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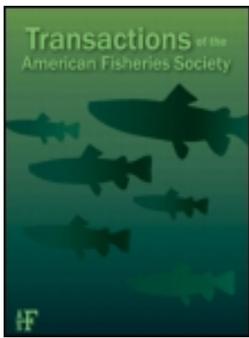
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Effects of Temperature and Streamflow on Time and Duration of Spawning by Smallmouth Bass

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Abstract.—The influences of eight water temperature and three discharge variables on the time and duration of spawning by smallmouth bass *Micropterus dolomieu* were evaluated in three mainstem sections and two tributaries of the New River in Virginia and West Virginia. Stepwise discriminant analysis was used to assess the relative importance of each variable in distinguishing between days when spawning did and did not occur. Spawning occurred from late April through mid-July at mean daily water temperatures ranging from 12.5 to 23.5°C. Frequency distributions of spawning dates were nearly identical among study sites, as was the timing of hydrologic events. Spawning activities were interrupted by flooding in June and resumed when water levels were receding. Mean daily water temperature explained most of the variation among groups of daily stream conditions related to spawning activities. Discriminant functions developed from three temperature variables and one discharge variable correctly classified 72% of the days on which spawning did and did not occur. The functions should be useful in predicting smallmouth bass spawning times in other streams.

Temporal variation in spawning times of the centrarchid basses *Micropterus* spp. affects growth and survival of young-of-year fish and may affect year-class strength (Christie and Regier 1973; Shelton et al. 1979; Miller and Storck 1984). Recognition of which factors influence smallmouth bass *Micropterus dolomieu* spawning times has aided population dynamics modeling (Shuter et al. 1980) and management decisions (MacLean et al. 1981). Most of the variability in annual spawning times of smallmouth bass in lentic environments is associated with variability in spring water temperature; the rate of increase in water temperatures is as important as absolute temperatures (Shuter et al. 1980; Vogeles 1981). In lotic environments, however, streamflow and associated hydrologic variables may also influence the timing of spawning by smallmouth bass (Surber 1943; Reynolds 1965; Pflieger 1975; Becker et al. 1981). Smallmouth bass spawning often occurs during times of receding or stable streamflows (Surber 1943; Reynolds 1965; Pflieger 1975), and flooding can divide the spawning season of smallmouth bass into two distinct periods (Cleary 1956; Clark and Mancini 1980). Therefore, the effects of streamflow on spawning times may be especially pronounced in streams regulated by dams, where releases can affect spring water temperatures as

well as flow rates. In this paper, we assess the relative influences of temperature and discharge variables on the time and duration of spawning by smallmouth bass in regulated and unregulated streams and present equations to predict spawning times of this species.

Methods

We selected five study sites in the New River drainage, Virginia and West Virginia, with dissimilar habitat types and temperature and discharge profiles (Table 1). The study sites included one unregulated section of the New River near Galax, Virginia, and two regulated sections, one near Eggleston, Virginia, and one near Meadow Creek, West Virginia (Figure 1). Releases from the Claytor Lake hydroelectric dam above Eggleston follow a peaking-mode schedule and releases from the Bluestone Lake dam above Meadow Creek are determined by flood-control needs. Two unregulated tributary streams of the New River were also selected for study, the Little River and Walker Creek, Virginia.

We used daily growth rings in the otoliths of young-of-year smallmouth bass to estimate spawning dates at each study site from the daily ages of fish collected at each site. Laboratory and field studies (Graham and Orth 1987) have confirmed that daily ring formation occurs in smallmouth bass otoliths beginning the day of swim-up and that the otolith aging technique is valid for estimating daily ages of young-of-year smallmouth

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TABLE 1.—Physical characteristics of study sites in the New River drainage.

Study site	Maximum temperature ^a (°C)	Mean width (m)	Dominant substrate	Gradient (m/km)	Mean discharge ^b (m ³ /s)
New River near Galax	24	163	Sand and cobble	0.4	43
New River near Eggleston	28	200	Bedrock and cobble	1.2	95
New River near Meadow Creek	27	207	Cobble and silt	1.6	221
Little River	24	39	Silt and sand	2.0	9
Big Walker Creek	22	14	Bedrock and cobble	3.2	8

^a Calendar year 1982.

^b U.S. Geological Survey water year 1982.

bass collected when water temperatures are greater than 10°C.

