Metabolism and Ram Gill Ventilation in Juvenile Paddlefish, *Polyodon spathula* (Chondrostei: Polyodontidae)

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Abstract

Metabolic rate, branchial morphology, and modes of gill ventilation were studied in young (2–10 g) North American paddlefish, Polyodon spathula, *with anatomical, behavioral, and physiological methods.* Polyodon *lacks the oral and opercular valves that are typical for fishes that rely on a buccal pump system to ventilate the gills, and the jaw opening system of* Polyodon *is poorly suited for regular pumping movements. Unrestrained, undisturbed juvenile paddlefishes swim constantly at a mean speed of 1.1–1.5 body lengths · s^{-1} (bls). The maximum speed sustainable for > 10 min is 1.6–1.8 bls. When forced to swim at slow speeds in flow tanks or water tunnels, ventilation of the gills by buccal pumping occurs at a frequency of 50–80 · min^{-1}. As swimming speed increases, buccal ventilation becomes intermittent and continuous ram ventilation occurs above 0.6–0.8 bls, which means that* Polyodon *is essentially an obligate ram ventilator under normal conditions. Oxygen consumption ($\dot{M}O_2$), carbon dioxide production ($\dot{M}CO_2$), and the gas exchange ratio (R) were determined as a function of inspired P_{O_2} during undisturbed swimming in still water at 25°C. Oxygen consumption, buccal pressure, and swimming performance were also measured at set swimming speeds in a flow tank and small water tunnel. Oxygen consumption at the preferred swimming speed of 1.25 bls was 6–7 μmol O_2 · g^{-1} · h^{-1}. Carbon dioxide production was 3–4 μmol CO_2 · g^{-1} · h^{-1}, yielding an* R *of 0.5–1.0. Paddlefishes are O_2 regulators in mild hypoxia (150 down to 90 mmHg) but die quickly at P_{O_2} < 90 mmHg. During steady swimming in normoxia, paddlefishes normally maintain 70%–80% of the maximum sustainable speed. This results in a normal minimum metabolic rate that is about twice that of the minimum (resting) rate of other acipensiform fishes. From a phylogenetic standpoint, other acipenseriforms also use ram ventilation, leading to the hypothesis that the evolutionary origin of a reliance on ram ventilation in* Polyodon *probably predates the origin of the filter feeding habit. Constant swimming may be metabolically expensive, but it would appear to allow some energy to be conserved by ram ventilation. This may*

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be particularly advantageous for species such as P. spathula *that combine filter feeding and ram ventilation.*

Introduction

The two major costs of gill ventilation are the energy loss due to resistance of the gills to water flow and the energy loss from cyclic acceleration and deceleration of water as it is pumped through the branchial chambers. The former will occur in both typical respiratory pumping and ram ventilation while the latter is completely eliminated during ram ventilation, in which the mouth is held open during swimming and the forward velocity of the fish generates water flow over the gills. Ram ventilation essentially transfers the work of respiration from the buccal and opercular muscles to the swimming muscles of the trunk (see Jones and Randall 1978; Roberts and Rowell 1988). The transition to ram ventilation somewhat reduces the profile drag caused by swimming at high velocities. Although the profile drag reduction is very species-dependent, in the bluefish and striped bass the transition to ram gill ventilation may allow as much as a 50% increase in swimming speed without an increase in metabolic rate (Freadman 1981).

Ram ventilation is common in large pelagic, predatory fishes (i.e., sharks, bluefish, striped bass, tuna), which swim frequently, if not constantly. Almost all our knowledge about the energetics of ram ventilation comes from studies of such pelagic species. However, ram gill ventilation also occurs in ram filter-feeding fishes such as anchovies and menhaden (Durbin et al. 1981; Lazzaro 1987; James and Probyn 1989), in which it is an obvious correlate of this feeding mode rather than simply a way to reduce drag during swimming (although this may also occur). From the perspective of energy acquisition, filter feeding is an energetically expensive mode of prey capture, requiring continual swimming movements instead of the sporadic brief movements of a sit-and-wait predator. The expense of continuous swimming for filter feeding could be partially offset by reduced metabolic costs for gill ventilation if filter feeding is coupled with ram ventilation.

To study the metabolic and respiratory consequences of filter feeding combined with ram ventilation in fishes, we examined ventilatory patterns and metabolism as a function of swimming speed in juveniles of the North American paddlefish, *Polyodon spathula*. *Polyodon* is the most derived genus in a small radiation of acipenseriform chondrostean fishes from North American and Asia. (Acipenseriformes is a group containing the sturgeons, Acipenseridae, and the paddlefishes, Polyodontidae; Grande and Bemis 1991.)

Like other acipenseriforms, paddlefishes have a jaw suspension that is highly modified from the plesiomorphic condition of actinopterygians (Patterson 1982) and that allows a great degree of kinesis in jaw movements. Unlike other fossil and living paddlefishes (*Paleopsephurus wilsoni, Crossopholis magnicaudatus,* and *Psephurus gladius*), *P. spathula* and the fossil species *Polyodon tuberculata* are morphologically specialized for filter feeding, as indicated by the presence of greatly elongated gill rakers in adults. There are other anatomical correlates of filter feeding in the genus *Polyodon,* including flattened and elongated gill arches and a secondary reduction in protrusibility of the upper jaw (Grande and Bemis 1991).

