across North America. Two subspecies have been recognized, the northern smallmouth and the Neosho smallmouth. The species occurs naturally in large, clear-water lakes and cool, clear streams having moderate current and rock and gravel substrate. In summer, smallmouth bass may be found in relatively shallow water at temperatures of

about 70°F. In winter, they move to deeper water, if available, take shelter in holes and crevices, and become torpid. Temperatures near the freezing point of water and lower, and above 90°F, are lethal. Most smallmouth have restricted home ranges in both lakes and streams.

As smallmouth bass grow, their diet changes from small to large food items. Typically, they begin eating zooplankton, then insects, and finally fish and crayfish. Growth rates, which are the same for both sexes, vary from one population to another, depending largely on temperature and food supply. An average growth rate would be represented by lengths of about 4, 7, 9, 11, 13, 14, 15, 16 and 17 inches at ages I through IX. The maximum age of smallmouth is about 15 years. The fish mature between ages II and V, and spawning females may contain 2,000 to 15,000 eggs.

Males move into spawning areas in spring when water temperature approaches 60°F. The male digs a nest, which is a circular, saucer-shaped depression, with vigorous sweeping motions of its tail. Then he courts a female and spawns with her in the nest. A female may spawn in several nests, and a male with more than one female in his nest. A second spawning period may occur a month or more after the first, whether or not eggs or fry from the first spawning are lost to adverse weather conditions. Eggs develop normally between temperatures of 59° to 77°F, and hatching takes place in about 2 to 10 days, depending on temperature. Newly hatched fry, which are nearly transparent, live in the nest while they absorb the attached yolk. As they grow, they begin to feed, become black, and rise and swim over the nest in a school. The school gradually becomes more diffuse and ranges farther from the nest, and when the fry are about 1/3 inch long or longer, they change from black to green and disperse.

The male guards the nest and the young from the time of egg deposition to fry dispersal. His defense is effective against a single potential predator, but often not against a school of predators or against such other hazards as temperature and water level fluctuation, humans, and fungus. A drop in water temperature may cause a male to desert a nest. Successful nests may produce 1,000 to 5,000 or more fry.

Wide fluctuations in year-class size occur in smallmouth bass populations. Although causes of the variations are not known, they seem to be related to temperature in the fish's first summer and not to number of spawners. Densities and standing stocks vary considerably, and many smallmouth bass populations, as well as the catch obtained from them, consist mainly of young, small fish. Typically half or more of the bass in a population die each year from fishing and from such natural causes as environmental catastrophies, predation, and diseases and parasites. Although anglers commonly catch fewer than 10 bass per 100 fishing hours, angling is the major cause of death in some populations.

Smallmouth bass management procedures include stocking and season, creel, and length limits. Stocking probably is not advisable for waters already containing the species unless the stocked fish would become a substantial part of a weak year class. Season limits probably are not beneficial for many populations, but creel limits can prevent occasional adept anglers from taking excessive numbers of fish. Length limits, which seldom are necessary to protect spawners, may be used to increase the average age and size of fish in a population. Length limits also can increase the weight harvested if increases in weight of young fish exceed losses from natural mortality.

Smallmouth bass fisheries can conservatively be estimated to be worth millions of dollars on the basis of tangible costs to anglers. Their esthetic values probably are worth much more.

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