The Spines of the Channel Catfish, *Ictalurus punctatus*, as an Anti-Predator Adaptation: an Experimental Study

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**Introduction**

Mechanisms to avoid predation include a variety of adaptations that can function in predator deterrence, which reduce the probability of attack, and as defenses, which reduce the risk of mortality from an attack (Alcock 2005). The pectoral spines of catfishes are thought to deter predation through warning behavior and by increasing the effective size of the catfish (Endler 1986; Fine & Ladich 2003). The channel catfish *Ictalurus punctatus* pectoral spine complex (spine and girdle) is a highly modified anatomical mechanism responsible for stridulatory sound production, binding and spine locking (Fine et al. 1997). When locked the fully abducted spine is held rigidly at a right angle to the fish by skeletal specializations. In binding, the position of the partially abducted spine is maintained by muscular force engaging two friction-locking mechanisms. The spine, a stout and sharp modified fin ray composed of dense bone tissue, is located along the mediolateral axis of the fish and equipped with serrated dentations along its posterior edge (Fig. 1). The junction of the spine forms a modified joint with the pectoral girdle. The mechanics of this junction allow the spine to be bound and locked making it resistant to

**Abstract**

Although experimental evidence is lacking, the stout pectoral spine of catfishes has been interpreted as a defensive adaptation. The spine can be rigidly locked and abducted to produce stridulation sounds, which have been hypothesized to serve a warning function. We studied spine function in channel catfish (*Ictalurus punctatus*) as a deterrent to predation by largemouth bass (*Micropterus salmoides*) by presenting individuals with pairs of catfish, one with its pectoral spines clipped and the other intact. The number of initial attacks on clipped and intact fish was similar, suggesting that bass do not recognize the spine visually. Bass showed evidence of learning across trials, striking clipped fish fewer times and consuming them. Conversely, intact fish were attacked more than clipped ones because intact fish were repeatedly disgorged and attacked again, suggesting that bass become sensitized to the spine. Ingestion times were longer for intact than clipped fish, and fewer intact fish were eaten. Eighty-eight percent of intact fish survived in the mouth of a bass one or more times. Catfish did not stridulate or use their spines to deter initial attacks, refuting the warning hypothesis. Locking and stridulation motions, only observed when catfish were held inside the mouth of a bass, did not deter subsequent attacks indicating that neither the spine nor stridulation carry a warning function. It is possible, therefore, that stridulation sounds function as a distress call. The spine functions against a gape-limited predator by increasing the difficulty of ingestion but not capture.
opposing forces (Fine et al. 1997; Fine & Ladich 2003).

Anecdotal evidence indicates catfish pectoral spines can harm or kill predators. However, experimental support for the role of the pectoral spine in deterring predation is lacking. Recher & Recher (1968) observed increased escapes by prey with spines from herons, but did not describe defensive use of these spines. Among the anecdotal reports, catfish spines of various species were implicated in wounds or death in largemouth bass (Krummrich 1969), midland water snakes (Nerodia sipedon) (Burr & Stoeckel 1999), great egrets (Ardea alba) (Werner et al. 2001), and brown pelicans (Pelecanus occidentalis) (Bunkley-Williams et al. 1994).

Forbes’ (1989) dangerous prey hypothesis is predicated on the notion that predators should tend to avoid prey with defensive structures in favor of more accessible prey. Forbes compared gape-limited birds (herons) and species that dismember prey (osprey) before ingestion and found that gape-limited species avoided ‘risky prey’ (channel catfish with locking pectoral spines) with greater frequency than non-gape-limited predators. Supporting the ‘dangerous prey hypothesis,’ Case (1970) (cited in Burr & Stoeckel 1999) observed northern pike (Esox lucius) cannibalizing conspecifics before taking a single tadpole madtom (Noturus gyrinus). Similarly, Glahn & Dorm (2002) concluded that alternative prey, golden shiner (Notemigonus crysoleucus), which are more easily handled and manipulated than channel catfish, are a probable moderator of catfish predation by double-crested cormorants (Phalacrocorax auritus) at aquaculture facilities. Although these observations support the pectoral spine as a deterrent to predation, experimental data as to how the spine might be used are lacking.