Filter feeding in juvenile and adult *P. spathula* occurs in bursts of variable duration, during which the lower jaw is strongly depressed and the gill arches and opercular flaps are broadly spread as the fish swims forward (Rosen and Hales 1980). Adult paddlefishes specialize on slow-swimming plankton such as cladocerans but occasionally prey on small fishes. In contrast to the filter feeding of juveniles and adults, larval paddlefishes "pluck" individual prey items from the water column (Michaletz et al. 1982; Russell 1986). Only at about 50 mm total length (TL) does rapid outgrowth of the gill rakers begin (W. Bemis and L. Grande, personal observations). From very soon after hatching, however, juvenile paddlefishes take up the habit of constant swimming, which persists throughout life.

Material and Methods

This study is one of several based on developmental series of paddlefishes obtained from the Missouri Department of Conservation and the Osage Catfisheries Company (Osage Beach, Mo.) from 1988 to 1990. Certain methods common to all of these studies are described elsewhere (Bemis and Grande 1992).

Animals

Fifty living paddlefishes were obtained in June 1989 and maintained in captivity in a square, filtered, aerated, and chilled freshwater holding tank (18°C; 100 × 100 × 30-cm water depth = 300 L in swimming tank, 550 L total system capacity) fitted with two glass panes for observations from the side and bottom. Filtration provided by the two Eheim 2017 cannister filters and a 250-L biological filter created a clockwise current in the tank at a velocity of 5.6 mm · s^{-1}. Fish were maintained in good health in this system for as long as 5 mo on a daily diet of brine shrimp supplemented with small

frozen prawns as the fish grew. Growth was rapid, although not as great as that observed for siblings reared on natural foods in outdoor ponds in Missouri. Individuals ranging in age from 14 to 17 wk, with body masses from 2 to 10 g, and TLs from 60–130 mm were used for the behavioral and physiological portions of this study. All fish studied here showed typical bursts of active filter feeding, defined by dropping the lower jaw, not by the degree of development of the gill rakers.

Morphology

Several types of preparations relevant to the analysis of respiration were studied.

Morphology of the Head and Gill Arches. Heads of several juvenile specimens fixed in 4% formalin were studied, dissected, drawn, and photographed with a Wild M5 stereomicroscope. Additional adult specimens were also examined. Cleared and double-stained specimens were available for study of the skeleton of the gill arches. The head of an additional 30-mm specimen was prepared as serial frontal sections through the low viscosity nitrocellulose (LVN) methods outlined by Thomas (1983) and Bemis (1984).

Vasculature of the Gills. Several specimens were used for studies of gill morphology and circulation. In five individuals anesthetized with MS-222, the heart was cannulated with fine polyethylene tubing and either yellow latex (Microfil) or Bateson's compound (Polysciences) was injected at estimated physiological pressures. The two specimens injected with Microfil were then fixed in 3% formalin, depigmented with hydrogen peroxide, macerated in trypsin solution (0.25 g trypsin in a buffer made with 30 mL saturated sodium borate and 70 mL distilled water), and dehydrated and cleared in glycerin for study of the major cranial vessels. The three specimens injected with Bateson's compound were allowed to cure for several hours and were then macerated overnight in concentrated (34%) potassium hydroxide. After the tissues had completely disintegrated, the corrosion preparations were washed in distilled water, dried, and mounted on stubs for study in a JEOL JSM-100 scanning electron microscope (courtesy of the Botany Department, University of Massachusetts).

Swimming Performance

Several different experiments were designed to assess swimming characteristics and performance and associated respiratory patterns and gas exchange. All swimming velocities are expressed in body lengths $\cdot$ s^{-1} (bls).

Unrestrained Specimens. Swimming speeds of undisturbed, unrestricted fish during voluntary swimming were calculated for specimens observed in the holding tank. An opaque, vertical partition was placed in the tank approximately 150 mm behind the front observation window. When undisturbed, fish swam continuously near the walls of the tank, passing through the "slot" created by the window and this partition. The time required for fish to swim along the linear path of the window (440 mm) was measured. The actual swimming velocity was then calculated by subtracting water current velocity (5.6 mm $\cdot$ s^{-1}) from apparent swimming velocity while the fish were swimming downstream.

Flow Tank. More detailed observations of swimming speed and associated ventilatory behaviors were made in a recirculating flow tank (fig. 1) based on the design described by Vogel and LaBarbera (1978). A speed control on the motor of the flow tank allowed us to control water flow precisely, and we calibrated flow speeds prior to tests by repeated timing and regression analysis of plumes of dye. The flow tank contained approximately 28 L of water held at room temperature (22°C). The water was aerated with an airstone. A restricted swimming chamber was constructed from screen, with dimensions 210 mm long by 130 mm deep by 55 mm wide (fig. 1). Water flow in this restricted chamber had a top velocity of 180 mm $\cdot$ s^{-1}. Larger specimens were unable to easily turn around in this chamber but were

