North American Journal of Aquaculture 70:328–337, 2008

DOI: 10.1577/A07-003.1

[Article]

Degree-Days as a Tool to Determine the Heating Requirement for Channel Catfish Spawning in Earthen Ponds

PATRICE PAWIROREDJO

Aquaculture Research Station, Louisiana Agricultural Experiment Station, Louisiana State University Agricultural Center, 2410 Ben Hur Road, Baton Rouge, Louisiana 70803, USA

JONATHAN LAMOUREUX AND STEVEN G. HALL

Department of Biological and Agricultural Engineering, Louisiana Agricultural Experiment Station, Louisiana State University Agricultural Center, 143 E. B. Doran, Baton Rouge, Louisiana, 70803 USA

TERRENCE R. TIERSCH*

Aquaculture Research Station, Louisiana Agricultural Experiment Station, Louisiana State University Agricultural Center, 2410 Ben Hur Road, Baton Rouge, Louisiana 70803, USA

Abstract.—Temperature and time are critical in determining when channel catfish *Ictalurus punctatus* will be physiologically ready to spawn (conditioned). Natural and hormone-induced spawning can occur when the fish are held at, above, or below specific temperatures for a largely undetermined minimum period of time. This period of conditioning can also be described as the heating requirement for spawning. We used degree-days as a standard unit to describe and quantify the heating requirement for channel catfish spawning, and we developed specific terminology and standard parameters to support the use of the degree-day concept for channel catfish spawning. The heating requirements for spawning were quantified by (1) retrospectively calculating degree-day values using previously collected data (2000–2003) from heated and ambient-temperature ponds before and during the natural spawning season and (2) calculating degree-days using data from fish conditioned for the 2004 natural spawning season at different thermal regimes in heated ponds at three threshold temperatures. These results were used to calculate spawning probabilities to enable future spawning predictions using degree-days. The values calculated using the 21°C threshold were more consistent than those calculated using the two other thresholds: 18°C and 24°C. The heating requirements for spawning in heated ponds before the natural spawning season were not different from the requirements for spawning in ambient-temperature ponds during the natural spawning season. Degree-day guidelines for channel catfish spawning were proposed based on the results of the degree-day calculations and spawning probabilities using a commercial definition that corresponded with the 21°C threshold. According to those guidelines, channel catfish spawning can begin in 0.04-ha ponds in southern Louisiana after the accumulation of 57–172 degree-days, with a median value of 99 degree-days.

The reproductive cycle of channel catfish *Ictalurus punctatus* is primarily influenced by environmental water temperature (Davis et al. 1986; Lang et al. 2003b). Reports on the range of water temperature required for their spawning vary between 21°C and 30°C (Table 1). Spawning activity can decrease rapidly when temperatures drop below 21°C or rise above 30°C (Huner and Dupree 1984) and can increase again when temperatures resume within the permissive range. Because natural spawning is dependent on weather conditions, catfish producers have little daily control over spawning and the production of seed stock. Controlled water temperatures and hormone treatments can be used to induce spawning and provide an alternative to natural spawning (Kelly and Kohler 1996). Controlled spawning offers considerable benefits for future seed stock production because it increases spawning predictability and provides opportunities for genetic improvement through selective breeding and hybridization of production lines. Early out-of-season spawning facilitates genetic selection and improvement and potentially allows for a constant supply of fry and fingerlings (Blythe et al. 1994) that could double or triple annual crops of fry in rearing ponds (Kohler et al. 1994). This greater fry production capacity could be advantageous for fingerling producers.

Studies addressing natural and out-of-season spawning of channel catfish report a combination of temperature and time as the main environmental variables in controlling spawning. Channel catfish broodstock held in small (<0.04 ha), shallow ponds with relatively warmer water have been reported to

* Corresponding author: ttiersch@agctr.lsu.edu

Received January 8, 2007; accepted October 5, 2007
Published online June 2, 2008

TABLE 1.—Selected spawning temperature ranges for channel catfish found in the literature.

Source	Temperature range (°C)	Spawning environment	Type of spawning
Brauhn (1971)	24–26	Ponds	Natural and induced
Lee (1979)	21–30	Ponds	Natural
Busch (1985)	21–29	Ponds	Natural
Davis et al. (1986)	24–26	Ponds	Natural
Steeby (1987)	18–29	Ponds	Natural
MacKenzie et al. (1989)	27.5	Ponds	Natural
Kelly and Kohler (1996)	25–28	Indoor tanks	Natural and induced
Bates and Tiersch (1998)	>21	Indoor tanks	Induced
Lang et al. (2003a)	27	Indoor tanks	Induced
Lang et al. (2003b)	27	Ponds	Natural

spawn about 2 weeks earlier than broodstock held in larger ponds (0.4–1.0 ha; Lee 1979; Huner and Dupree 1984). Using a combination of water temperature manipulation and injection of carp pituitary, channel catfish in Missouri were spawned in ponds in August and November (i.e., after the natural season; Brauhn 1971). These fish were maintained at 17 ± 2°C for 109 d followed by an increase in water temperature to 24°C over 7 d where they were maintained for 7 d. The females were injected with macerated fresh carp pituitary at 20.8 g/mL of 0.15 M sodium chloride and were paired with a male in compartments with water temperatures of 26°C. Fish were also spawned out of season (November through January) in indoor water recirculating systems in Illinois by holding them at 17 ± 2°C for 6, 9, or 15 months followed by 3 months at 25–28°C (Kelly and Kohler 1996). One-half of the fish received injections of luteinizing hormone releasing hormone analog at 100 mg/kg of body weight and human chorionic gonadotropin at 1,000 IU/kg of body weight to induce ovulation, while the other half spawned naturally.