Four hundred seven young-of-year smallmouth bass were collected between 30 May and 20 October 1982. Several gear types were required due to difficulty in collecting fish less than 30–40 mm total length, differences in water depths and substrate among sites, and changes in gear selectivity as the fish grew. Collected fish were individually packaged, labeled, and frozen until their sagittae could be prepared for ring counts. Procedures for

preparation of sagittae and daily ring counts are described by Graham and Orth (1987).

The date on which each young of year had been spawned was estimated from $SP = SU - 7 - I$; SP and SU are the Julian dates of spawning and swim-up, respectively; 7 is the number of days required between hatching and swim-up; and I is the number of days required between egg fertilization and hatching. The Julian date of swim-up for each fish was estimated as the Julian date of capture minus the number of sagittal rings. We assumed the number of days between hatching and swim-up was constant (7 d) and that number of days from fertilization to hatching could be estimated for each fish with a regression equation ($r = 0.99$; $P < 0.01$) derived from Webster's (1948) data on incubation times in relation to water temperatures.

From our estimates of spawning dates, we constructed frequency distributions of spawning dates for each study site. Kolmogorov–Smirnov tests for general distributions were used to compare frequency distributions of spawning dates among sites (Hollander and Wolfe 1973).

We assumed that collections of young-of-year smallmouth bass were representative of the actual number of fish spawned on any particular date and the frequency of spawning activity. These assumptions may have been violated for the following reasons. The number of fish collected at each study site was probably a relatively small fraction of the number present, so it is unlikely that we collected fish that were spawned on every day that spawning did indeed occur. Differential survival of fish may also have influenced our frequency distributions of spawning dates. Most of the fish we collected were greater than 30 mm total length; therefore, broods that underwent high mortality during the early life history stages were underrepresented. However, due to the precision of the otolith aging technique (Graham and Orth 1987),

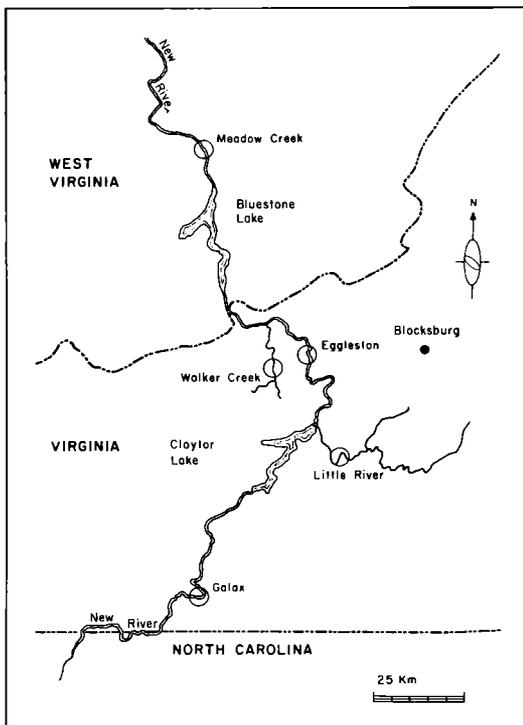


FIGURE 1.—Location of study sites in the New River drainage, Virginia and West Virginia.

back-calculation of spawning dates from daily ages of collected fish did give us reasonable evidence of spawning activity on those dates.

Temperature data were obtained from continuously recording thermographs placed at all study sites prior to the 1982 smallmouth bass spawning season. All sites were in close proximity to U.S. Geological Survey gauging stations, from which daily discharge data were obtained. At two sites, the New River near Eggleston and Walker Creek, temperature data were lost for 29 d (10 June–9 July) and 24 d (26 June–20 July), respectively. Missing temperature data for the New River near Eggleston were estimated by least-squares regression of mean daily water temperatures near Eggleston against corresponding mean daily water temperatures near Galax ($r = 0.95$; $P < 0.01$). Missing Walker Creek temperature data were similarly estimated from water temperatures of nearby Big Reed Island Creek ($r = 0.97$; $P < 0.01$).

The physical variables examined in relation to smallmouth bass spawning times included eight water temperature and three discharge variables (Table 2) thought to be important in determining spawning times of smallmouth bass. All rates of change are the algebraic differences between any particular day's variable value and that of the same variable's value on the previous day. The daily accumulation of degree-days greater than 15°C was based on mean daily water temperatures and defined as the sum of the number of degree-days greater than 15°C for all days previous to and including any particular day of 1982.

