THE UNIVERSITY OF MANITOBA

ADJUSTMENT OF BUOYANCY BY CATFISH (ICTALURIDAE) IN RESPONSE TO A CHANGE IN WATER VELOCITY

by

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ABSTRACT

Adjustment of swimbladder volume in response to a change in water velocity was studied in four species of catfish (Ictaluridae). All four species were more buoyant in still water than when held in current. Within three species; tadpole madtom (*Noturus gyrinus*), black bullhead (*Ictalurus melas*) and stonecat (*Noturus flavus*) extent of adjustment and buoyancy attained in still and current varied with size. Whether in still or current, stonecat were less buoyant than the other species. To maintain position in current, tadpole madtom and black bullhead move to the bottom and reduce buoyancy. Tadpole madtom adjust buoyancy within 96 - 192 hours with partial adjustments within 12 - 48 hours. Year 0 fish were found to make a more rapid decrease in buoyancy than year 1 or 2 while no differences between age groups could be found in rate of increase. During buoyancy decrease tadpole madtom (year 0 and 1) showed significant changes in internal gas pressure; however, no significant change was detected during buoyancy increase. Tadpole madtom were found to have no ability to secrete gases in comparison with the black bullhead.

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INTRODUCTION

This study seeks to determine if certain species of catfish (Ictaluridae) adjust buoyancy by altering swimbladder volume in response to a change in water velocity and if so to describe the rate and mechanisms involved. Enlarging swimbladder volume as current decreases and reducing it as current increases is an important adaptation to life in streams and rivers where water velocity varies greatly over time and space (Gee 1970). Such adjustment of buoyancy has been only recently described in Atlantic salmon parr and smolts (Saunders 1965; Neave *et al*. 1966; Pinder and Eales 1969), brook trout (Saunders 1965) and in longnose and blacknose dace (Gee 1968, 1970, 1972; Gee and Machniak 1972). Environment occupied and size of fish are known to influence both buoyancy (Saunders 1965; Gee and Northcote 1963) and extent of adjustment (Gee 1968, 1972).

Four species were examined to determine if buoyancy (1) differed in still water and in current, and (2) was related to size of fish and environment occupied. The tadpole madtom (*Noturus gyrinus*) and black bullhead (*Ictalurus melas*) are common in still water, channel catfish (*Ictalurus punctatus*) are found in faster velocities and stonecat (*Noturus flavus*) occupy areas of rapid current.

Although the rate of adjustment in dace (Gee 1968, 1970), brook trout (Saunders 1965) and Atlantic salmon parr (Saunders 1965; Neave *et al*. 1966) have been described, no attempt has been made to determine if within a species, fish of different ages adjust buoyancy at different rates. This was examined in the tadpole madtom.

The swimbladder of catfish, as in other Cypriniformes, contains gases at a pressure greater than that of the surrounding water (Alexander 1959, 1961). Gee (1970) found that blacknose dace appeared to alter internal pressure of gases in the swimbladder during adjustment of buoyancy thereby affecting the rate and extent of alteration of swimbladder volume. The internal pressure of gases in the swimbladder of the tadpole madtom was examined to determine if changes occurred during adjustment of buoyancy.

Until recently (Jones and Marshall 1953), gulping air at the surface had been believed to be the sole means by which physostomes increased swimbladder volume. However, a variety of fishes are now known to be able to secrete gas into the swimbladder when denied access to the surface (Wittenberg 1958; Alexander 1966 b; Gee 1968). The tadpole madtom and black bullhead were examined to determine if they could secrete gas to enlarge swimbladder volume when denied access to the surface.

The advantages of reduced buoyancy to maintain position in running water have been described in previous studies (Gee and Northcote 1963; Saunders 1965; Alexander 1966b; Gee 1968).

Hartman (1963) has indicated that behavioural adaptations could be an important feature in maintenance of position in current. Tadpole madtom and black bullhead were compared to determine if swimming behaviour and vertical distribution differed between still water and current.

MATERIALS AND METHODS

Each of the four species of Ictaluridae was collected from different environments as follows:

Species	Tadpole madtom	Black bullhead	Stonecat	Channel catfish
River	Rat River	La Salle River	Red River	Red River
Location	St. Malo	La Barriere Pk.	St. Norbert	Lockport
Method of Collection	Seine	Seine, angling	Angling	Angling
Surface velocity (cm /sec)	0 - 8	0 - 15	>45	0 - 30
Substrate	silt, sand, gravel	mud	silt, boulders	silt, mud, boulders
Depth (m)	0.2 - 0.9	0.6 - 1.5	3	2 - 3
Vegetation	*Potomageton* sp., *Elodea canadensis*	*Elodea canadensis*	None	None

Fish were collected during the months of May to August in 1971 and 1972. They were held in the laboratory under a normal photo period and water temperature of $21 \pm 2^{\circ}C$. Small fish were fed Tetramin flakes and brine shrimp while larger fish ate trout pellets, canned dog food, and ground perch fillets.

To determine the extent of adjustment of buoyancy fish of each species were placed in batches of 4 - 10 fish for 8 - 10 days in aquaria of either still or current, usually within a week of capture. Since Gee (1968, 1972) has shown that the degree of buoyancy attained and range of adjustment is dependent on length of fish a representative number of all available sizes was examined. Large aquaria (122 x 61 x 61 cm) were used to hold channel catfish and black bullhead exceeding 150 mm total length while smaller aquaria (92 x 46 x 46 cm) were used for smaller fish including all tadpole madtom and stonecat.