In addition to locking their spines, catfish voluntarily produce stridulatory sounds, bursts of short-duration pulses, by depressing ridges on the dorsal process of the pectoral spine against a cleithral surface (Fig. 1) during pectoral spine movement (Kaatz 1999; Heyd & Pfeiffer 2000; Fine & Ladich 2003). Channel catfish favor their left or right fins in sound production (Fine et al. 1996), and stridulation pulses are radiated by the pectoral girdle rather than the swimbladder (Fine et al. 1997). Sörensen (1895) originally hypothesized that pectoral stridulation in South American catfishes could alert predators to the spine, and Kaatz (1999) therefore suggested that these sounds may have an aposematic function.

This study examined predatory interactions between largemouth bass and channel catfish; largemouth bass are a generalized fish predator and can be important catfish predators in aquacultural ponds (Krummrich & Heidiger 1973). Our goal was to determine whether the spine protected the catfish, and if so, how it works. We tested the predictions that largemouth bass would (1) attack and (2) ingest fewer channel catfish with intact than clipped pectoral spines, and (3) tested the hypothesis that pectoral spines and sound production serve a warning function.

Methods

In each trial, two catfish were matched for size (total length, TL in mm) and simultaneously introduced into a tank (120 cm diameter × 70 cm deep) with a
single largemouth bass. The tank housed a table structure (61 × 46 × 46 cm) constructed from PVC pipe and a plastic cover as a refuge for the bass. The tanks were covered with lattice material, which was removed prior to predation trials. Ambient lighting was constant during all trials. The spines of the experimental fish were bilaterally removed, and the control was left intact after sham surgery (see below). The experimental protocol and surgical procedures were approved by the VCU Institutional Animal Care and Use Committee and comply with principles of animal care publication No. 86-23, revised 1985, of the National Institute of Health. Smaller sized catfish were presented initially to gauge the size preferences of each bass. Sizes were then increased according to the ease with which bass ingested catfish, although size limitations were dictated by the individuals in our catfish stock. The pair was introduced into the bass tank from a bucket containing approx. 6 l of water. Experiments utilizing each bass lasted about 2 mo; trials were conducted every second to third day to maximize feeding motivation in the bass. Experiments with seven separate bass were conducted, each for at least 15 trials with predation (18–23 trials in all) except for bass 3 (13 trials), terminated due to a lack of catfish and bass 7, which exhibited escape behavior (erratic bursts of swimming and long-axis spiraling) upon catfish introduction. Data from bass 7 were not included in the analysis. During observations, we recorded which catfish was struck first, the number of strikes on each fish, ingestion of one or both fish, orientation of ingested fish (head first or tail first), ingestion time (in seconds) and presence or absence of pectoral fin sweeps, a reliable indicator of stridulatory sound production (Fine et al. 1997; Kaatz 1999; Heyd & Pfeiffer 2000). Ingestion time was defined as the time elapsed from capture to disappearance of the catfish inside the mouth of a bass. Trials lasted 1 h unless a catfish was being ingested in which case the trial was extended until release or ingestion. Remaining catfish were removed from the bass tank.

We collected largemouth bass (n = 7) via boat electrofishing in Lake Chesdin (six bass) in Petersburg, Virginia and Lake Charles (one bass) in Charles City County, Virginia. Bass were stored in a community tank and fed golden shiners weekly until used sequentially in experiments. Bass ranged from 380 to 500 mm TL and 847 to 1866 g, and catfish ranged from 111 to 205 mm TL. Lengths of intact and clipped (respectively) catfish pairs were within 3–4 mm (the mean difference was 0.2 ± 0.3 mm) and did not vary significantly for any of the seven bass (paired t, NS). Upon completion of experiments bass were returned to their home lakes. Channel catfish of varying lengths were obtained from Virginia State’s aquaculture facility, held in a stock tank and fed twice weekly.