Early out-of-season (March–April) spawning of channel catfish in southern Louisiana was achieved in heated outdoor ponds through temperature manipulation by adding geothermal 36°C water (Lang et al. 2003b). Ponds were heated from ambient temperatures (13–17°C) at a rate of 2°C/d to 24–30°C. Spawning was advanced by 20–62 d, occurring 12–30 d after ambient water temperatures were raised to within the spawning range (24–30°C) or 21–30 d after the start of initial heating (Lang et al. 2003b). Broodstock were also conditioned to spawn in geothermally heated ponds and were artificially spawned indoors in male–female pairs or groups of 2–8 females (Lang et al. 2003a). These studies indicate that temperature is a dominant variable influencing the timing of channel catfish spawning. In all of these studies, spawning was manipulated by maintaining fish at, above, or below specific temperatures for a minimum period. The combination of temperature and time thus appears to be critical in determining when spawning will occur in channel catfish. The calculation of degree-days combines the variables of temperature and time to create a consistent parameter that can be used to compare spawning studies and provide more accurate and consistent predictions of catfish spawning.

The degree-day concept has been used to describe different developmental processes in traditional row crops and in several fish species. The product of the number of days required to reach a developmental stage and the temperature (°C) above a biological threshold can be viewed as constant (Howell et al. 1998). In this case, the threshold refers to the temperature below which development is negligible. Hatching for several coldwater fish species has been described using degree-days. For example, the degree-days required for hatching was 500 in Atlantic salmon *Salmo salar*, 490 in brown trout *Salmo trutta*, 375 in rainbow trout *Oncorhynchus mykiss*, and 450 in Arctic char *Salvelinus alpinus* (Jobling 1996).

The relationship between temperature and growth in fish has also been described in units similar to degree-days. The U.S. Fish and Wildlife Service adapted the monthly thermal unit (MTU), originally developed by Haskell (1959), to describe the growth-temperature relationship of salmonid species (Soderberg 1992). The MTU is defined as 1°C above 0°C for 1 month. In this scenario, 0°C is the minimum threshold temperature above which growth occurs. Assuming an average month of 30 d, 1 MTU would generally equal 30 degree-days. The MTU requirements for each centimeter of growth have been described (Soderberg 1992) for channel catfish, blue tilapia *Oreochromis aureus*, brook trout *Salvelinus fontinalis*, rainbow trout, lake trout *Salvelinus namaycush*, Atlantic salmon, and tiger muskellunge (northern pike *Esox lucius* × muskellunge *E. masquinongy*).

Temperature has also been shown to play a major role in the timing of ovulation in common carp *Cyprinus carpio* (Horvath 1986) and other fish species. The reproductive heating requirements of common carp and

TABLE 2.—Channel catfish broodstock strains and sex ratios in geothermally heated ponds during the extended spawning seasons (February–July) in 2000–2004 at Louisiana State University Agricultural Center's Aquaculture Research Station (ARS). The channel catfish strains are as follows: LSU = a population maintained at ARS; GKD = Gold Kist strain D, obtained from Harvest Select Farms, Inverness, Mississippi; and LCC = fish obtained from Haring's Pride Catfish, Wisner, Louisiana, and identified as Louisiana commercial catfish. Most of the broodstock used during this experiment (LSU, LCC) were obtained from two locations 200 km apart within the state of Louisiana. Only in 2002 were broodstock from outside of Louisiana (GKD) used.

Year	Ponds per trial	Number of trials	Sex ratio (females : males)	Strain
2000	4	3	16–20:8–10	LSU
2001	4	2	16–20:8–10	LSU
2002	4	3	12–18:5	LSU/GKD
2003	4	3	16:5	LCC
2004	4	1	20:10	LCC

grass carp *Ctenopharyngodon idella* have been described using degree-days. The optimal interval between consecutive ovulations for common carp was reported as 2,000 degree-days above 17°C (Horvath 1986). In Israel, however, common carp were reported to require an accumulation of 1,000–1,200 degree-days above 15°C to complete ovarian development (Rothbard and Yaron 1995). Grass carp were reported to require 1,350–1,450 degree-days above 15°C to complete ovarian development (Zonneveld 1983). The degree-day concept has received criticism; that is, it does not always correctly describe the relationship between developmental times and temperature (Jobling 1996) because the actual relationship between time and temperature in embryonic development is an exponential function (Howell et al. 1998). However, the degree-day concept has proven accurate over the limited temperature ranges experienced during egg development and is still useful in practical hatchery management (Jobling 1996).

The goal of our study was to evaluate the utility of the degree-day concept for determining the heating requirement for channel catfish spawning in natural and geothermally heated earthen ponds. Our objectives were to (1) explain the rationale behind the application of the degree-day concept to the heating requirements of spawning, (2) introduce terminology that relates the degree-day concept to catfish spawning, (3) use previously collected data from heated and ambient temperature ponds to quantify the heating requirements for spawning by retrospectively calculating degree-day values, (4) quantify the heating requirements for broodstock conditioned at different target temperatures in heated ponds before the natural spawning season, (5) compare the heating requirements for spawning in heated ponds before the natural spawning season and in ambient-temperature ponds during the natural spawning season, and (6) provide degree-day guidelines and recommendations to different user groups when reporting studies regarding channel catfish spawning.