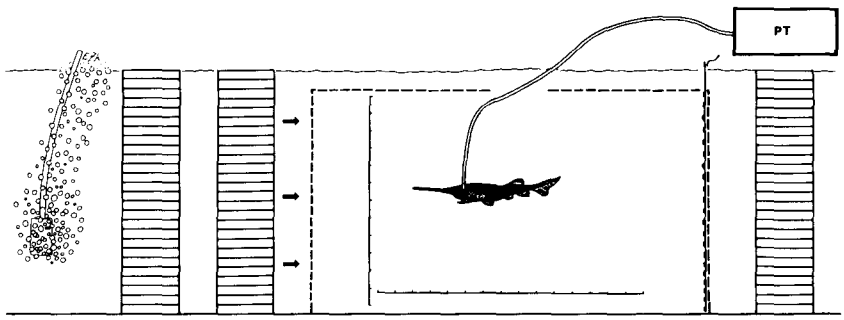

*Fig. 1. Diagram of the swimming chamber used for observations of gill ventilation. A fish with a polyethylene catheter inserted in the spiracle is shown in the swimming chamber. Two upstream and one downstream honeycomb flow laminizers are indicated outside the swimming chamber proper. The vertical and horizontal scales inside the tank are graduated in 10-mm units. The position of the downstream electrified grid is indicated by black bars, and the catheter is connected to a pressure transducer (*PT*).*

readily oriented to the flow. A grid with a weak electric current at the downstream end of the chamber forced the fish to continue swimming. The transparent sides of the swimming chamber allowed direct observations and videotape records to be made. Videotapes were made with a Panasonic NV 8950 motion analysis tape deck, a Xybion shuttered video camera with a zoom telephoto lens that allowed us to frame the entire swimming chamber within the field, and illumination provided by synchronized strobe lamps (Chadwick-Helmuth Corp).

In the first flow-tank experiment, videotape records of 10 individuals were made for fish swimming for 5 min at each of three water velocities: 0.5 bls, 1.0 bls, and 1.5 bls. Respiratory movements at each of the three speeds were studied during slow-speed replays of the tapes.

In the second flow-tank experiment, two individuals were anesthetized with MS-222 (1:10,000), and a 50-cm-long PE 50 water-filled catheter was implanted in the buccal cavity via the spiracle (see Burggren 1978). The catheter was attached to a Narco P-1000b pressure transducer. Buccal pressure signals were recorded on a Narco Mark IV chart recorder. After recovery from anesthesia, the fish were placed in the flow tank and put through the same swimming protocol used in the first experiment.

In a third series of observations designed to determine water flow patterns into the oral cavity, freshly killed specimens mounted on steel rods were placed in the middle of the cross section of the tank. A fine pipette was used to introduce a dye stream into the tank, and the pipette was moved to direct the dye stream into the mouth. These fish had a cross-sectional area of about 20 mm^2, which accounted for less than 0.5% of the total cross-sectional area of the swimming chamber.

Respirometry

Two different "closed" respirometer systems were used to determine O_2 consumption ($\dot{M}O_2$) and CO_2 production ($\dot{M}CO_2$). Values are expressed as mass-specific consumption in units of μmol gas · g^{-1} · h^{-1}.

Flask Respirometry. In the first system, designed to determine the metabolic effects of progressive hypoxia on $\dot{M}O_2$ and $\dot{M}CO_2$, individual fish approximately 80–90 mm in length were measured, weighed, and placed in 1,060–1,080 mL Erlenmyer flasks containing aerated water thermostated to 24°C. The fish were allowed 12 h to acclimate to the flasks, which were large enough to allow voluntary swimming at an apparently normal speed. At the end of the acclimation period, a rubber stopper with a single 1-mm-diameter port was inserted into each flask. The 1-mm-diameter sampling probe from

a respiratory mass spectrometer (VG Medical Instruments) was inserted through the port into the water. With this probe, water P_{O_2} and water P_{CO_2} were continuously measured over the course of about 3–4 h as the fish slowly depleted the O_2 from the water in the closed respirometer. After P_{O_2} in the water fell to approximately 80–90 mmHg (or if the animals suffered sudden-onset disequilibrium, see Results, below), the respirometer was opened and an airstone was carefully introduced into the water to restore quickly the P_{O_2} of the water to air-saturated levels, taking care to disturb the fish as little as possible. The flask was then stoppered once again, and $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ measurements were continued over a second period of shorter duration (1–2 h) to determine any posthypoxic effects on metabolism. The $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ were calculated in the standard fashion from the rate of decline of water P_{O_2} and P_{CO_2}, the volume of the flasks and the solubility of O_2 and CO_2 in water. The respiratory quotient, R, was determined as the ratio of $\dot{M}_{CO_2}$ to $\dot{M}_{O_2}$.