Stepwise discriminant analysis (Sarle 1982) was used to assess the relative importance of the temperature and discharge variables in differentiating among three selected groups of daily stream conditions associated with spawning times. The groups were: (1) daily stream conditions approximately 1 month prior to the spawning season at each study site; (2) daily stream conditions when spawning occurred at each site; (3) daily stream conditions when spawning did not occur during the spawning season at each site. Each site's spawning season was defined as the period between the first and last estimated spawning dates, inclusive of those dates. Each group's data set consisted of daily measurements of the 11 physical variables previously described for all days that were associated with the appropriate group.

To determine if stream conditions prior to actual spawning were more influential than conditions on the day of spawning, all variables for the three groups were lagged 1 and 2 d and applied to

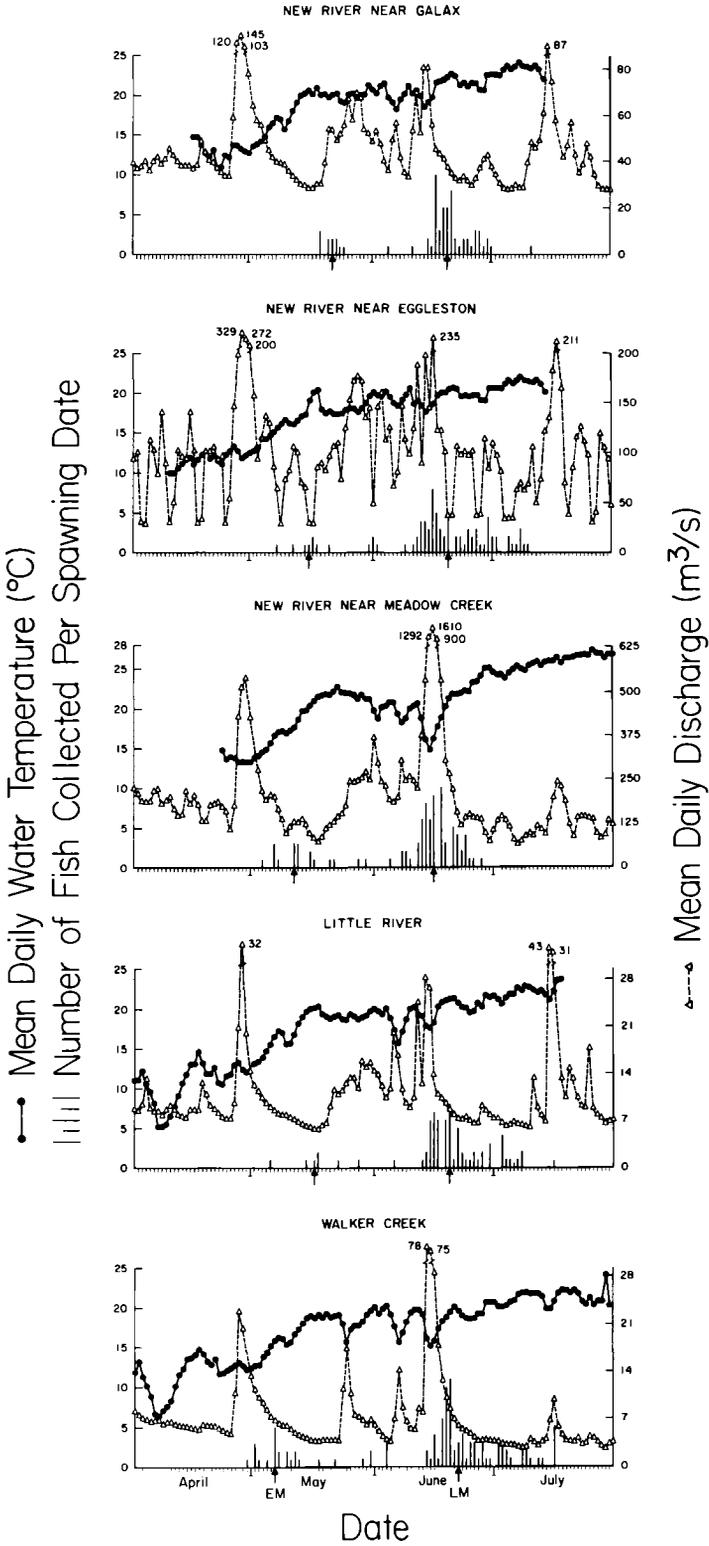
TABLE 2.—Temperature and discharge variables examined in relation to smallmouth bass spawning times in the New River drainage.