Methods

Degree-day calculations and terminology.—Degree-days were calculated from pond temperature measurements during the spawning season. Celsius degree-days were calculated retrospectively for 254 spawns at the Aquaculture Research Station (ARS; Louisiana State University Agricultural Center) in heated ponds before the start of natural spawning and from ambient temperature ponds after the start of the regular 2000–2004 spawning seasons (Table 2). Degree-days were calculated from measured and threshold temperatures. The threshold temperature was assumed to be the lower limit below which no activity was expected in the described process. The exact lower temperature limit for channel catfish spawning has not been determined; thus, three threshold temperatures were selected—18, 21, and 24°C—based on three conceptually different definitions.

(1) Biological definition: This designation describes the biological time and temperature requirements for channel catfish spawning. The threshold temperature selected for this definition was 18°C to ensure that the starting point of the degree-day accumulation was below or equal to the previously reported minimum spawning temperatures for channel catfish. Two studies (Brauhn 1971; Kelly and Kohler 1996) reported prevention of spawning by maintaining broodstock at 17°C during the spawning season.
(2) Commercial definition: This definition was intended to aid in the development of a tool to predict a reliable starting point of natural spawning for commercial producers. This threshold temperature, 21°C, is the lower temperature limit for channel catfish spawning, and it is generally used as a guideline by commercial producers (Grizzle 1985; Avault 1996).
(3) Research definition: This definition, derived from the thermostatic set point used in previous experiments conducted in small (0.04-ha) broodstock ponds at the ARS, has become part of the established, documented method for early out-of-season spawning experiments at the ARS (Lang et al. 2003b). The threshold temperature selected for this definition was 24°C, which was the median temperature of the spawning range in these experiments (21–27°C).

Three spawning parameters were also created to permit consistent comparison of the numerical data among the different temperature thresholds: (1) "spawning onset" (the number of degree-days accumulated when 10% of the total spawns had been collected), (2) "median spawning" (the number of degree-days accumulated when 50% of the total spawns had been collected), and (3) "spawning conclusion" (the number of degree-days accumulated when 90% of the total spawns had been collected). These three spawning parameters were used to compare the three definitions described above.

Celsius degree-days were calculated by using the maximum–minimum (max–min) method (Wilson and Barnett 1983). This method calculates degree-days by summing the daily difference between the mean daily temperature (°C) and the established threshold temperature from the starting date to the date the spawn was collected, that is,

$$\sum_{t=0}^{\text{final}}(\text{mean daily temperature} - \text{threshold temperature}) \times 1\ \text{d}.$$

The temperature and spawning data used for these calculations were collected at the ARS over a 5-year span (2000–2004), as previously described (Lang et al. 2003b; Pawiroredjo 2004). The start dates of these temperature measurements were between January 1 and February 27 and varied among the years these data sets were collected. Degree-days were calculated from the earliest available measurement below the threshold temperature to minimize the risk of missing degree-days accumulated before measurements started. The degree-day values were calculated using the macros function of the Microsoft Excel 2003 spreadsheet software.

Broodstock.—In the winters (December–February) of 2000 through 2004, twelve 0.04-ha ponds were stocked in various combinations with channel catfish broodstock (Table 2). From 2000 to 2002, the ponds were stocked with broodstock from two sources: (1) males and females from a research population maintained at ARS (LSU broodstock) and (2) females of the Gold Kist strain D (GKD broodstock) obtained from Harvest Select Farms (formerly Gold Kist Farms, Inverness, Mississippi); these two sources were located 200 km apart. In 2003 and 2004, all the broodstock (males and females) were obtained from Haring's Pride Catfish (Wisner, Louisiana) and were identified as Louisiana commercial catfish (LCC). For this study, only ponds stocked with a mixture of males and females were evaluated for spawning. These and adjacent ponds were also used in other studies during this time period to evaluate stocking with females only, stocking of broodstock in cages, and hormonally induced spawning. These results are presented elsewhere (Lang et al. 2003a, 2003b; Pawiroredjo 2004; Lang and Tiersch 2007). Ponds were stocked with 12–20 females and 5–10 males based on the experimental design for that year (Table 2). Although the number of broodstock in the ponds varied each year, the stocking scheme was similar to that of the 2003 spawning season (Figure 1).

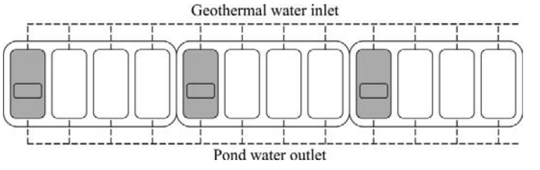

FIGURE 1.—Schematic showing the stocking of Louisiana commercial channel catfish (LCC) in nine ponds (three ponds per trial) in the 2003 spawning season. All nine ponds (white) received 16 females and 5 males. An additional pond (gray) in each trial was stocked with 16 free-swimming females and 10 caged males. No spawns were collected from these "all-female" ponds.