Water Tunnel Respirometry. The second respirometry system was essentially a miniaturized water tunnel (volume, 2 L) with a 100-mm-long, 25-mm^2-diameter swimming chamber equipped with front and back screens to keep fish inside. The remainder of the repirometer system was composed of 16-mm-diameter clear plastic tubing and a large Vortex Diatom filter (Inner-space Products) in which the filter bag had been removed and the filter bottle filled with glass marbles to reduce the total volume of the closed system. The filter bottle was placed in a container of temperature-controlled water (24°C) to limit water-temperature changes in the respirometer. The velocity of water recirculating through the swimming chamber was regulated by a speed control on the pump motor, and water velocity was calibrated by timing the passage of a bolus of injected dye as it passed through the empty swimming chamber. Fish used in these experiments had a body length of 70–90 mm. Their cross-sectional area at the shoulder girdle was approximately 80 mm^2 (the shoulder is the widest part of the body, with the trunk tapering sharply from that point). This area was less than 16% of the total cross-sectional area of the swimming chamber. Consequently, on the basis of standard hydrodynamic considerations, the presence of the fish was unlikely to have resulted in an overall increase in water velocity along the length of the swimming chamber. Fish swam normally within the tube provided that water velocity remained above 0.5 bls. Fish confined in the swimming chamber with no water flow (i.e., water velocity = 0 mm/s) showed immediate distress. Thus, for the initial 2-h acclimation period, during which water was maintained in an air-saturated condition, water velocity was maintained at 0.5 bls. The probe of the respiratory mass spectrometer was inserted

through a water-tight port into the water within the tunnel, and the rate of decline in water P_{O_2} and P_{CO_2} was recorded during each of three swimming regimes. Each fish within the respirometer was made to swim at velocities corresponding to 0.5, 1.0, and 1.5 bls for 15-min periods, with the water being returned to air saturation during a 10-min rest period (water velocity = 0.5 bls) between each run.

Statistical Analyses

Reduced major axis and least-squares regressions were fitted to data from the flask respirometry; repeated measures ANOVAs and paired comparisons tests were used to compare data from the water tunnel respirometry. All group means are presented as mean ± 1 SD. A fiducial level of 0.05 was used in all statistical analyses.

Results

Morphology of the Respiratory System

Basic features of the branchial circulation of *Polyodon* were described by Danforth (1912). *Polyodon* has holobranchs on both the cerato- and epibranchial portions of gill arches 1, 2, and 3 and a complete anterior hemibranch on the ceratobranchial portion of gill arch 4. On the posterior face of gill arch 4, however, there is only a partial hemibranch, associated with the ceratobranchial and most ventral portion of the epibranchial. Dorsal to this point, the gill slit between arches 4 and 5 is closed (see Danforth 1912, p. 422, for further discussion). There is also a pseudobranch, associated with the minute spiracle. These features are readily comparable to those reported for sturgeons by Burggren, Dunn, and Barnard (1979).

An isolated first gill arch of juvenile *Polyodon* is shown in figure 2*B*. The cartilaginous elements of the first gill arch are laterally flattened. The gill arches remain predominantly cartilaginous throughout life, and those small centers of ossification that do develop probably do not provide great additional mechanical support. At the point in ontogeny for specimens used in respiratory experiments, the gill rakers are only beginning to protrude from the arch. Clearly, well-developed gill rakers are unnecessary for effective filter feeding in juvenile *Polyodon*. Sanderson, Cech, and Patterson (1991) have shown that adult blackfish (*Orthodon microlepidotus*) do not use gill rakers directly for filter feeding, although the rakers are well developed as adults in this species and are used to guide water to the roof of the oral cavity, where food particles are retained. Also, in the *Polyodon* used for