Surgery
Catfish were anesthetized in 100 mg/l MS 222 in oxygenated water, and pectoral spines were clipped near their base with a small pair of wire snips. Caution was taken to avoid damaging the soft pectoral fin rays. Sham surgery was conducted by touching the snips to both pectoral spines without clipping. Fish were held for 24 h prior to experiments but usually recovered normal swimming behavior within several minutes. We held 20 fish with clipped spines for a week in the lab to determine mortality and effect on swimming behavior. No mortality occurred and swimming appeared normal. Pectoral fins are retracted in normal swimming and escape although they are extended during turning and breaking. In a tank with five clipped and five intact catfish it was difficult to even distinguish whether a fish was clipped or not without focusing on a single individual.

Data Analysis
Statistical tests compared data from clipped and intact fish, including number of fish ingested, number of initial strikes, strikes per session, and ingestion time for each bass. Measurements were averaged for each bass, which was then treated as a single replicate, and mean values for clipped and intact fish were compared with a paired t-test. One outlier (an ingestion period of 150 min for an intact fish) was deleted from the analysis (Fig. 2c). With the deletion of this observation, all data conformed to a normal distribution, although in one case (number of strikes), data were log transformed to achieve a better approximation of normality. To test for learning effects, %eaten, %struck and number of strikes were compared across trials. Linear regressions of percentage eaten for intact and clipped fish were compared using ANCOVA. Stridulation, determined by the presence of pectoral fin sweeps, was evaluated as a percentage of trials with stridulatory behavior. Analyses were conducted using Prism statistical software (GraphPad Software, San Diego, CA, USA) and evaluated at a significance level of alpha = 0.05.
Results

Response to Attack

Burst swimming was the initial, although unsuccessful, reaction of intact and clipped catfish to predatory pursuit. Bass captured catfish and attempted to ingest them whole. Catfish that had been partially ingested and then disgorged typically remained motionless on the bottom or swam near the top of the water. Sitting on the bottom decreased the attack stimulus, particularly later in the trial. Immediately after release by a bass, catfish remained motionless for a period normally lasting <3 s, followed by slow retreat. Locking was witnessed in all catfish whose pectoral spines were not obstructed from view (headfirst or completely inside the mouth of a bass). Variability in duration of locked spines after release was apparent with some fish unlocking immediately, and others maintaining the locked position for extended periods, including the duration of the trial. Catfish that remained stationary typically kept spines locked longer than ones that continued swimming. Locked spines hindered swimming behavior causing wobbling during forward movement. Often, bass released fish with locked spines and struck them again to obtain a better position. Release occurred most frequently when a fish was captured tail first, and the spines were braced against the outside of the mandible of the bass.

Bass were injured by the spines. In two instances, the spine pierced interior mouthparts causing bleeding and subsequent release. One of the bass resumed attacks on both catfish after bleeding ceased. In three other instances, a bass with a spine protruding through its mandible or lodged inside its mouth, completed a series of shakes beneath the surface before vaulting from the water, shaking violently in an attempt to dislodge the catfish. After dislodging the catfish, these bass did not resume predatory behavior during the trial. One bass had difficulty ingesting an intact fish, requiring 150 min. Bass that experienced troubles with the spine exhibited relative caution in future encounters. Decreased aggressiveness in attacks, particularly on intact fish was the most common response in subsequent trials.

Twenty-eight of 139 (20.3%) intact catfish performed pectoral stridulatory sweeps. Twenty-seven of these fish were partially inside the mouth of the bass, grasped tail first, and one fish had just been released by a bass. Most fish were grasped head first, precluding observation of pectoral movement. This number may therefore be an underestimate. Five of the 28 fish were eaten, and seven were attacked repeatedly resulting in death, yielding a 44% mortality rate for stridulating fish.

Quantitative Data

Bass exhibited no preference for attacking clipped or intact fish on the first strike of the session (Fig. 2a, t = 0.18, p = 0.86). Bass struck intact catfish more than clipped fish (Fig. 2b, t = 3.17, p = 0.025; note data were log transformed to achieve a better fit). Bass had difficulty ingesting an intact fish, requiring 150 min. Bass that experienced troubles with the spine exhibited relative caution in future encounters. Decreased aggressiveness in attacks, particularly on intact fish was the most common response in subsequent trials.
approximation of normality) because intact catfish were repeatedly struck and disgorged more frequently. Bass took longer to ingest intact than clipped fish (Fig. 2c, \( t = 3.316, p = 0.0045 \)) although they ate more clipped than intact fish (Fig. 2d, \( t = 7.95, p = 0.0003 \)). These results suggest that bass did not visually recognize the spine prior to attack, and that the spine did not reduce vulnerability to attack, although it did increase survival.