Pond heating.—The ponds were heated in groups of four by adding 36°C water from a 760-m geothermal well (30°22′ 13.803″N, 91°11′ 12.827″ W. Ponds were heated at a rate of 2°C/d from ambient temperatures to the target spawning temperature (Hall et al. 2002; Lang et al. 2003b). Water was delivered to the ponds through 10-cm polyvinyl chloride ball valves (Model LB308; Hayward Industrial Products, Elizabeth, New Jersey). The valves were controlled by an automatic thermostatic system (Hall et al. 2002). Water temperatures were recorded with data loggers (CR-23X; Campbell Scientific, North Logan, Utah) that were an integral part of the control system and separate individual data loggers (HOBO data logger; Onset Computer Corporation, Pocasset, Massachusetts) that were submerged 1 m below the water surface in the middle of each pond (Figure 2). The actual measurements collected by the Campbell Scientific CR-23X were made using a type-T copper constantan thermocouple. The accuracy of both types of data loggers was ±0.1°C for a temperature range between 0°C and 40°C. The ponds were maintained within ±1°C of the target temperatures until the end of the heating period or until temperatures in the unheated ponds rose to equivalent temperatures. The target temperature was 27°C from 2000 to 2003, but in 2004 the ponds were programmed at target temperatures of 21, 24, and 27°C. Actual pond water temperatures regularly reached the target temperatures and all treatments accumulated degree-days above the threshold temperatures. Although the mean pond

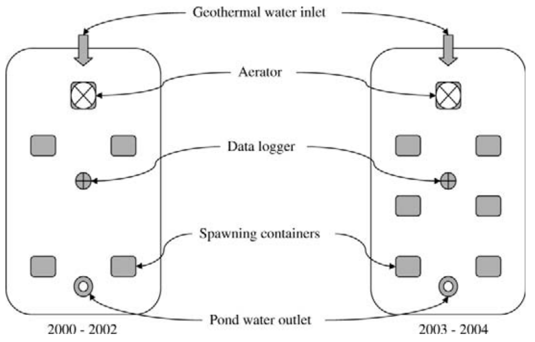

FIGURE 2.—Placement of spawning containers and other equipment in ponds used to study heating requirements for channel catfish spawning during the 2000–2002 and 2003–2004 spawning seasons.

temperatures for some ponds were similar, degree-days were accumulated at different rates because of the variation around the mean values. Degree-day values for spawns collected in 2004 were also calculated using the three threshold temperatures (18, 21, and 24°C) corresponding with the spawning definitions.

Spawning containers.—Channel catfish are cavity spawners, normally spawning in natural cavities available to them. In the experimental ponds, these cavities were provided in the form of metal containers ($70 \times 40 \times 20$ cm) with a circular opening of 15 cm. From 2000 to 2002, four spawning containers (sites) were placed in each pond; in 2003 and 2004 all ponds received six spawning containers (Figure 2). The spawning containers were checked for egg masses at least every 3 d, but often every other day, beginning when water temperatures reached the target range. It is possible that multiple females were ready to spawn at the same time but were prevented from doing so by the limited number of spawning sites. Accordingly, degree-days were calculated for the first four spawns in 2000 to 2002 and the first six spawns in 2003 and 2004 to minimize the effect of spawning site limitations on the degree-day values. These data points were referred to as degree-day values "without spawning site limitations" because the spawns for which they were calculated occurred when at least one spawning site was available. When all spawns were included in data analysis the data set was referred to as degree-day values "with spawning site limitations."

Statistical analysis.—The temperature and spawning data collected between 2000 and 2004 were analyzed to determine the heating requirement for channel catfish spawning in heated and ambient-temperature ponds. These requirements were used to predict future spawning readiness of broodstock. The degree-day data set was analyzed using the Proc Freq function of the SAS system (Statistical Analysis Software system, version 9 for Windows; SAS Institute, Cary, North Carolina) to create frequency tables displaying the frequency of spawns at intervals of 25 degree-days. The degree-day value for each spawn was compared with a range of degree-day values between 0 and 500 (at 25 degree-day intervals) to determine the interval in which the spawn occurred. If the degree-day value calculated for the spawn was less than the value with which it was compared, the number recorded was zero, meaning that the spawn had not occurred yet. However, if the value was greater than the value with which it was compared, the number was recorded as one, indicating that the spawn had occurred. This created a series of zeros and ones for each spawn, resulting in a binomial data set describing the spawning occurrence at degree-day values between 0 and 500 degree-days. This data set was used to perform regression analysis using the Proc Logistic function of SAS system to generate mathematical functions that describe the probability of spawning related to degree-day accumulation. The results of this analysis yielded the slope and intercept of functions that allowed calculation of spawning probabilities for each threshold. All other data were analyzed using the Proc Mixed function of SAS for analysis of variance Differences were considered to be significant at $\alpha = 0.05$.

Results

The cumulative percentages of spawns at different degree-day values above the three thresholds were calculated for the data with spawning site limitations and for the data without spawning site limitations (Figure 3). The values for the onset of spawning, median spawning, and conclusion of spawning at the three threshold temperatures for both data sets (Table 3) were determined through interpolation of the values of the frequency tables produced by the Proc Freq function of the SAS system. The relationships between spawning probability and degree-day values were determined by using the logistic procedure of the SAS system (Table 4). Using these functions, the spawning probability at different degree-day values was calculated for the data with spawning site limitations and for the data without spawning site limitations (Figure 4). The degree-day values that represented 10, 50, and 90% spawning probability (using the three threshold temperatures for both data sets; Table 5) were derived from the data presented in Figure 3. In 2004, 18 spawns were collected from three ponds (the first 6 spawns/pond) that were maintained at the three target temperatures (21, 24, and 27°C). Degree-day values were calculated above the 18, 21, and 24°C thresholds for spawns collected