T_m	= mean daily water temperature (°C)
dT_m	= the rate of change in mean daily water temperature, d^{-1}
T_{min}	= minimum daily water temperature (°C)
dT_{min}	= the rate of change in minimum daily water temperature, d^{-1}
T_{max}	= maximum daily water temperature (°C)
dT_{max}	= the rate of change in maximum daily water temperature, d^{-1}
D-days	= the daily accumulation of degree-days greater than 15°C
dD-days	= the rate of change in the daily accumulation of degree-days greater than 15°C, d^{-1}
pFlow	= the ratio of mean daily discharge to mean annual discharge for water year 1982
dpFlow	= the rate of change in the ratio of mean daily discharge to mean annual discharge for water year 1982, d^{-1}
Flow	= mean daily discharge (m^3/s)

the stepwise discriminant analysis; results were compared with those for unlagged variables. Daily measurements of physical variables from New River sites, tributary sites, and all sites combined were pooled by group to aid in the determination of generalities associated with the physical variables examined. Classification functions were developed with data from all sites combined by stepwise discriminant analysis; these functions were tested with the jackknife procedure (Dixon 1983) to determine the misclassification probabilities.

Results

Smallmouth bass in the New River drainage spawned between 29 April and 20 July 1982, mainly in mid-June (Figure 2). Mean daily water temperatures on days when spawning occurred ranged from 12.5°C at Walker Creek to 23.5°C near Meadow Creek. The spawning season was divided into two distinct spawning periods (early and late) at each study site. Median spawning dates for the early spawning period ranged from 6 to 21 May among sites, a 16-d interval. Median spawning dates for the late spawning period were very similar among sites, ranging from 15 to 21 June, a 7-d interval. It appeared that a major flood in mid-June was responsible for delineating the two spawning periods at most sites; early spawning activities ceased at the onset of flooding and late spawning activities began when water levels were receding. The magnitude of the mid-June flood varied from 1.4 (New River at Galax) to 8.4 (Walker Creek) times the average discharge for the period of record.



In general, fluctuations in daily stream conditions were similar among study sites, although the absolute values of temperature and discharge variables differed among sites at any time. Discharge profiles followed a consistent pattern at all sites except for the New River near Eggleston, where hydropower generation altered hydrographs considerably (Figure 2). Water temperatures were slightly warmer at the New River near Meadow Creek, due to surface releases from Bluestone Lake, and at the New River near Galax. Walker Creek, which flows through heavily wooded, montane topography, was the coolest study site.

Frequency distributions of spawning dates among most study sites did not differ greatly. Only at the New River near Meadow Creek did the distribution differ significantly from the others ($P < 0.05$); the late spawning period there was sharply curtailed in late June, whereas it continued into July at other sites (Figure 2).

Five temperature-related variables differed consistently among groups of daily stream conditions (Table 3): mean, minimum, and maximum daily water temperatures; the daily accumulation of degree-days greater than 15°C; and the rate of change in the daily accumulation of degree-days greater than 15°C. Differences in the magnitude of these variables were greatest between days prior to and days of the spawning season. Little difference in any variable's mean value was apparent between days on which spawning did and did not occur during the spawning season. Discharge variables did not exhibit consistent differences among the three groups (Table 3).

Stepwise discriminant analyses confirmed that temperature variables accounted for most of the significant variation among the three groups of daily stream conditions at most sites (Table 4), although different variables were important at each site; Walker Creek and the New River near Meadow Creek were the only sites where flow variables contributed significant sources of variation among the three groups. At each site, the importance of variables did not appreciably change when variables were lagged 1 and 2 d.

Results of pooling data from the three New River study sites, from the two tributary sites, and from all sites varied (Table 5). Mean daily water

temperature or minimum daily water temperature explained most (>60%) of the variability among the three groups in the different analyses of pooled data. Temperature variables were the only significant sources of variation in analyses of pooled New River data, but flow variables were significant for pooled tributary sites. The analyses of pooled data highlighted generalities arising from results at individual sites. Overall, mean daily water temperature accounted for greater than 50% of the variation among the three groups in 15 of the 24 separate analyses. Minimum daily water temperature accounted for more than half of the variation in six analyses. The rate of change in the daily accumulation of degree-days accounted for over 25% of the variation in four analyses. The daily accumulation of degree-days accounted for 10% of the variation in seven analyses, and was the only variable identified as important in all analyses. The importance of the remaining temperature variables and all discharge variables in differentiating among the three groups of daily stream conditions appeared to be minimal in most analyses.