The probability of an intact fish being eaten across all bass was 26% (30 of 114) compared with 74% (84 of 114) for clipped fish (\( p < 0.0001 \), binomial test). The average number of strikes to ingest intact fish was 4.1 ± 1.2 compared with 2.2 ± 0.3 for clipped fish. Eighty percent (91 of 114) of fish were ingested head first, and 20% (23 of 114) tail first. Ninety-six of 109 (88%) intact catfish survived after being inside the mouth of a bass one or more times. After multiple partial ingestions, which resulted in superficial skin abrasions, most fish were capable of normal swimming. One bass killed eight of 13 (62%) intact fish without ingestion, frequently striking them multiple times. These catfish were badly wounded and killed immediately upon removal. This behavior was atypical of other bass.

Learning Effects

The percentage of initial strikes on clipped and intact catfish did not change across trials (Fig. 3a). The slopes of both regressions were not significantly different from zero indicating a 50:50 chance of striking a clipped or an intact fish and no change with experience. The chance of being eaten, however (Fig. 3b), increased over time for clipped fish (\( r^2 = 0.48, p = 0.0002 \)) but declined insignificantly for intact ones (\( r^2 = 0.085, p = 0.1748 \)). The difference between clipped and intact was significant (\( \text{ANCOVA: } F_{1,42} = 13.64, p = 0.0006 \)). This difference was caused by different predatory behavior of the bass over time (Fig. 3c). Total number of strikes on clipped and intact fish was similar throughout the first six trials and exhibited some variability between the sixth and ninth trial. From the tenth trial on, clipped fish were ingested after a small number of strikes, and intact fish were repeatedly disgorged and attacked. The greater number of attacks on intact fish reflects the greater number of escapes, and not a feeding preference. The large standard errors for strikes on intact fish was caused primarily by the largest bass in the study which was capable of eating intact fish with little trouble and required fewer attacks for ingestion than other bass in the study.

Finally some increases in strikes on clipped fish (e.g. trials 8 and 19) appear to reflect transfer of spine sensitization to the clipped fish. This transfer occurred in certain individuals which had been con-
summing clipped fish readily and then shifted to the pattern for intact fish of repeatedly attacking and disgorging.

Discussion

Our observations indicate that channel catfish utilize their spines to avoid predation, but that the spines do not deter attack in an experimental situation without alternative prey. Given the size variation of our bass predators, these results are quite robust. Spine locking appears to be the most common and effective defense in deterring ingestion by largemouth bass. Channel catfish can also bind their spines, an action maintained by muscle contractions that engage two friction locking mechanisms when the spine is partially abducted (Fine et al. 1997). Binding has been evoked experimentally by holding or attempting to move the spine. Because catfish in the mouth of a bass fully abduct their spines to the locked position, locking appears to be the defensive posture of choice. Note that locking and stridulation are opposite behaviors, and a fish cannot accomplish both simultaneously.

Pectoral spines do not deter attacks by largemouth bass. In fact, based on initial attacks, bass do not appear to visually recognize the spine. Rather, the spine functions as a hindrance to ingestion but not attack, and mortality of catfish that are attacked but not ingested is low. Spinelli et al. (1985) report even lower mortality rates (6.3%) of non-ingested catfish. Our conclusion is consistent with findings of palatability and esophageal-size constraints as factors in a largemouth bass’s decision to ingest captured prey (Lawrence 1957; Winemiller & Taylor 1985; Linser et al. 1998). In this sense, the bass chooses to abort or complete an ingestion attempt based on the ease of handling the prey item during ingestion. Optimal foraging theory considers that the energetic benefits of a prey item are weighed against the costs of capturing, ingesting, and digesting the prey (Pyke 1979; Townsend & Winfield 1985; Turesson et al. 2002).