To create current, long air-diffusor stones (27.5 cm) were placed across the width of one end of the aquaria and supplied with compressed air. A glass deflector plate was placed at an angle of 45° above the airstones so that the rising bubbles of air created a circular current of water that passed along the surface; down the opposite end and along the bottom at a velocity of approximately 20 - 35 cm/sec. Three or more stones 3 - 7 cm high (10 - 15 cm diam) were placed on the bottom to provide a turbulent flow and refuge areas similar to a stream environment. Compressed air could be shut off and aquaria used as a still water situation.

After the appropriate period in either still or current, fish were captured individually in a beaker to prevent gulping air and transferred to a solution of tricane methanesulfonate.

Once immobilized the swimbladder volume (± 0.001 ml), the weight of the gas-free fish in water (± 0.001 g), and the volume of gases released from the swimbladder at atmospheric pressure (± 0.001 ml for fish $<$ 110 mm total length; ± 0.1 ml for fish $>$ 110 mm total length) were determined using the procedure given by Gee (1970). Floatation pressure (Saunders 1953) was used as a measure of buoyancy and was obtained by dividing the volume of the swimbladder (ml) by the weight of the gas-free fish in water (g) (neutral buoyancy = 1.0 ml/g; negative buoyancy $<$ 1.0 ml/g; positive buoyancy $>$ 1.0 ml/g). Internal pressure of gases was measured by dividing the volume of gases released from the swimbladder at atmospheric pressure by the volume of the swimbladder.

To determine the role of swimming behaviour in association with floatation pressure in maintenance of position in current; black bullhead and tadpole madtom (32 - 59 mm) were observed in both still and current in the laboratory. A week after capture, six black bullhead and ten tadpole madtom were each placed into still or current aquaria (92 x 46 x 46 cm). Each aquarium was divided into three 13 cm intervals from top to bottom to record vertical distribution. Three small rocks (7.5 - 13 cm diam) were placed on the bottom of these aquaria to provide cover and in the case of current to simulate the turbulent flow of a stream environment. Observations were made at 8:00 a.m., 2:30 p.m. and 5:30 p.m. with nightly observations at least every second day after 9:00 p.m. Each fish was treated as an individual observation and its position recorded. Because tadpole madtom are nocturnal (Taylor 1969) and black bullhead diurnal (Darnell and Meierotto 1965) only those observations associated with most active period were used in determining vertical distribution. This gave a cumulative total of 72 individual observations on black bullhead and 130 on tadpole madtom in still water, while in current there were 84 and 120 observations respectively. The number of fish observed in each section was totalled and expressed as a percentage of the total number of observations made in all sections during the period of the experiment. After 8 days, fish were removed and floatation pressures determined.

To describe the rate of decrease in buoyancy 72 tadpole madtom were held for 8 days in still water. A group of 8 fish were selected at random and floatation pressure and internal pressures were recorded (0 hr). Then the compressed air was turned on creating current. The remaining groups of fish were examined after 1, 3, 6, 12, 24, 48, 96 and 192 hours in current. Rate of increase in buoyancy was determined by holding 72 fish in current for 8 days and then they were examined at the above time intervals in still water. The procedure was carried out on three age classes: year 0 (24 - 41 mm), year 1 (44 - 59 mm) and year 2 (61 - 101 mm) to determine if rate of adjustment varied with age (size) of fish. Division into age categories was derived from length frequency distribution. In the current aquarium many of the smaller year

0 fish did not remain near the bottom in the area of current but moved to a mid-depth position of little current. To overcome this, year 0 fish were contained in a stainless steel screen cage (61 x 42 cm) of 3 meshes/cm with a plexiglass bottom and suspended in the top portion of the aquarium in 10 cm of water through which water current flowed at 20 - 30 cm/sec.

Swimbladder volume was reduced in tadpole madtom and black bullhead in an attempt to induce gas secretion by the following methods: (1) increase in water velocity and (2) reduction in pressure. Gas secretion would be indicated if floatation pressure increased after a period in still water when a fish was denied access to the surface following a reduction in swimbladder volume.

Tadpole madtom (24) were held in current for one week, then eight were removed and floatation pressures determined. The remainder were placed into aquaria (24 x 17 x 14 cm) with six having access to the surface while eight were denied access by a stainless steel screen (3 meshes/cm). The former were held in 21.5 cm of water and the latter in 38 cm of water. After two weeks in still water floatation pressures were measured.

The ability of tadpole madtom and black bullhead to secrete gas was compared following a pressure reduction. Fish held in small plastic vials to restrict movement were weighed in water, placed into a water-filled dessicator jar and exposed to a vacuum of 13 - 30 cm Hg and weighed again. Twenty-four tadpole madtom were so treated and 12 were each placed in access and non-access situation. Of the 10 black bullhead treated, four were given access to the surface and six were denied access. Floatation pressures were determined after two weeks in still water. Floatation pressures prior to and following the pressure reduction were estimated using the weight of the intact fish in water obtained at these times and the weight of the gas-free fish in water after two weeks in still. It is assumed that no significant change in the latter occurred over the two week period.