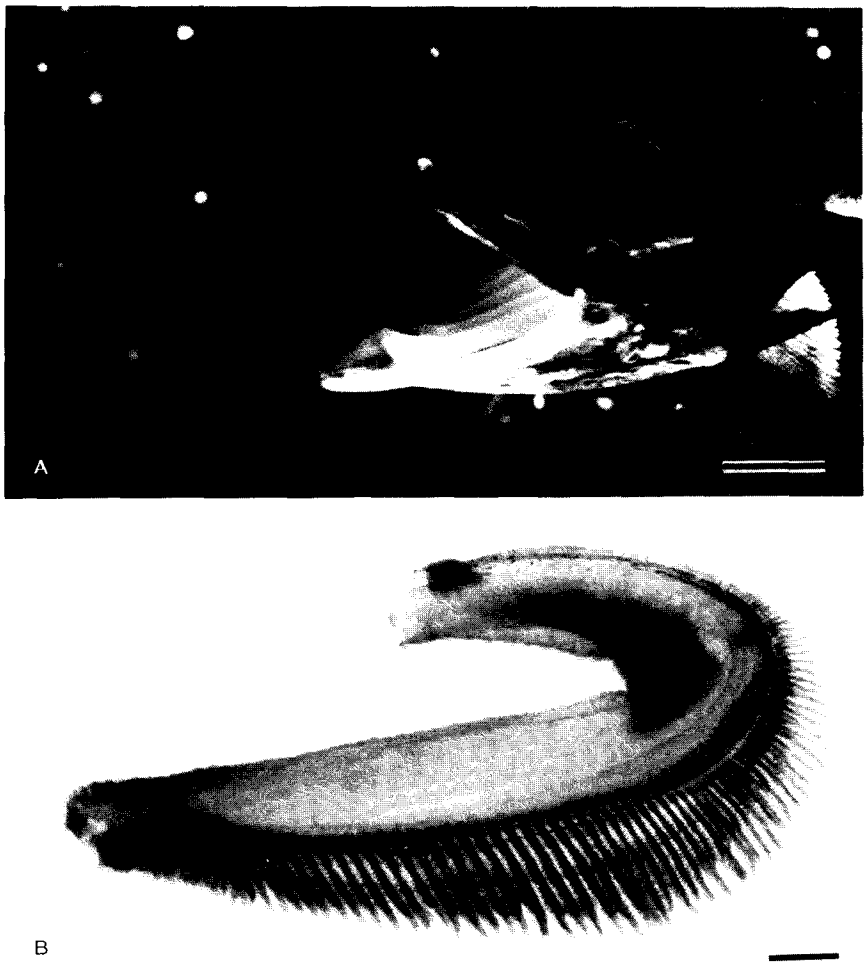

Fig. 2. A, *Photograph of filter-feeding paddlefish showing position of the gill arches and opercular flap. The white reflective spots are* Daphnia, *on which this fish is feeding. Total length of fish is 150 mm; scale = 10 mm.* B, *Photograph of isolated left gill arch. Preparation is from an individual comparable in size to the specimens used for physiological studies reported here. Total length of fish is 75 mm; scale = 1 mm.*

physiological experimentation, the gill filaments are best developed along the posterior two-thirds of the ceratohyal (fig. 2*A*). In older animals, gill filaments develop on all parts of the gill arch, but even in very large adults the filaments are longest in the posteroventral portion of the gill arches.

Histologically, the gills of *Polyodon* are similar to those of other basal actinopterygians. A frontal section through portions of four gill arches is

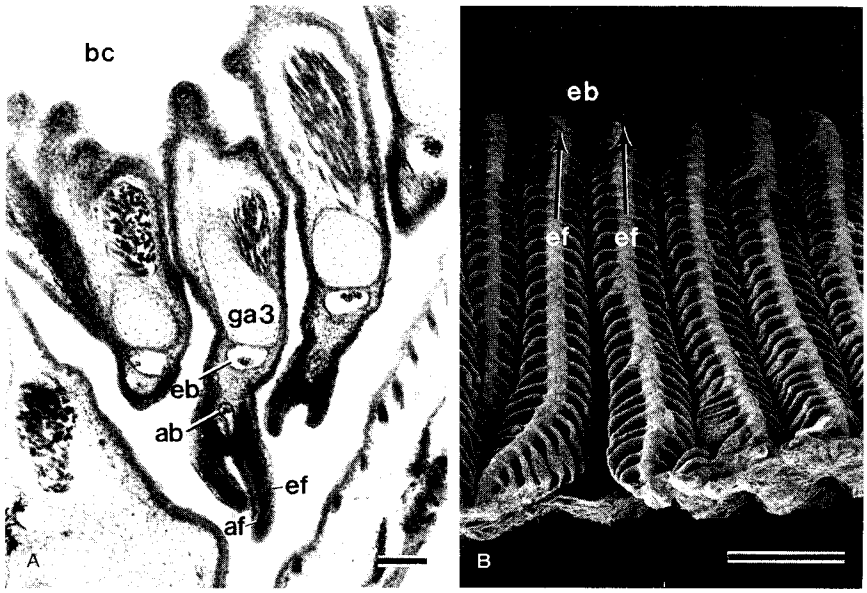

Fig. 3. A, *Frontal section through gill region of a paddlefish. Anterior to top of page. Vasculature of the typical third gill arch (*ga3*) is labeled:* ab, *afferent branchial artery;* af, *afferent branchial vessel;* bc, *buccal cavity;* eb, *efferent branchial artery;* ef, *efferent branchial vessel;* op, *opercular flap. Total length of fish is 30 mm; scale bar = 100 μm.* B, *Scanning electron micrograph of corrosion cast of gill vasculature. Preparation shows a portion of the gill filaments along the ceratohyal as in pt.* A. *The secondary lamellae are apparent as a series of leaflets connecting into the efferent filament vessels (*ef*), which in turn lead to the efferent branchial artery (*eb*). Total length of fish is 60 mm; scale bar = 500 μm.*

shown in figure 3*A*. The buccal cavity (*bc*) is at the upper left, and the opercular flap (*op*) is at the lower right. Details of the vasculature of the third typical gill arch (*ga*3) are labeled. The large efferent branchial artery (*eb*) lies adjacent to the cartilage of the arch. In larger specimens, a distinct groove for the vessels develops along the posterior margin of the arch. From the posterior of the arch, two gill filaments are visible extending into the opercular cavity. The afferent branchial artery (*ab*) is shown giving rise to an afferent filament (*af*) vessel, which extends along the posterior margin of the right gill filament. The *af* vessel in turn connects to the efferent filament (*ef*) vessel by a series of secondary lamellae, just beyond the resolution of this micrograph. Figure 3*A* shows that very young paddlefishes (30 mm TL, in this case) lack a gill septum linking the filaments within a holobranch. However, in the larger individuals (>60 mm) studied physiologically, the septum is present, as can be seen in the SEM view of a corrosion

cast of ceratobranchial filaments in figure 3*B*. A well-developed septum appears to be typical (i.e., plesiomorphic) for acipenseriforms (see Burggren et al. 1979 and Laurent 1984 for more information on structure of gills of *Acipenser*). Figure 3*B* also shows the secondary lamellae and the efferent vessels of *Polyodon,* which are generally similar to those of other acipenseriforms. Finally, a series of cartilages supports the gill filaments in older individuals (see, e.g., Danforth 1912, fig. 8). These filamental cartilages are beginning to develop in individuals of the sizes used for physiological study.