The following discriminant functions were developed from unlagged data on all sites pooled.

Group 1 (days before the spawning season):

$$Y_1 = -27.274 + 2.214T_m + 1.438T_{max} + 3.886pFlow - 0.064D\text{-days.}$$

Group 2 (days of spawning):

$$Y_2 = -48.122 + 4.063T_m + 0.852T_{max} + 4.668pFlow - 0.060D\text{-days.}$$

Group 3 (days of no spawning within the spawning season):

$$Y_3 = -48.683 + 4.289T_m + 0.731T_{max} + 4.484pFlow - 0.069D\text{-days.}$$

To classify an "unknown" day, values of T_m , T_{max} , $pFlow$, and D -days for that day are entered into each of the three group equations. The largest value of Y that results defines the group most closely matched by the data. The greater the difference between the three Y values, the greater the reliability of the prediction.

These discriminant functions correctly classified

←

FIGURE 2.—Temperature and discharge conditions and number of smallmouth bass collected per spawning date, April–July 1982, at five sites in the New River drainage. Median dates of the early and late spawning periods are indicated by EM and LM, respectively, and arrows along the abscissas.

TABLE 3.—Group means and standard deviations (in parentheses) of temperature and discharge variables for five study sites in New River drainage. Group 1 represents daily conditions prior to the smallmouth bass spawning season and groups 2 and 3 represent daily conditions when spawning did and did not occur during the spawning season, respectively. Daily rates of change are prefixed d; ratios of mean daily to mean annual flow are prefixed p.

Group, <i>N</i>	Daily temperature (T) °C						Degree-days (D-days) > 15°C		Discharge (m ³ /s)		
	Mean		Minimum		Maximum		D-days	dD-days	pFlow	dpFlow	Flow, mean daily
	T _m	dT _m	T _{min}	dT _{min}	T _{max}	dT _{max}					
New River near Galax											
1, 30	15.3 (3.1)	0.2 (0.9)	13.6 (2.8)	0.2 (1.2)	17.4 (3.5)	0.3 (1.3)	7.3 (12.3)	1.4 (2.1)	1.2 (0.6)	0.0 (0.4)	49.6 (27.7)
2, 26	21.1 (1.2)	0.0 (0.8)	19.9 (1.2)	0.0 (0.7)	22.9 (1.5)	0.1 (1.2)	195.0 (86.3)	6.1 (1.3)	1.0 (0.3)	0.0 (0.2)	42.7 (11.5)
3, 28	21.2 (1.7)	0.1 (0.7)	19.8 (1.5)	0.1 (0.8)	22.9 (2.2)	0.1 (1.4)	191.4 (103.2)	6.1 (1.7)	1.1 (0.3)	0.0 (0.2)	45.7 (1.5)
New River near Eggleston											
1, 27	12.3 (1.3)	0.2 (0.6)	11.5 (1.4)	0.2 (0.8)	13.1 (1.4)	0.2 (0.9)	0.0 (0.0)	0.0 (0.0)	1.2 (0.7)	0.0 (0.6)	114.7 (70.0)
2, 38	19.7 (1.5)	0.1 (0.8)	18.5 (1.4)	0.2 (0.8)	21.2 (1.9)	0.2 (1.1)	140.2 (78.5)	4.7 (1.5)	1.0 (0.5)	0.0 (0.5)	95.9 (47.2)
3, 26	18.4 (1.5)	0.0 (0.7)	17.6 (1.3)	0.0 (0.5)	19.4 (1.8)	0.0 (1.0)	68.5 (59.5)	3.4 (1.5)	1.1 (0.4)	0.0 (0.3)	103.2 (42.3)
New River near Meadow Creek											
1, 10	13.7 (0.5)	-0.1 (0.4)	12.9 (0.7)	-0.1 (1.0)	14.4 (0.4)	-0.1 (0.3)	0.0 (0.0)	0.0 (0.0)	1.4 (0.7)	0.0 (0.5)	311.6 (157.9)
2, 29	19.7 (2.5)	0.2 (0.9)	18.7 (2.6)	0.2 (1.0)	20.7 (2.5)	0.2 (1.2)	145.0 (88.8)	4.8 (2.5)	1.4 (1.6)	0.0 (1.0)	307.4 (356.0)
3, 27	20.0 (2.2)	0.2 (0.7)	19.1 (2.4)	0.1 (0.9)	20.9 (2.2)	0.1 (1.0)	100.8 (72.9)	5.0 (2.1)	0.9 (0.4)	-0.1 (0.4)	201.8 (96.8)
Little River											
1, 29	11.0 (2.8)	0.1 (1.1)	9.7 (2.9)	0.2 (1.5)	12.3 (2.8)	0.1 (1.3)	0.0 (0.0)	0.0 (0.0)	1.2 (0.6)	0.0 (0.5)	10.3 (5.2)
2, 30	20.1 (1.7)	0.0 (0.7)	19.1 (2.6)	0.1 (0.9)	21.4 (1.7)	0.0 (0.9)	171.0 (82.4)	5.2 (1.7)	1.0 (0.6)	0.0 (0.5)	9.3 (5.5)
3, 36	19.0 (1.7)	0.2 (0.8)	17.6 (1.9)	0.2 (0.9)	20.5 (2.3)	0.2 (1.1)	90.7 (72.7)	4.0 (1.7)	1.1 (0.4)	0.0 (0.3)	10.1 (3.8)
Walker Creek											
1, 30	11.5 (2.3)	0.1 (1.1)	10.2 (2.5)	0.1 (1.5)	12.7 (2.3)	0.0 (1.2)	0.0 (0.0)	0.0 (0.0)	0.9 (0.5)	0.0 (0.3)	7.3 (3.9)
2, 43	18.5 (2.6)	0.2 (0.7)	17.1 (2.7)	0.2 (0.9)	19.9 (2.8)	0.2 (0.9)	125.3 (90.7)	3.6 (2.3)	1.1 (1.8)	0.0 (1.6)	9.7 (15.5)
3, 40	18.8 (2.2)	0.2 (1.3)	17.5 (2.2)	0.1 (0.8)	20.0 (2.3)	0.0 (1.4)	107.5 (96.9)	3.9 (2.0)	0.7 (0.4)	0.0 (0.3)	6.1 (3.2)