RESULTS

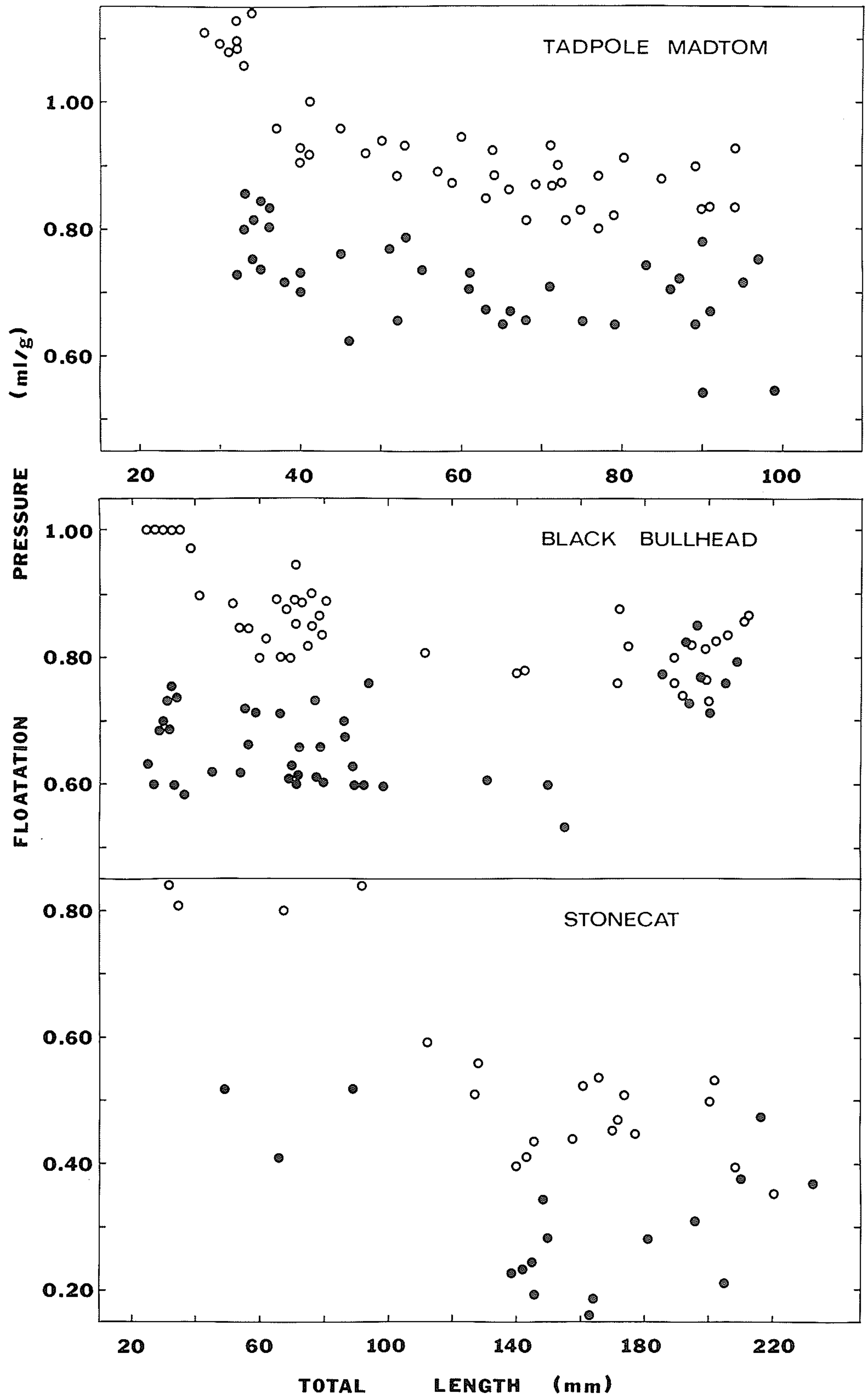
Extent of Adjustment of Buoyancy

All species demonstrated an ability to adjust buoyancy when exposed to a change in water velocity. Differences existed between species in buoyancy attained in both still and current with tadpole madtom reaching a higher buoyancy than black bullhead while stonecat attained the lowest buoyancy. Within each of these species the ability to adjust buoyancy and the buoyancy attained in still or current appeared to be related to size (Fig. 1).

Year 0 tadpole madtom attained a significantly ($p < 0.05$) higher floatation pressure in both still and current than did year 1 or 2 (Cochran's modified t - test). Within each age group fish held in still had a significantly higher floatation pressure than those in current although the difference decreased with age. Mean floatation pressures and numbers of fish (in parentheses) used in this analysis were as follows:

Year	Length (mm)	Still	Current	Difference
0	28-36	1.098 (8)	0.795 (9)	0.303
1	50-65	0.903 (7)	0.689 (7)	0.214
2	75-90	0.861 (11)	0.688 (8)	0.173

FIGURE 1. Relationship between floatation pressure and total length of tadpole madtom, black bullhead and stonecat held in still water (open circles) and current (closed circles).



TADPOLE MADTOM
BLACK BULLHEAD
STONECAT
FLOATATION PRESSURE (ml/g)
1.00
0.80
0.60
0.40
0.20
20
40
60
80
100
140
180
220
TOTAL LENGTH (mm)

Year 0 and 1 black bullhead in still attained a significantly higher buoyancy than those in current. Year 3+ did not make a significant adjustment. In still water year 0 were significantly more buoyant than year 1 or 3+ while that attained by year 3+ was significantly less than year 1. Mean floatation pressures and number of fish (in parentheses) used in this analysis were as follows:

Year	Length (mm)	Still	Current	Difference
0	25-34	1.000 (8)	0.678 (8)	0.322
1	60-80	0.858 (15)	0.645 (10)	0.213
3+	180-200	0.792 (9)	0.781 (8)	0.011

Too few stonecat were caught to permit aging by length frequency. But in still water, buoyancy attained decreased with increasing size as did buoyancy in current. Those fish less than 180 mm total length attained a lower buoyancy in current than in still but among larger fish (> 200 mm) the difference is not as apparent (Fig. 1).