The fleshy gill cover contains a sheet of contrictor musculature (Danforth 1913) and numerous ampullary organs and is supported by the subopercular and branchiostegal bones (Grande and Bemis 1991). Flaring of the gill cover is caused by protraction of the hyomandibular bone, an event that is also linked with jaw opening in *Polyodon* (Bemis 1987). The trailing posterior tip of the gill cover lengthens greatly in animals older than the ones studied here. The posterior border of the gill cover is uniformly thick and is unsuited to function as a membranous opercular flap valve as in other fishes. In fact, in specimens of the size range we studied, the trailing opercular flap is incapable of even covering the dorsal portion of the opercular cavity. The right and left gill covers merge on the ventral surface of the head, forming a continuous "chute" ventral to the anterior portion of the pectoral girdle and isthmus region. Thus, water can flow out of the opercular chamber dorsally, caudally, or ventrally. The fact that gill filaments are best developed on the ventral portions of the gill arches suggests that most of the flow will occur in the posteroventral direction.

Observations of Ram Ventilation and Water Flow

Paddlefishes swim constantly from soon after hatching. During normal, steady swimming as observed in the main tank, the mouth was always held slightly agape so that water flows continuously through the oral cavity, over the gill surfaces, and out behind the opercular flap. Relevant features of the respiratory system can be seen easily in individuals in which the mouth is fully opened for active filter feeding, as in figure 3*A*. This figure demonstrates that there is no oral valve in *Polyodon,* as there typically is in those species of fishes with well-developed buccal pumping systems. Primarily because of the skeletal structure of the gill arches as opposed to any active abduction, there is always a gap between adjacent gill arches. This is particularly apparent in figure 3*A*. Also, whether engaged in steady swimming movements or in filter feeding, the entire set of gill arches is typically held so that they are elevated above the floor of the buccal cavity, exposing the gill filaments as nearly as possible to the direct flow of water through the oral cavity (e.g.,

fig. 3*A*, where the left ceratohyal and elements of the basibranchial series are visible in lateral view).

Figure 4 shows a lateral view of the head of a freshly killed specimen mounted in the flow tank for study of flow into the oral cavity. This photograph is one of a series in which the position of the pipette generating the dye stream was moved vertically to trace patterns of flow along the ventral surface of the paddle. In this case, the dye stream intersected the elevated series of gill arches and was deflected into the oral cavity. Even though the flow regime used to produce this photograph was far slower than the typical speed recorded for freely swimming fish, it suggests that the raised position of the gill arches may help to play a role in directing flow into the oral cavity.

Swimming Speed and Ventilation Mode Transition

The habit of steady forward swimming in *Polyodon* is only interrupted for fractions of a second to allow rapid turning movements that produce a new course of direction. Voluntary swimming speed, measured in 15 undisturbed fish (mean fork length = 76 ± 19 mm), was 1.25 bls.

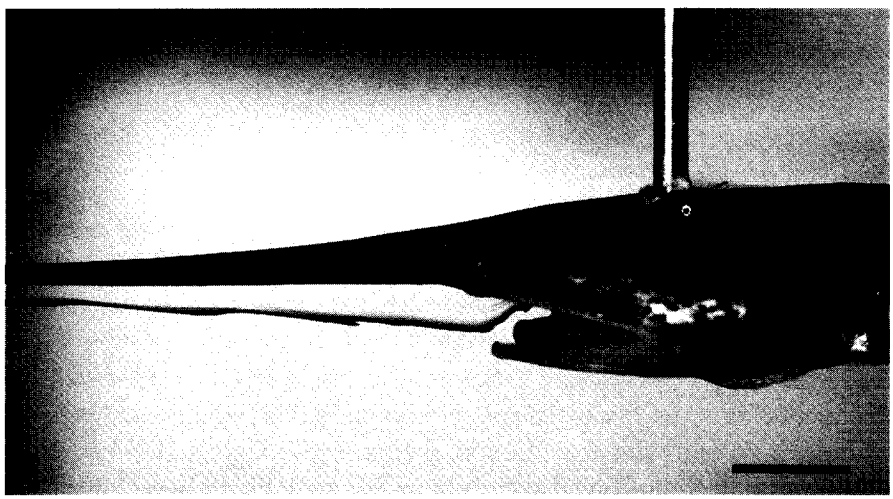

Fig. 4. Photograph of dye stream intersecting the basibranchial series. This freshly killed specimen was attached to a steel rod and inserted into the flow tank as shown. This picture was taken at a low-speed flow (ca. 0.25 bls) and is included primarily to show how water flow might be directed into the oral cavity by the elevated anterior portion of the gill arches. Scale = 10 mm.