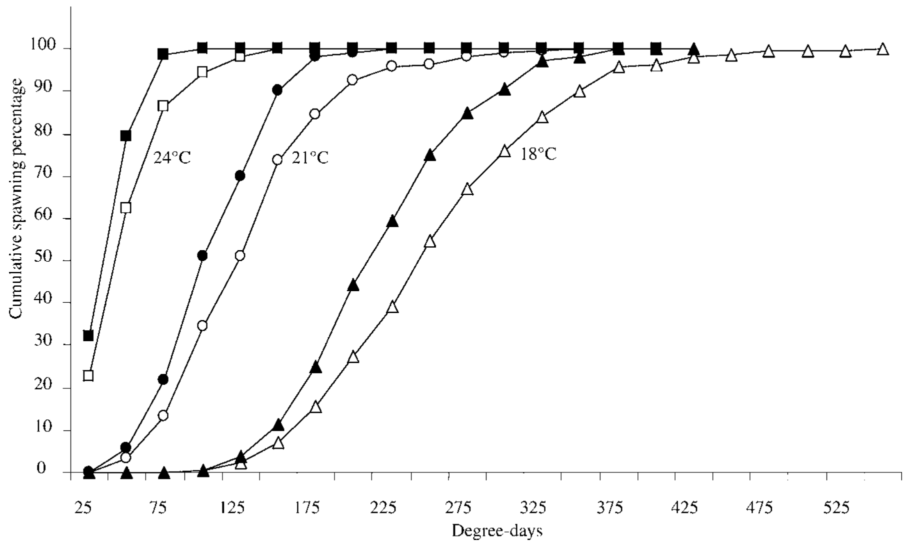

FIGURE 3.—Cumulative percentage of channel catfish spawns at different numbers of degree-days above three temperature thresholds—18°C (triangles), 21°C (circles), and 24°C (squares). The data points indicated by the white symbols were calculated from the first four spawns per pond in 2000–2001 and the first six spawns per pond in 2002–2004. The data points indicated by the black symbols were calculated from all 254 spawns collected between 2000 and 2004.

from the ponds with the target temperatures of 21, 24, and 27°C (Table 6). The three ponds with different temperature regimes produced a constant value of 98 ± 4 degree-days (mean ± SD) above the 21°C threshold. The actual temperatures in the ponds differed from the expected target temperatures because of unequal head pressure at the three outlet valves leading to fluctuating distribution of the geothermal water. The ponds with target temperatures of 21, 24, and 27°C had actual temperatures of 23.1 ± 1.5, 23.1 ± 2.6, and 24.6 ± 3.0°C. Two ponds had the same average temperature but were considered different temperature regimes because of unequal variation (SD) and differential accumulation of degree-days.

The average degree-day values for the spawns collected from heated ponds without spawning limitations ($N = 136$) were 207 ± 60 for the 18°C threshold, 104 ± 34 for the 21°C threshold, and 36 ± 17 for the 24°C threshold. The spawns without spawning limitations collected from ambient temperature ponds ($N = 45$) had average degree-day values of 214 ± 43 for the 18°C threshold, 92 ± 34 for the 21°C threshold, and 25 ± 21 for the 24°C threshold. For spawns without spawning site limitations, there was no significant difference in the degree-day values between spawns collected from heated ponds and those collected from ambient-temperature ponds, as calculated using the 18°C threshold ($P = 0.38$), the 21°C threshold ($P = 0.52$), and the 24°C threshold ($P = 0.32$). For ponds with spawning site limitations, there were also no significant differences among spawns collected from

TABLE 3.—Degree-day values calculated for channel catfish ponds in southern Louisiana with spawning limitations (spawning sites possibly limited; includes all 254 spawns) and without spawning limitations (using only the first four spawns per pond in 2000 and 2001 and the first six spawns in 2002, 2003, and 2004; total = 153) at the onset (10% of all spawns), median (50%), and conclusion (90%) of spawning above three threshold temperatures (18, 21, and 24°C) between 2000 and 2004.

Temperature threshold (°C)	Threshold type	Spawning site limitations	Degree-days		
			Onset	Median	Conclusion
18	Biological	Yes	159	242	349
		No	149	209	296
21	Commercial	Yes	67	124	192
		No	57	99	150
24	Research	Yes	11	42	86
		No	8	36	64

TABLE 4.—Relationships between the probability of channel catfish spawning (y) and degree-day value (x) in southern Louisiana ponds for situations with and without spawning site limitations (as explained in Table 3).

Temperature threshold (°C)	Without spawning site limitations	With spawning site limitations
18	$y = 0.033x - 6.97$	$y = 0.024x - 5.97$
21	$y = 0.051x - 5.31$	$y = 0.035x - 4.39$
24	$y = 0.104x - 3.62$	$y = 0.065x - 2.98$

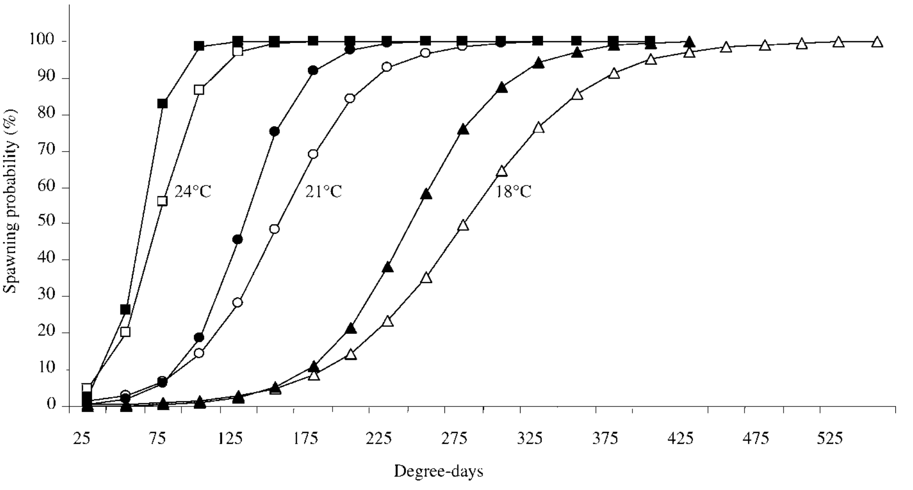

FIGURE 4.—Spawning probability for channel catfish at different numbers of degree-days above three temperature thresholds. See Figure 3 for further details.

heated and ambient-temperature ponds (Table 7), as calculated using the 18°C threshold ($P = 0.60$), the 21°C threshold ($P = 0.59$), and the 24°C threshold ($P = 0.54$).