Channel catfish also attained a lower mean floatation pressure in current than in still shown as follows:

Length (mm)	Still	Current
287-382	0.851 (6)	0.753 (5)

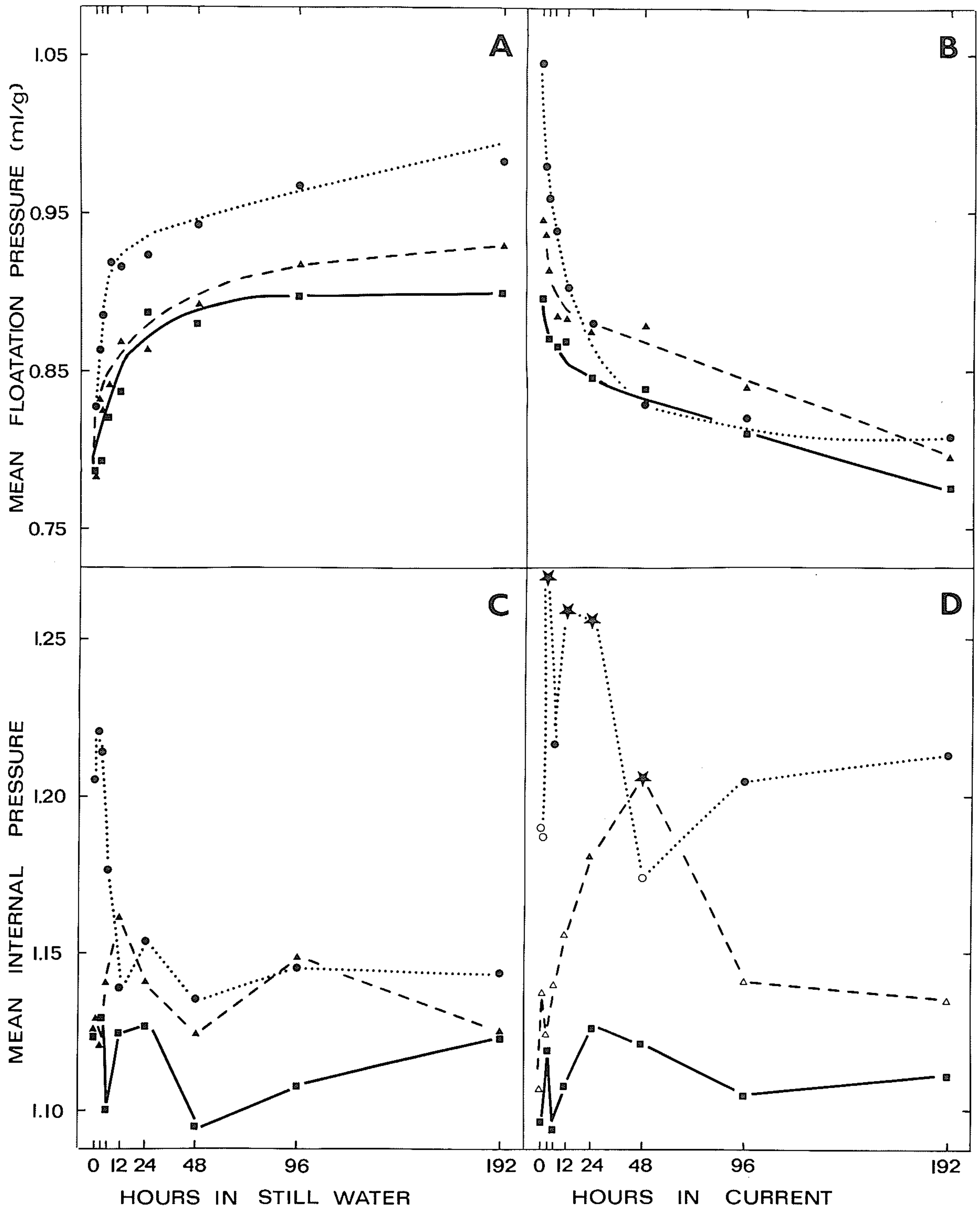
Because of the restricted size range examined no conclusion could be made on the effect of size on ability to adjust buoyancy.

Rate of Buoyancy Adjustment

Tadpole madtom increased their buoyancy rapidly when water velocity changed from current to still (Fig. 2A). Most of the adjustment was made within 48 - 96 hours. Adjustment was completed within 96 - 192 hours. Appendix I gives the range and 95% confidence limits for the means illustrated. Regression lines were calculated with a logarithmic transformation of time for the rate of increase during the first 24 hours. The regression lines were: $y = 0.838 + 0.071 \log x$ (year 0), $y = 0.795 + 0.056 \log x$ (year 1) and $y = 0.768 + 0.071 \log x$ (year 2). A test of homogeneity on regression coefficients ($p < 0.05$) showed no significant difference between the rate of increase (slope) for the three age groups.