More detailed observations of swimming speed and ventilatory behavior were made by videotaping fish swimming in the flow tank at speeds ranging from 0.5 to 1.5 bls. At all swimming speeds juvenile *Polyodon* held the blade of the paddle closely parallel to the flow. At the highest speed (1.5 bls), even a brief upward or downward misorientation of the paddle was sufficient to sweep the fish to the opposite end of the tank. As we observed in the holding tank, individuals that were steadily swimming in the flow tank at speeds between 1–1.5 bls also held the mouth slightly agape with the gill arches in the elevated position described above. When complete closing of the mouth occurred in this speed range, it was an irregular and brief occurrence. Finally, the tip of the opercular flap was always slightly separated from the trunk during steady swimming, although not as greatly abducted as in active filter feeding.

Tracings of a video of a fish swimming in the flow tank at 0.5 bls are shown in figure 5. These diagrams indicate that regular buccal pumping occurs when fish are forced to swim at this slow speed. The basic phases of cyclic buccal pumping typical for other fishes can be identified. In the sequence shown, the prominent posteroventral bulge of the gill cover in figure 5*A* indicates expulsion of water from beneath the gill cover. In figure

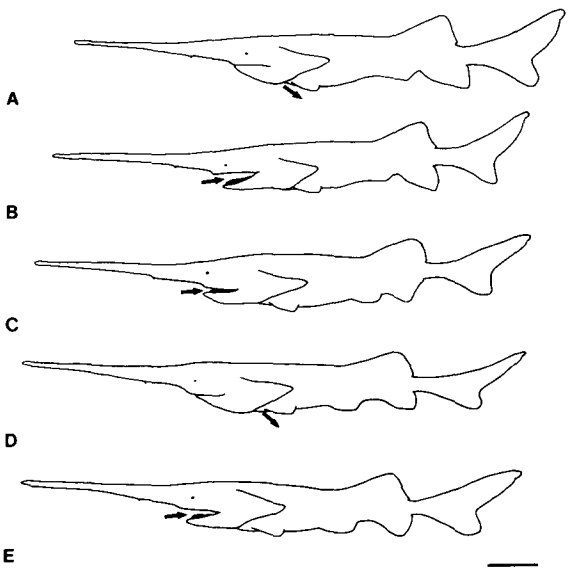

Fig. 5. Representative buccal pumping movements for a specimen at 0.5 bls over a 2-s period, traced from videotapes. These diagrams document that the sequence of actions during buccal pumping is generally comparable to that seen in other fishes that rely on buccal pumping. Arrows indicate direction of water flow. Scale = 10 mm.

5*B*, the mouth is open, and water is drawn into the buccal cavity. Insofar as its morphology allows, the gill cover is being sucked onto the side of the head to provide a crude opercular flap valve. In figure 5*C*, mouth closing is underway, and water is accumulating in the opercular chamber after having passed over the gill filaments. Figure 5*D* shows expulsion of water from the opercular chamber, to begin the cycle again.

Direct observation and videotape analysis revealed that the pattern of gill ventilation was correlated with swimming speed. At slow speeds (0.5 bls) buccal pumping to ventilate the gills was continuous while at higher swimming speeds the regular pumping movements decreased and then ceased altogether. This is most easily shown by the results of the second flow-tank experiment (fig. 6), in which water pressure in the oral cavity was measured by means of a catheter in the spiracle (fig. 1). At swimming speeds below 0.5 bls, buccal ventilation of the gills occurred at a frequency of 50–80 cycles · min^{-1} (fig. 6). However, the effectiveness of such pumping move-

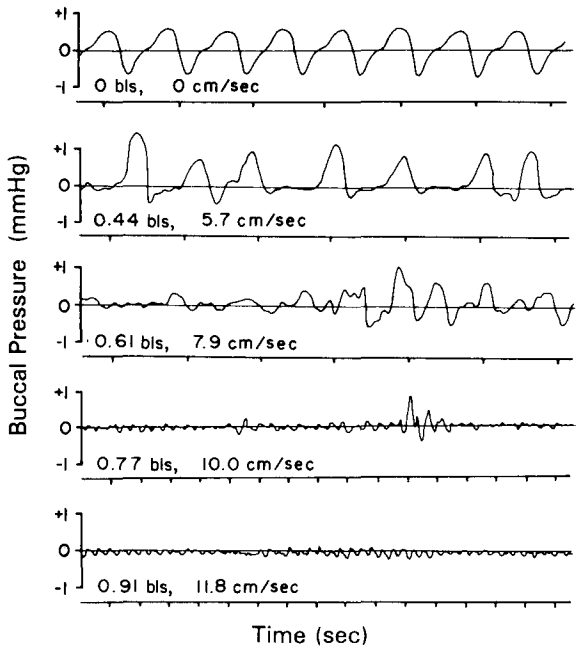

Fig. 6. Gill ventilation patterns as a function of swimming speed in a 7.11-g (13.0 mm fork length) Polyodon *swimming freely in a flow tank at 24° C. Buccal pressures were recorded continuously during swimming bouts at each of five water velocities (expressed in both relative and absolute terms). Note that the time scale differs in the two lowest panels. Small oscillations in pressure in the buccal cavity reflect trunk and tail movements associated with swimming.*

ments in ventilating the gills is uncertain, for paddlefish prevented from swimming showed extreme distress. Swimming speeds of 0.6–0.8 bls represent a transition speed, in which buccal ventilation becomes intermittent and periods of ram ventilation with no buccal movements begin to occur. Above a swimming speed of 0.8 bls, ram ventilation was continuous and buccal pumping ceased in all fish observed.