The average degree-day values for the data with spawning site limitations were 250 ± 76 for the 18°C threshold, 127 ± 51 for the 21°C threshold, and 45 ± 27 for the 24°C threshold; for the data without spawning site limitations the average values were 214 ± 56 for the 18°C threshold, 103 ± 35 for the 21°C threshold, and 34 ± 19 for the 24°C threshold. The degree-day values for the data with spawning site limitations were 16% greater at both initial and median spawning and 21% greater at the conclusion of spawning. This means that the difference in onset, median, and final spawning using the 18°C threshold was between 10 and 50 degree-days. This difference was between 10 and 42 degree-days for the 21°C threshold and between 3 and 22 degree-days for the 24°C threshold. The degree-day value at which channel catfish will spawn with a 10% probability was 7% greater at the 18°C threshold, 6% greater at the 21°C threshold, and not different at the 24°C threshold in comparisons between data with and without spawning site limitations. The same comparisons done for the 50% spawning probability were 13% greater at the 18°C threshold, 16% greater at the 21°C threshold, and 14% at the 24°C threshold and for the 90% spawning probability were 16% greater at the 18°C threshold, 23% greater at the 21°C threshold, and 20% at the 24°C threshold.

TABLE 5.—Degree-day values calculated for channel catfish ponds in southern Louisiana with spawning limitations and without spawning limitations (as explained in Table 3) above three temperature thresholds (18, 21, and 24°C) at which there is a 10, 50 or 90% spawning probability.

Temperature threshold (°C)	Threshold type	Spawning site limitations	Spawning probability		
			10%	50%	90%
18	Biological	Yes	183	275	367
		No	171	240	308
21	Commercial	Yes	86	153	217
		No	81	129	172
24	Research	Yes	33	71	109
		No	33	61	87

Discussion

The difference in degree-day values between spawns collected without spawning site limitations and those collected with spawning site limitations could be explained by the lag that occurred between the first four to six spawns and the rest of the spawns collected from a pond. It is possible that females could have been ready to spawn, but there may not have been enough

TABLE 6.—Average degree-day values for channel catfish spawns above three temperature thresholds in southern Louisiana ponds maintained at different temperatures. Within columns, values with the same letter are not significantly different.

Temperature (°C)		Temperature threshold		
Target	Actual	18°C	21°C	24°C
21	23.1 ± 1.5	234 z	95 z	8 x
24	23.1 ± 2.6	203 zy	98 z	22 y
27	24.6 ± 3.0	184 y	102 z	41 z

spawning sites and males available. Once all spawning sites in a pond were occupied by male–female pairs, it took 2–3 d for the eggs to be removed from the spawning container and additional days for another spawning pair to occupy the site and complete the spawning interactions. This could have increased the degree-day values in situations with spawning site limitations and could inaccurately extend the range of degree-day values for channel catfish spawning. Plans for future studies involving degree-day calculations for spawning should recognize the effect of spawning site limitations on the accumulation of degree-days and the possible distortion of the collected data. Accordingly, this discussion will henceforth focus on the data derived from the first four to six spawns collected from each pond.

Our study was conducted as part of a broader research program aimed at developing economically feasible methods for the commercial production of hybrid catfish. One aspect of that program is the early extension of the channel catfish spawning season through geothermal heating of ponds. With pond heating, commercial producers can synchronize females conditioned in outdoor ponds at scheduled times for induction of final oocyte maturation in indoor facilities. Efficient conditioning of females calls for reliable heating requirements, so the process is conducted using specific temperature and time benchmarks. Knowledge of the correct heating requirements for channel catfish spawning will also improve the management efficiency of costly geothermal water resources. Future studies need to establish the lower threshold temperature for channel catfish spawning, which will increase the accuracy of the heating requirements. The application of these requirements in commercial conditions could lead to the development of other less costly methods of water heating. This would also include the use of greenhouses or raceways to hold broodstock in heated water. The calculation in this study of degree-day values from temperature and spawning data collected over a 5-year span in heated and ambient temperature ponds provides a baseline for the heating requirements of channel catfish spawning. There was no significant difference among the years (2000–2004) in degree-day values calculated for spawns above the 18°C threshold ($P = 0.61$), the 21°C threshold ($P = 0.94$), or the 24°C threshold ($P = 0.61$) for spawns collected with no spawning limitations and, in the same analysis done for spawns collected with spawning limitations, no significant difference for the 18°C threshold ($P = 0.87$), the 21°C threshold ($P = 0.74$), and the 24°C threshold ($P = 0.57$). This analysis shows that the degree-day values were consistent for each year and broodstock strain (LSU in 2000 and 2001, GKD in 2002, and LCC in 2003 and 2004) and that they can be used to predict spawning readiness for at least the three populations of channel catfish broodstock we used. Although the retrospective data provides a strong baseline, the degree-day data from the heated ponds were collected mainly from ponds heated to 27°C followed by calculations at different threshold temperatures.