Fish decreased their buoyancy when exposed to current; most of the decrease in buoyancy occurred within 24 - 96 hours with a complete adjustment requiring 96 hours for year 0 and 192 hours for older fish. Appendix II gives range of variation and 95% confidence limits for the means illustrated in Fig. 2B. Regression lines calculated for the rate of decrease in floatation pressure during the first 48 hours were: $y = 1.033 - 0.117 \log x$ (year 0), $y = 0.940 - 0.044 \log x$ (year 1) and $y = 0.895 - 0.033 \log x$ (year 2). A significant difference ($p < 0.05$) between the slope of year 0 fish compared with each of the older groups was shown by a test of homogeneity on regression coefficients signifying a more rapid decrease in buoyancy by year 0 fish.

FIGURE 2. Rate of adjustment of mean floatation pressure (A,B) and mean internal pressure (C,D) in tadpole madtom in still water and current (n = 8). No observations were made at one hour for year 2 fish. Circles connected by dotted lines = year 0; triangles connected by broken lines = year 1; squares connected by solid lines = year 2. Within each age group means represented by stars differ significantly from those with open symbols (D).



A
B
C
D
MEAN FLOATATION PRESSURE (ml/g)
1.05
0.95
0.85
0.75
MEAN INTERNAL PRESSURE
1.25
1.20
1.15
1.10
0
12
24
48
96
192
HOURS IN STILL WATER
HOURS IN CURRENT

During the change from current to still, year 0 fish showed a decrease (1.21 - 1.14) in internal pressure within 12 hours, while year 1 and 2 had less discernible changes. Appendix III gives the range of variation and 95% confidence limits for the means illustrated in Fig. 2C. Within each age group means were compared in a single factor analysis of variance combined with the Student - Newman - Keuls' test but no significant differences were found.

When water velocity changed from still to current year 0 fish increased internal pressure during the first 24 hours (Fig. 2D). This was then followed by a decrease year 1 showed a similar pattern of change while in year 2 fish this pattern was less evident. Appendix IV gives the range of variation and 95% confidence limits for the means illustrated in Fig. 2D. Within each age group these means were compared in a single factor analysis of variance combined with the Student - Newman - Keuls' test and significant differences ($p < 0.05$) were revealed (Fig. 2D).

Swimming Behaviour in Still and Current

The swimming behaviour of tadpole madtom and black bullhead differed in still water. Black bullhead when swimming, hovering, or resting on the bottom did so with the body horizontal. Tadpole madtom adopted an oblique position with the head up, when hovering or moving slowly. On a number of occasions they were observed near the surface in a vertical position. When resting tadpole madtom either laid on their side, or obliquely with only the tail touching the bottom.

As fish in current were displaced they associated more with the bottom. In running water, black bullhead swam close to the bottom with their head directly into the current and body parallel to the bottom. There was little attempt to use rocks as cover against the current. Tadpole madtom swam obliquely into the current with head down and tail at a slight angle off the bottom. During the course of the experiment, they utilized the space behind rocks and air-diffusor stones to escape the current. Most tadpole madtom preferred the sides of the aquarium where the current was less due to frictional drag.

Vertical distribution of fish and corresponding floatation pressures were as follows:

Environment	Still			Current		
Floatation pressure (ml/g):						
Tadpole madtom	0.918			0.717		
Black bullhead	0.850			0.566		
Section of aquarium	Top	Middle	Bottom	Top	Middle	Bottom
Distribution (%):						
Tadpole madtom	21.4	29.8	48.8	8.3	16.7	75.0
Black bullhead	4.1	45.2	50.7	0.0	3.6	96.4

Differences between species in sections occupied in still and current were examined with a chi-square contingency table. In still water, there was no significant difference in the bottom section, but there were differences ($p < 0.01$) in the top and middle sections between tadpole madtom and black bullhead. Tadpole madtom were observed more frequently in the top section while black bullhead were observed more frequently in the middle section. In current, both species showed a significant downward shift in distribution with black bullhead more frequent in the bottom than tadpole madtom.

Gas Secretion

With access to the surface tadpole madtom were able to increase floatation pressure significantly (Cochran's modified t-test; $p < 0.05$) after two weeks in still water (Table 1). Those without access made no significant increase in buoyancy retaining floatation pressures similar to those immediately following a reduction in buoyancy. However, black bullhead in both access and non-access were able to increase floatation pressures significantly after two weeks attaining a floatation pressure similar to that prior to buoyancy reduction.

TABLE 1

Mean floatation pressures of tadpole madtom and black bullhead in response to buoyancy reduction followed by a two week period in still water with access and without access to the surface.

Method of buoyancy reduction	Species	Floatation pressure (ml/g)			
		Prior to buoyancy reduction	Following buoyancy reduction	After two weeks in still	
				access	no access
Current	Tadpole madtom		0.786	0.941	0.800
Pressure Reduction	Tadpole madtom	0.958	0.829	0.967	
		0.954	0.851		0.843
	Black bullhead	0.882	0.758	0.909	
		0.924	0.744		0.923

DISCUSSION

Adjustment of buyoancy and the means by which such adjustment might occur in response to water velocity were studied in catfish. All four species of catfish alter swimbladder volume in response to a change in water velocity becoming more buoyant in still and less buoyant in current. Within three species; tadpole madtom, black bullhead and stonecat, extent of adjustment and buoyancy attained in still and current varied with size. Behaviour of tadpole madtom and black bullhead indicate that a strong tendency for association with the bottom along with lowered buoyancy serve as important mechanisms against displacement by current. Tadpole madtom adjust buoyancy on the average within 96 hours with year 0 fish making a more rapid decrease in buoyancy than older fish. Tadpole madtom appear to have little ability to secrete gas in comparison with the black bullhead.