72.2% of all days, 91% of days prior to the spawning season, 68% of the days when spawning did occur, and 62% of the days when spawning did not occur during the season; most incorrect classifications occurred between consecutive days when spawning did and did not occur during the spawning season. To test the hypothesis that 1-d errors in estimates of spawning dates and small sample sizes could result in misclassifications, the analysis was repeated after data were omitted for days of no spawning that were bracketed by days on which

spawning did occur. The discriminant functions developed for this subset of the data were similar to those reported here except T_{max} was not included as an important variable. Overall correct classification was improved to 77% because the omission of data on days of no spawning increased correct classification of group-3 days to 72%. Classifications of days prior to the spawning season and spawning days were unchanged.

The discriminatory power of the functions to identify the onset of spawning is due solely to mean

TABLE 4. — Variables identified by stepwise discriminant analyses as important sources of variation (measured by partial R^2) among days prior to the smallmouth bass spawning season and when spawning did and did not occur during the spawning season by site, New River drainage, 1982. See Table 2 for descriptions of variables.

No lag			One-day lag			Two-day lag		
Variable	R^2	P	Variable	R^2	P	Variable	R^2	P
New River near Galax								
Tmin	0.69	<0.01	Tmin	0.72	<0.01	Tmin	0.75	<0.01
dTmin	0.10	0.01	dTmin	0.12	<0.01	dTmin	0.12	<0.01
D-days	0.09	0.02	dD-days	0.09	0.02	Tmax	0.07	0.06
Tmax	0.08	0.04	dTmax	0.08	0.05	Tm	0.06	0.10
Tm	0.08	0.05	Tmax	0.07	0.07			
dTmax	0.07	0.07						
New River near Eggleston								
Tm	0.84	<0.01	Tm	0.79	<0.01	Tm	0.81	<0.01
D-days	0.24	<0.01	D-days	0.24	<0.01	dD-days	0.35	<0.01
dTm	0.10	0.01	dD-days	0.11	<0.01	D-days	0.17	<0.01
			dTmin	0.10	0.01	Tmin	0.10	0.01
			dTm	0.08	0.02	dTmin	0.08	0.03
			Tmin	0.07	0.06			
New River near Meadow Creek								
Tmax	0.54	<0.01	Tmax	0.48	<0.01	Tmax	0.43	<0.01
dD-days	0.32	<0.01	dD-days	0.25	<0.01	dD-days	0.25	<0.01
Tm	0.21	<0.01	Tm	0.19	<0.01	Tm	0.15	<0.01
Flow	0.12	0.02	D-days	0.11	0.03	D-days	0.09	0.06
D-days	0.08	0.08						
Tmin	0.07	0.14						
Little River								
Tm	0.78	<0.01	Tm	0.79	<0.01	Tm	0.80	<0.01
D-days	0.15	<0.01	D-days	0.14	<0.01	D-days	0.14	<0.01
dD-days	0.06	0.05				Tmax	0.08	0.02
dTm	0.05	0.09						
Walker Creek								
Tm	0.64	<0.01	Tm	0.62	<0.01	Tm	0.61	<0.01
pFlow	0.09	<0.01	Flow	0.11	<0.01	Flow	0.08	0.01
D-days	0.07	0.02	D-days	0.07	0.02	D-days	0.08	0.01
dpFlow	0.04	0.13	dpFlow	0.05	0.07	dpFlow	0.04	0.14