TABLE 7.—Average degree-day values (means ± SDs) for spawns collected from southern Louisiana ponds heated with geothermal water before the start of the natural channel catfish spawning season and from spawns collected from ambient temperature ponds during the natural spawning season. The degree-day values were calculated using three threshold temperatures. Within columns, values with the same letter are not significantly different.

Temperature threshold (°C)	Heated ($N = 119$)	Ambient ($N = 32$)
18	211 ± 57 z	218 ± 42 z
21	105 ± 32 y	86 ± 31 y
24	37 ± 17 x	23 ± 23 x

We also calculated degree-day values using different thresholds for channel catfish broodstock held in ponds heated and maintained at different temperature regimes to further investigate whether there was a constant heating requirement. All 16 spawns produced by these fish had values of 98 ± 4 degree-days above the 21°C threshold. The degree-day values calculated for the other two thresholds (18°C and 24°C) were not as consistent and were significantly different among the ponds, indicating that 21°C was the threshold temperature that yielded consistent degree-day values for channel catfish spawning. This temperature has been reported in the literature as the minimum required for the spawning of channel catfish (Huner and Dupree 1984; Busch 1985). Thus, the commercial definition results in the more constant degree-day values than the biological and research definitions. These findings can be applied to heated and ambient-temperature ponds because there was no significant difference in the degree-day values calculated for spawns collected before and during the natural spawning seasons. This indicates that the heating requirement for channel catfish spawning is a consistent value above a certain threshold and that the heating requirement for spawning is not affected by the rate of temperature change we evaluated.

The degree-day terminology we developed was intended to be applied by different user groups when reporting channel catfish spawning studies. The three degree-day definitions (biological, commercial, and research) and threshold temperatures (18, 21, and

24°C) provide reference points that can be used to compare results from future studies and past data about channel catfish spawning. This is an important step toward standardizing research findings concerning catfish reproduction.

Regular monitoring of water temperatures provides a general indication as to when channel catfish will spawn barring unexpected weather events that can delay spawning or cause it to cease completely. The degree-day values accumulated in heated ponds with water temperatures that fluctuate in and out of the spawning temperature range but still produce spawns before the natural spawning season (e.g., Lang et al. 2003b) can be calculated if water temperatures are recorded, and they can be used to predict spawning readiness. The results of these degree-day calculations also provide confidence intervals that can serve as guidelines for the timing of catfish spawning. The degree-day values and spawning probabilities can be used as targets to predict the spawning readiness of broodstock based on water temperature, weather data, and climate records. Automatic data loggers are important to systematically collect temperature data because degree-day calculations should factor in multiple daily measurements to reflect the actual temperature regime of the pond and make accurate spawning predictions. For example, ponds with unequal fluctuations in water temperatures but similar average temperature can produce spawns at different times because the pond with the greater positive temperature variation will accumulate degree-days at a faster rate resulting in earlier spawning. The commercial definition produced the most consistent values and is recommended for use when applying degree-days to channel catfish spawning for predictive and comparative functions. This definition yielded 57 degree-days for the onset, 99 degree-days for the median, and 150 degree-days for the conclusion of spawning for the subsamples of fish analyzed in each pond (the first four or six spawns from approximately 20 females per pond). The spawning probability results were 81 degree-days for the 10% spawning probability, 129 degree-days for the 50% probability, and 172 degree-days for the 90% probability. Accordingly, spawning will start after the accumulation of 57–81 degree-days and most broodstock will begin to spawn between 99 and 129 degree-days in earthen ponds. For practical application it would be most suitable to use the 90% probability values for estimating the timing of spawning readiness. These calculations should be used as guidelines and spawning containers should be provided in the ponds to ensure that fish are indeed ready to be collected for hormone injection and induced spawning.

This initial work needs to be extended to natural and commercially cultured populations of catfish in other environments. Different populations of channel catfish may respond differently to temperature, based on factors such as age, genetics, or nutrition. This work was performed in southern Louisiana, and catfish in other regions may respond differently. In addition, it will be important to evaluate the relationship of degree-days for spawning throughout the early, median, and concluding portions of the natural spawning season in a variety of channel catfish populations. Future studies need to focus on the application and fine-tuning of these definitions and degree-day values and establish the lower threshold temperature and minimum requirement for cold temperatures to induce gonadal development for channel catfish. This true threshold can only be established if broodstock in ponds are consistently held below that temperature and do not show gonadal development that leads to spawning. Detailed degree-day data on channel catfish spawning could provide the basis for computer programs that predict the pond spawning probability of wild or cultured channel catfish in a geographic region based on climate data or in facilities with control of pond temperatures. This would enhance the predictability and control of channel catfish spawning and simplify planning for fingerling producers and hatchery and resource managers. Future studies should also define the degree-day relationship for conditioning of catfish for hormonal induction of spawning in the hatchery before and during the natural spawning season (e.g., Lang and Tiersch 2007) and apply a degree-hour calculation approach to standardize the timing of final oocyte maturation after injection of spawning hormones.

Acknowledgments

The authors thank N. Mandhani for assistance with the degree-day calculations and W. Campbell, F. Jimenez, J. Hargreaves, C. Lambert, A. Horvath, P. Paz, R. Reigh, and R. Romaire for technical advice and help in collecting data. This research was supported in part by funding from the Cooperative State Research, Education, and Extension Service of the U.S. Department of Agriculture, the Louisiana Catfish Promotion and Research Board, and the Southern Regional Aquaculture Center. It has been approved for publication by the Director the Louisiana Agricultural Experiment Station as manuscript 07-11-0280.