Catfish held in current became less buoyant than those held in still water. Saunders (1965) showed that after a week in still water brook trout and Atlantic salmon parr had a higher floatation pressure than those held in fast water. Similarly, Gee (1968, 1970, 1972) showed that longnose and blacknose dace were more buoyant in still water than in current.

Extent of buoyancy adjustment in tadpole madtom, black bullhead and stonecat is a function of size. Smaller fish made greater adjustments than larger fish. A similar pattern was found in longnose dace (Gee 1968); although in blacknose dace extent of buoyancy adjustment increased with increasing size (Gee 1972). In still water smaller catfish had a higher buoyancy than larger fish. In both stonecat and tadpole madtom, larger fish had a lower buoyancy in current than did smaller fish, while in the black bullhead it was the reverse. Gee (1968) found that small longnose dace had a higher buoyancy in both still and current than did large dace. Gee (1972) showed that in current large blacknose dace had a lower buoyancy than did smaller fish. Saunders (1965), Neave et al (1966), Pinder and Eales (1969) found that differences in buoyancy in Atlantic salmon were more likely the result of changes in mode of life or seasonal effects rather than fish size.

Differences in the range of buoyancy attained between species of catfish are probably the result of adaptations to different environments. The higher buoyancy of tadpole madtom and black bullhead contrasts sharply with that of the stonecat. Both tadpole madtom and black bullhead were obtained from quiet waters, the typical environment of these species (Taylor 1969; Trautman 1957). But stonecat are common in riffles or rapids of streams and are also found along wave-washed shores of Lake Erie (Taylor 1969). Fish exposed to flowing or turbulent water of rivers and wave-washed lake shores have a reduced swimbladder volume (Hora 1922; Gee 1968, 1972; Gee and Machniak 1972). The slender and depressed shape of the stonecat is an additional adaptation to life in turbulent water. A depressed shape enables a fish to take advantage of reduced current speeds near the bottom (Alexander 1966 a).

Saunders (1965) suggested that differences in buoyancy between brook trout and young Atlantic salmon are indicative of the different environments that they occupy. Whereas buoyancy of brook trout (typical of pools and slow-moving waters) were near neutral buoyancy, salmon parr (typical of fast waters) were negatively buoyant. Similar relationships between buoyancy and environment occupied have been described for species of the genus Rhinichthys (Gee and Northcote 1963; Gee 1972; Gibbons and Gee 1972.

Ability to alter vertical distribution and swimming behaviour may supplement changes in buoyancy and assist in maintenance of position in increasing water velocities. In still water tadpole madtom and black bullhead were distributed from top to bottom although the former were observed more frequently nearer the surface. The higher floatation pressure of tadpole madtom, 0.92 ml/g compared to 0.85 ml/g for black bullhead, may account for this. In current both species showed a significant downward shift in distribution along with a decrease in floatation pressure. Fish can maintain their position more efficiently by exploiting negative buoyancy and staying on the bottom than they can with neutral buoyancy swimming perpetually against the current (Alexander 1966 b). Black bullhead showed a greater association with the bottom than tadpole madtom in running water, possibly due to their lower floatation pressure. In current, floatation pressure of black bullhead was 0.57 ml/g compared to 0.72 ml/g for tadpole madtom.

Hartman (1963) showed that association with bottom, areas of slow water or other cover offered protection from displacement by current for brown trout (Salmo trutta). According to Allen (1969) stream fishes must resist movement downstream over their life cycle to maintain a localized population. By moving to the bottom and reducing swimbladder volume as water velocity increases fish can take advantage of frictional forces of their body against the bottom to hold position.

Year 0 tadpole madtom had a quicker initial rate of decrease in floatation pressure than older fish. This would seem logical considering that fry were positively buoyant to begin with and made a greater adjustment in current than older fish who already had an advantage in running-water by the possession of negative buoyancy. No difference in initial rate of increase in buoyancy in still water could be found among the three year classes. Tadpole madtom adjusted from minimum to maximum buoyancy within 96 hours, while the reverse adjustment required up to 196 hours. This rate of adjustment is slower than rates of some other species. Saunders (1965) showed that Atlantic salmon parr and brook trout could adjust buoyancy in 14 hours when transferred from fast to slow-moving water and vice-versa. A complete adjustment required 36 hours. Atlantic salmon fry took longer to complete adjustment (46 hrs). Adjustment in buoyancy for longnose dace was completed in 24 - 96 hours with partial adjustments in 3 hours or less (Gee 1968). However, Gee (1970) found blacknose dace took longer to reach maximum buoyancy (84 hr) and 132 hours to reach minimum buoyancy. Tadpole madtom made a quicker gain in buoyancy than a decrease as did longnose and blacknose dace (Gee 1968, 1970).

Internal pressure of gases may be an important factor in rate and extent of buoyancy adjustment. A change in swimbladder volume can result from an increase or decrease in internal gas pressure. An increase in internal gas pressure might result from muscular compression of the swimbladder, or increase in rate of gas secretion, or swallowing air at the surface or decrease in rate of gas absorption. A decrease in internal gas pressure might result from relaxation of the swimbladder, or decrease in rate of gas secretion, or gas-spitting or increase in rate of gas absorption. Changes observed in internal pressure of gases during adjustment of buoyancy probably reflect some or all of the above processes.