daily temperature. Functions based on mean daily temperature alone could correctly classify 91% of days prior to the spawning season.

Discussion

Previous studies have indicated the importance of stream discharge in controlling smallmouth bass spawning time. However, our analyses indicated mean daily water temperature was the single most important variable. Only water temperature changed progressively over time. Discharge variables did not undergo any such trend over time; identical discharge variable values were often associated with all three groups of daily stream conditions. Because temperature variables exhibited the most variation among the three groups of daily stream conditions, it seems probable that water temperature exerted a dominant influence in determining spawning times.

Although discharge variables were generally identified as minimally important in differentiating between the three groups of daily stream conditions, they undoubtedly can influence smallmouth bass spawning times and reproductive success. The early and late spawning periods at most study sites began when water levels were receding following flooding events (Figure 2). Relatively few young-of-year smallmouth bass were collected that had been spawned during the early spawning period compared to the numbers that were spawned during the late spawning period. High flows accompanied by a rapid decline in water temperatures occurred between the two spawning periods at most study sites. Cleary (1956), Pflieger (1975), and Clark and Mancini (1980) have implicated flooding as the cause for smallmouth bass spawning seasons being broken into two distinct spawning periods. Rapid drops in water temper-

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TABLE 5.—Results of stepwise discriminant analysis of temperature and discharge data pooled among sites for smallmouth bass spawning times in the New River drainage, 1982. See Table 2 for descriptions of variables.

No lag			One-day lag			Two-day lag		
Variable	R ²	P	Variable	R ²	P	Variable	R ²	P
New River study sites								
Tmin	0.65	<0.01	Tmin	0.65	<0.01	Tmin	0.65	<0.01
dD-days	0.07	<0.01	dD-days	0.08	<0.01	dD-days	0.07	<0.01
D-days	0.06	<0.01	D-days	0.06	<0.01	D-days	0.07	<0.01
dTmin	0.05	<0.01	dTmin	0.04	<0.01	dTmin	0.05	<0.01
Flow	0.02	0.07	dTm	0.02	0.05	Flow	0.02	0.07
dTm	0.02	0.09				dTm	0.02	0.09
Tributary study sites								
Tm	0.70	<0.01	Tm	0.69	<0.01	Tm	0.68	<0.01
D-days	0.08	<0.01	D-days	0.09	<0.01	D-days	0.09	<0.01
pFlow	0.05	<0.01	pFlow	0.06	<0.01	pFlow	0.08	<0.01
Flow	0.04	0.02	Flow	0.04	0.02	dpFlow	0.04	0.01
dD-days	0.02	0.10				dTmin	0.02	0.12
All study sites								
Tm	0.63	<0.01	Tm	0.63	<0.01	Tm	0.62	<0.01
D-days	0.06	<0.01	D-days	0.05	<0.01	D-days	0.06	<0.01
pFlow	0.03	<0.01	pFlow	0.03	<0.01	pFlow	0.04	<0.01
Tmax	0.02	0.01	Tmax	0.02	0.02	Tmax	0.02	0.01
dTmin	0.02	0.03	dpFlow	0.01	0.08	dD-days	0.01	0.04
			dTmin	0.01	0.10	dTmin	0.01	0.10

ature, as occurred during New River drainage flooding, have caused smallmouth bass nest desertion (Rawson 1945; Henderson and Foster 1957; Vogele 1981) and increased egg (Rawson 1945; Cleary 1956) and larval mortality (MacLean et al. 1981). Therefore, the low numbers of smallmouth bass collected from the early spawning period may reflect high mortality of eggs or young (or both) during the June flood.