References

Avault, J. W. 1996. Fundamentals of aquaculture. AVA Publishing Company, Baton Rouge, Louisiana.

Bates, M. C., and T. R. Tiersch. 1998. Preliminary studies of artificial spawning of channel catfish as male–female pairs or all-female groups in recirculating systems. Journal of the World Aquaculture Society 29:325–334.

Blythe, B., L. A. Helfrich, W. E. Beal, B. Bosworth, and G. S. Libey. 1994. Determination of sex and maturational status of striped bass (*Morone saxatilis*) using ultrasonic imaging. Aquaculture 125:175–184.

Brauhn, J. L. 1971. Fall spawning of channel catfish. Progressive Fish-Culturist 33:150–152.

Busch, R. L. 1985. Channel catfish culture in ponds. Pages 13–78 *in* C. S. Tucker, editor. Channel catfish culture. Elsevier, Amsterdam.

Davis, K. B., C. A. Goudie, B. A. Simco, R. Mac Gregor, and N. C. Parker. 1986. Environmental regulation and influence of the eyes and pineal gland on the gonadal cycle and spawning in channel catfish (*Ictalurus punctatus*). Physiologia Zoologica 59:717–724.

Grizzle, J. 1985. Reproductive biology. Pages 229–282 *in* C. S. Tucker, editor. Channel catfish culture. Elsevier, Amsterdam.

Hall, S. G., J. Finney, R. P. Lang, and T. R. Tiersch. 2002. Design and development of a geothermal temperature control system for broodstock management of channel catfish *Ictalurus punctatus*. Aquacultural Engineering 26:277–289.

Haskell, D. C. 1959. Trout growth in hatcheries. New York Fish and Game Journal 6:205–237.

Horvath, L. 1986. Carp oogenesis and the environment. Pages 109–117 *in* R. Billard and J. Marcel, editors. Aquaculture of cyprinids. Institut National de la Recherche Agronomique, Paris.

Howell, B. R., D. J. Owen, T. Ellis, and S. M. Baynes. 1998. Early life stages of farmed fish. Pages 27–55 *in* K. D. Black and A. D. Pickering, editors. Biology of farmed fish. Sheffield Academic Press, Sheffield, UK.

Huner, J. V., and H. K. Dupree. 1984. Methods and economics of channel catfish production, and techniques for the culture of flathead catfish and other catfishes. Pages 44–82 *in* J. V. Huner and H. K. Dupree, editors. Third report to the fish farmers. U.S. Fish and Wildlife Service, Washington, D.C.

Jobling, M. 1995. Development of eggs and larvae. Pages 357–390 *in* Environmental biology of fishes. Chapman and Hall. London.

Kelly, A., and C. Kohler. 1996. Manipulation of spawning cycles of channel catfish in indoor water recirculating systems. Progressive Fish-Culturist 58:221–228.

Kohler, C. C., R. J. Sheehan, C. Habicht, J. A. Malison, and T. B. Kayes. 1994. Habituation to captivity and controlled spawning of white bass. Transactions of the American Fisheries Society 123:964–974.

Lang, R. P., K. L. Riley, J. E. Chandler, and T. R. Tiersch. 2003a. The use of dairy protocols for the cryopreservation of blue catfish sperm *Ictalurus furcatus*. Journal of the World Aquaculture Society 34:66–75.

Lang, R. P., R. P. Romaire, and T. R. Tiersch. 2003b. Induction of early spawning of channel catfish in heated earthen ponds. North American Journal of Aquaculture 65:73–81.

Lang, R. P., and T. R. Tiersch. 2007. Early out-of-season induced spawning of channel catfish *Ictalurus punctatus* (Rafinesque) conditioned in heated earthen ponds. Aquaculture Research 38:498–507.

Lee, J. S. 1991. Spawning and producing fry, fingerlings, and stockers. Pages 209–233 *in* Commercial catfish farming, third edition. Interstate Publishers, Danville, Illinois.

MacKenzie, D. S., P. Thomas, and S. M. Farrar. 1989. Seasonal changes in thyroid and reproductive steroids in female channel catfish *Ictalurus punctatus* in pond culture. Aquaculture 78:63–80.

Pawiroredjo, P. A. 2004. Temperature effects on spawning and fingerling production of channel catfish, *Ictalurus punctatus*. Master's thesis. Louisiana State University, Baton Rouge.

Rothbard, S., and Z. Yaron. 1995. Carps (Cyprinidae). Pages 321–352 *in* N. R. Bromage and J. R. Roberts, editors. Broodstock management and egg and larval quality. Blackwell Scientific Publications, Cambridge, Massachusetts.

Soderberg, R. W. 1992. Linear fish growth models for intensive aquaculture. Progressive Fish-Culturist 54:255–258.

Steeby, J. A. 1987. Effects of spawning container type and placement depth on channel catfish spawning success in ponds. Progressive Fish-Culturist 49:308–310.

Wilson, L. T., and W. W. Barnett. 1983. Degree-days: an aid in crop and pest management. California Agriculture 37(1 and 2):4–7.

Zonneveld, N. 1983. The spawning season and the relation between temperature and stripping time of grass carp (*Ctenopharyngodon idella* Val.) in Egypt. Bamidgeh 36:21–28.