During the decrease in buoyancy in the first 96 hours there was a significant increase followed by a decrease in internal pressure in year 0 and 1 fish. It appears that compression of swimbladder gases occurs until a "critical" pressure is reached. Release of gases through the pneumactic duct may require a certain pressure before gas can be lost from the swimbladder. It appears that both an increase in internal pressure and a loss of swimbladder gases result in a decrease in swimbladder volume and floatation pressure. Evans (1925) found that the pneumactic duct possessed a sphincter mechanism. A number of recent studies have confirmed that changes in internal pressure may be the result of muscular activity changing the volume of the swimbladder (McCutcheon 1958, 1962; Long 1959; Qutob 1962).

The pattern of change in internal pressure that occurred when tadpole madtom increased buoyancy was more variable. The only pronounced trend occurred in year 0 fish in which internal pressure dropped sharply during the first 12 hours of buoyancy decrease. Increased buoyancy appeared the result of addition of gases into the swimbladder with accompanying internal pressure.

Gee (1970) found that blacknose dace decreased internal pressure during buoyancy increase and increased internal pressure during buoyancy decrease. Extent of changes in internal gas pressure was greater in younger tadpole madtom (year 0 and 1) in both still and current than year 2. The considerable variation observed in internal pressures within and among age groups is probably the result of different rates at which fish adjust buoyancy by various means.

The increase in floatation pressure of black bullhead when denied access to the surface indicated these fish secreted gases to enlarge swimbladder volume. In comparison tadpole madtom showed no ability to secrete gas. This illustrates the importance of the pneumactic duct to buoyancy adjustment in tadpole madtom. Gulping air appears to be the major means of increasing swimbladder volume. This does not preclude the possibility that tadpole madtom can secrete gas, possibly very slowly.

In non-access, black bullhead were continually swimming about while tadpole madtom remained on the bottom relatively inactive. The inability of tadpole madtom to secrete that amount of gas to alter significantly their buoyancy in such circumstances might be due to this inactivity. Jacobs (1930), and Meesters and Nagel (1934) using yellow perch (Perca) and Copeland (1952) using the mummichog (Fundulus heteroclitus) (both physoclists) demonstrated that gas secretion is greatly inhibited if the fish does not swim about. More recently, McCutcheon (1962) showed that gas secretion was more active when the pinfish (Lagodon rhomboides) showed periodic swimming movements. Fänge (1966) states that it seems as if fishes secrete gas if they are "aware" that they are too heavy. Such an "awareness" could come about through motions of swimming. However, greater activity of black bullhead may simply be the result of a quicker rate of gas secretion rather than the cause of such an effect.

In conclusion, the ability to adjust the volume of the swimbladder is seen as an important adaptation of fishes living in streams and rivers where water currents change rapidly.

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APPENDIX I. Mean and range of floatation pressures measured on groups of eight fish each after water velocity changed from current to still water.

Hours in Still water	Floatation Pressure Mean	Range	Standard Deviation	95% confidence limits on mean
Year 0				
0	0.827	0.867-0.750	0.039	0.860-0.795
1	0.859	0.923-0.778	0.046	0.897-0.821
3	0.885	1.143-0.760	0.113	0.979-0.791
6	0.919	1.000-0.875	0.042	0.954-0.884
12	0.915	1.071-0.844	0.085	0.986-0.845
24	0.923	0.962-0.875	0.033	0.951-0.896
48	0.942	1.048-0.885	0.047	0.981-0.903
96	0.967	1.000-0.931	0.029	0.991-0.943
192	0.982	1.000-0.933	0.026	0.999-0.965
Year 1				
0	0.781	0.886-0.710	0.065	0.835-0.727
1	0.830	0.968-0.675	0.084	0.900-0.760
3	0.823	0.953-0.678	0.084	0.893-0.753
6	0.840	0.975-0.708	0.103	0.926-0.754
12	0.868	0.984-0.717	0.093	0.947-0.790
24	0.862	0.919-0.798	0.044	0.898-0.825
48	0.892	0.942-0.817	0.042	0.928-0.857
96	0.917	0.937-0.899	0.014	0.929-0.906
192	0.929	0.971-0.910	0.020	0.946-0.913
Year 2				
0	0.783	0.901-0.685	0.071	0.842-0.724
3	0.793	0.949-0.587	0.109	0.884-0.703
6	0.823	0.975-0.584	0.142	0.942-0.705
12	0.837	0.966-0.671	0.091	0.913-0.761
24	0.888	0.932-0.843	0.024	0.908-0.867
48	0.880	0.935-0.738	0.077	0.944-0.816
96	0.897	0.961-0.811	0.054	0.942-0.852
192	0.899	0.987-0.818	0.061	0.950-0.849

APPENDIX II. Mean and range of floatation pressures measured on groups of eight fish each after water velocity changed from still to current.