At one study site, the New River near Meadow Creek, spawning occurred during the June flood as well as during the following interval of receding water levels. Spawning during flooding at the New River near Meadow Creek study site may have been successful because of the site's physical characteristics. All other study sites were typical riffle-run riverine habitats. At normal flows (approximately 200 m³/s), the New River near Meadow Creek study site is one large pool approximately 1,400 m long by 200 m wide; depths average in excess of 2 m. Pflieger (1975) noted that rises in water levels occurring during the spawning season are only detrimental to smallmouth bass reproductive success if they cause extensive scouring of the stream bottom. Smallmouth bass in the New River near Meadow Creek had more access to both deep waters and eddy areas than those spawning at other study sites, and may have used these waters for spawning; protection from current is an estab-

lished criterion for smallmouth bass nest site selection (Pflieger 1966; Winemiller and Taylor 1982).

MacLean et al. (1981) and Vogele (1981) have noted that the rate at which water temperature increases, i.e., the thermal history of the fish, exerts a dominant influence in determining the duration of smallmouth bass spawning seasons in lakes. This relationship was also observed in the New River drainage. The spawning season of smallmouth bass in the New River near Meadow Creek was of shorter duration than those of other study sites and was sharply terminated in late June. Water temperatures at this site rose more rapidly during the spawning season than at other sites (Figure 2). A water temperature of approximately 24°C was reached by late June, and temperatures remained above this value for the next several weeks. Robbins and MacCrimmon (1977) have observed that a potamodromous stock of smallmouth bass abandoned its spawning area when temperatures reached 25°C, a temperature near which spawning in the New River near Meadow Creek was sharply curtailed. In contrast, Walker Creek, the site with the coolest temperatures, supported the most prolonged spawning. Pflieger (1966) has suggested that smallmouth bass spawning will continue so long as temperatures are within a range suitable for spawning. Based on our studies and those by pre-

vious investigators (Surber 1943; Cleary 1956; Robbins and MacCrimmon 1977; Shuter et al. 1980), the range of mean daily water temperature suitable for spawning appears to be 12–25°C.

The relationships between discharge, temperature, and spawning by smallmouth bass in lotic systems seem to be analogous to those alluded to by Shuter et al. (1980) concerning wind direction, temperature, and spawning of smallmouth bass in northern lakes. In northern lakes, offshore winds produce upwellings that bring cold, hypolimnetic water into littoral spawning areas, interrupting smallmouth bass spawning. When offshore winds die down, the shallow littoral areas are warmed by the sun and spawning begins again. Similarly, rising water levels during flooding in the New River drainage were generally associated with falling water temperatures and cessation of spawning activity. After floods peaked and water levels declined, water temperatures rose and spawning again commenced. Therefore, it seems that the interaction of discharge and temperature variables, not the sole influence of either one, determined smallmouth bass spawning times in the New River drainage during 1982.

As noted previously, the discriminant functions were more than 90% successful in identifying daily stream conditions prior to the spawning season over a variety of stream systems. This was expected, given the large differences in group mean temperature variable values between daily conditions prior to the spawning season and those of the spawning season. However, the functions were only about 70% successful in differentiating between days when spawning did and did not occur during the spawning season. Many days when no spawning occurred were classified as days on which spawning should have occurred by the discriminant functions. These misclassification errors probably could have been minimized by increased sampling effort.

The discriminant functions developed may prove useful to fisheries managers dealing with regulated streams inhabited by smallmouth bass. Given adequate discharge and meteorological data, seasonal water temperatures of streams can be estimated for different discharge release schedules (Theurer and Voos 1984). When simulated discharge and temperature regimes are applied to the discriminant functions, the effects of these variables on the time and duration of smallmouth bass spawning can be compared and evaluated. However, further testing of the generality of the discriminant functions will be needed. The discriminant functions

we present should be used primarily to distinguish between stream conditions prior to spawning seasons and stream conditions during spawning seasons. The predictive abilities of the discriminant functions (>90% correct classifications) are sufficient for this purpose, but not for differentiating between days when spawning will and will not occur during a spawning season (72% correct classifications).

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