Bass generally attack intact fish more often than clipped fish. One bass frequently attacked intact fish to the point of death without ingesting them. Such behavior has been previously reported in largemouth bass used in experiments with channel catfish (Krummrich & Heidiger 1973) and Japanese dace (Tribolodon hakonensis) (Katano et al. 2002). Most attacks on intact fish occurred after ingestion of clipped fish. We suggest that swallowing a catfish with an erect spine can be punishment to the bass. Even an uneventful ingestion permits sharp bony projections against soft oral and esophageal tissues, and punctures by the spine or difficulties in swallowing can curtail attack and feeding. Therefore, bass may be undergoing an approach-avoidance conflict in which they attack the catfish as a food stimulus and disgorge it because of the spine. Learning by the bass is indicated by the changes in percentage of clipped fish eaten and the increasing number of strikes on intact catfish over time (Fig. 3). The most parsimonious hypothesis for the increasing strikes is that hungry bass disgorge catfish, sometimes almost completely ingested, because the bass has become sensitized to the spine. Note the avoidance behavior of bass 7 to catfish introduction. Although there were individual differences in behavior, bass generally swallow clipped fish with less difficulty. Some bass swallowed them more quickly over the course of the trials, and in other bass the sensitization appeared to transfer to the clipped fish, and bass that had easily ingested clipped fish started to release them and attack again.

Numerous sonic fishes produce disturbance calls when held by a human or electrically shocked (Fish & Mowbray 1970). To our knowledge the function of such sounds has not been formally investigated. However, stridulatory behavior and spine erection are not observed during initial attacks, failing to support hypotheses of a warning function for the spine and sound production, at least in interactions between channel catfish and largemouth bass. Absence of stridulation prior to attack also indicates these sounds do not carry a warning function. Stridulatory behavior was witnessed in about 20% of intact catfish, almost exclusively, when they were clenched in the jaws of a bass predator. Clearly, stridulation does not deter further attacks by largemouth bass, which are known to utilize visual cues for feeding (McMahon & Holanov 1995; Linser et al. 1998). These results, which need to be replicated with other catfish species and various predators, indicate that stridulatory behavior is ineffective in thwarting predation by largemouth bass. Therefore, it is likely that stridulatory sounds serve as a distress call that could potentially summon other predators and increase the emitter’s chances of escape (Bradbury & Vehrencamp 1998).

Spines in aquatic invertebrates and in fish fins are generally believed to discourage predation. The situation in fishes is complicated by effect of body shape (a deeper body makes successful attack more difficult) and maneuverability (Webb 1986; Brönmark & Miner 1992). Esocids (muskellunge, tiger
muskellunge and northern pike) capture fewer bluegills (with spines) and take longer (handling time) to ingest them than for fathead minnows and gizzard shad (without spines), and they grow slower in ponds dominated by bluegills (Gillen et al. 1981; Wahl & Stein 1988). In sticklebacks (Hoogland et al. 1957; Reimchen & Nosil 2002) and channel catfish (this study), these specialized spines appear to have a similar though exaggerated function compared with typical fin spines, and Hoogland et al. (1957) found that removing stickleback spines increased predation in an experimental tank. Spines have similar effects in Daphnia and other aquatic invertebrates (Kolar & Wahl 1998).

Our experiment did not directly test a deterrent effect of catfish spines. However, small bluegill rapidly decrease their strike rate on long-spined Daphnia lumholtzi compared with Daphnia pulex after a spine lodged in their buccal cavity indicating a deterrent effect (Kolar & Wahl 1998), and sticklebacks are rejected in favor of prey without spines (Hoogland et al. 1957). Our results suggest that largemouth bass might avoid channel catfish if other prey were available. This notion is supported by our fish 7 which quickly consumed golden shiners while avoiding catfish and evidence of sensitization to the spine (repeated disgorging and attacking intact catfish). Furthermore, the addition of alternative prey to catfish ponds has mitigated bird predation (Glahn & Dorr 2002).

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