Hours in running-water	Floatation pressure Mean	Range	Standard Deviation	95% confidence limits on mean
Year 0				
0	1.045	1.167-1.000	0.067	1.100-0.989
1	0.979	1.091-0.889	0.077	1.043-0.915
3	0.958	1.143-0.875	0.083	1.027-0.889
6	0.938	1.063-0.875	0.071	0.998-0.879
12	0.902	1.000-0.806	0.056	0.948-0.856
24	0.880	0.938-0.765	0.051	0.922-0.837
48	0.828	0.875-0.774	0.035	0.857-0.799
96	0.821	0.885-0.750	0.041	0.855-0.787
192	0.809	0.857-0.727	0.047	0.848-0.770
Year 1				
0	0.945	1.000-0.904	0.028	0.969-0.922
1	0.936	0.966-0.875	0.030	0.961-0.911
3	0.913	1.022-0.786	0.077	0.977-0.848
6	0.884	1.000-0.727	0.095	0.963-0.805
12	0.883	1.000-0.801	0.084	0.953-0.812
24	0.876	0.957-0.710	0.077	0.941-0.812
48	0.880	0.955-0.770	0.060	0.930-0.830
96	0.840	0.967-0.712	0.083	0.909-0.771
192	0.796	0.897-0.685	0.047	0.848-0.729
Year 2				
0	0.896	0.964-0.872	0.033	0.924-0.868
3	0.871	0.914-0.810	0.033	0.898-0.843
6	0.865	0.919-0.823	0.026	0.887-0.843
12	0.869	0.925-0.798	0.051	0.912-0.827
24	0.846	0.949-0.720	0.077	0.911-0.782
48	0.838	0.984-0.706	0.096	0.918-0.758
96	0.811	1.000-0.638	0.130	0.919-0.702
192	0.771	0.836-0.653	0.064	0.825-0.718

APPENDIX III. Mean and range of internal pressures measured on groups of eight fish each after water velocity changed from current to still water.

Hours in Still water	Internal pressure Mean	Internal pressure Range	Standard Deviation	95% confidence limits on mean
Year 0				
0	1.205	1.333-1.077	0.088	1.278-1.132
1	1.220	1.286-1.118	0.060	1.270-1.170
3	1.213	1.357-1.103	0.089	1.287-1.139
6	1.176	1.278-1.095	0.051	1.218-1.133
12	1.139	1.240-1.071	0.062	1.190-1.087
24	1.151	1.222-1.074	0.056	1.198-1.105
48	1.135	1.200-1.087	0.032	1.161-1.109
96	1.145	1.222-1.087	0.045	1.182-1.107
192	1.143	1.214-1.083	0.052	1.187-1.100
Year 1				
0	1.125	1.171-1.043	0.040	1.158-1.091
1	1.129	1.183-1.094	0.028	1.152-1.105
3	1.120	1.167-1.097	0.024	1.142-1.098
6	1.141	1.183-1.093	0.030	1.168-1.114
12	1.161	1.288-1.071	0.065	1.215-1.107
24	1.141	1.193-1.093	0.032	1.167-1.114
48	1.124	1.207-1.034	0.057	1.171-1.077
96	1.148	1.175-1.117	0.020	1.165-1.131
192	1.125	1.188-1.075	0.039	1.157-1.093
Year 2				
0	1.124	1.156-1.070	0.026	1.146-1.102
3	1.129	1.170-1.113	0.017	1.145-1.113
6	1.110	1.144-1.063	0.022	1.131-1.089
12	1.124	1.160-1.054	0.033	1.152-1.097
24	1.126	1.148-1.077	0.022	1.147-1.106
48	1.094	1.129-1.060	0.022	1.115-1.074
96	1.108	1.147-1.056	0.028	1.132-1.085
192	1.124	1.170-1.072	0.037	1.155-1.092

APPENDIX IV. Mean and range of internal pressures measured on groups of eight fish each after water velocity changed from still water to current.

Hours in running water	Internal pressure Mean	Internal pressure Range	Standard Deviation	95% confidence limits on mean
Year 0				
0	1.190	1.286-1.143	0.045	1.227-1.152
1	1.187	1.250-1.100	0.065	1.241-1.133
3	1.271	1.357-1.188	0.049	1.311-1.230
6	1.217	1.286-1.111	0.057	1.264-1.169
12	1.259	1.353-1.192	0.054	1.306-1.214
24	1.256	1.333-1.200	0.046	1.294-1.217
48	1.174	1.214-1.143	0.026	1.196-1.152
96	1.205	1.267-1.150	0.046	1.243-1.167
192	1.213	1.267-1.154	0.045	1.250-1.176
Year 1				
0	1.107	1.172-1.025	0.045	1.145-1.070
1	1.138	1.193-1.069	0.037	1.169-1.107
3	1.123	1.163-1.100	0.024	1.143-1.103
6	1.140	1.214-1.075	0.048	1.180-1.100
12	1.156	1.229-1.078	0.057	1.203-1.109
24	1.183	1.265-1.077	0.057	1.230-1.136
48	1.207	1.273-1.130	0.045	1.244-1.169
96	1.141	1.190-1.119	0.022	1.160-1.123
192	1.135	1.189-1.098	0.035	1.164-1.106
Year 2				
0	1.096	1.126-1.071	0.020	1.114-1.078
3	1.119	1.187-1.049	0.040	1.152-1.085
6	1.094	1.140-1.033	0.039	1.130-1.058
12	1.108	1.148-1.066	0.020	1.124-1.091
24	1.126	1.200-1.087	0.035	1.154-1.097
48	1.121	1.150-1.099	0.020	1.137-1.104
96	1.115	1.214-1.065	0.049	1.156-1.074
192	1.121	1.183-1.080	0.028	1.145-1.098