Fish in the flow tank showed a maximum sustainable speed (more than 10 min) of about 1.6–1.8 bls. Thus, voluntary swimming speed is about 70%–80% of maximum swimming in *Polyodon*.

Oxygen Consumption and Swimming Speed

The $\dot{M}O_2$ as a function of swimming speed was measured in five *Polyodon* (mean BL = 2.47 ± 0.22; mean fork length = 76 ± 19 mm); $\dot{M}O_2$ increased significantly ($P < 0.03$, df = 9, for each paired comparison) with swimming speed (fig. 7). At 1.5 bls, the fastest speed at which fish would swim in the apparatus, $\dot{M}O_2$ at 7.77 μmol $O_2 \cdot g^{-1} \cdot h^{-1}$ was more than double

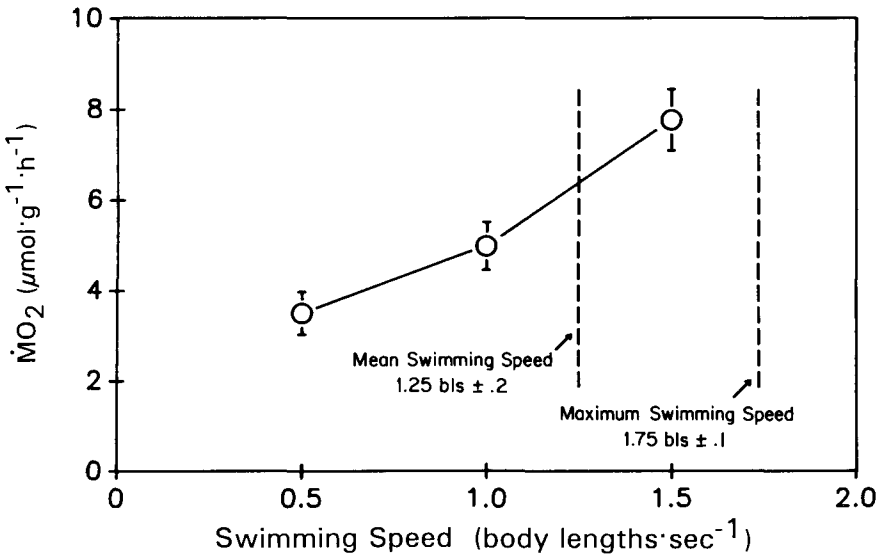

Fig. 7. Relationship between swimming speed and $\dot{M}O_2$ *(μmol* $O_2 \cdot g^{-1} \cdot h^{-1}$*) in* N = 5 *juvenile* Polyodon. *The vertical dashed lines indicate the mean swimming speed (measured in the large holding tank) and the maximum swimming speed (measured in the flow tank). Range bars indicate ± 1 SD. The relationship between swimming speed and* $\dot{M}O_2$ *is significant* (P < *0.03) on the basis of sequential paired-comparisons tests. Average body mass = 2.47 + 0.22 g; average fork length = 76 ± 19 mm.*

the 3.5 μmol $O_2 \cdot g^{-1} \cdot h^{-1}$ measured at 0.5 bls, the lowest speed at which fish swam constantly. These data allow estimation of the range of $\dot{M}O_2$ that would be associated with the typical range of swimming speed exhibited voluntarily by undisturbed individuals. At the mean swimming speed of 1.25 bls, $\dot{M}O_2$ would be approximately 6.4 μmol $O_2 \cdot g^{-1} \cdot h^{-1}$. Extrapolating $\dot{M}O_2$ at 1.5 bls to 1.75 bls, $\dot{M}O_2$ at the maximum swimming speed observed in the flow tank would be about 9 μmol $O_2 \cdot g^{-1} \cdot h^{-1}$. Thus, $\dot{M}O_2$ at the mean speed at which *Polyodon* constantly swim under undisturbed conditions is at least 70% of the maximum $\dot{M}O_2$ at maximum swimming speed.

Metabolism during Hypoxic Exposure and Recovery

Respirometry was performed on 10 freely swimming paddlefishes (average body mass = 2.02 ± 0.33 g) within glass flask respirometers. The $\dot{M}O_2$, $\dot{M}CO_2$, and R were measured at 25°C as a function of inspired water P_{O_2} (fig. 8). The value of $\dot{M}O_2$, approximately 8 μmol $\cdot g^{-1} \cdot h^{-1}$ at a P_{O_2} of 150 mmHg, did not change significantly with a decrease in P_{O_2} from 150 mmHg to slightly below 90 mmHg ($P > 0.5$ that the slope of the line describing the relationship between P_{O_2} and $\dot{M}O_2$ is not significantly different from zero). Thus, at mild levels of hypoxia *Polyodon* is an O_2 regulator. It is interesting, however, that the difference in degree of hypoxia between that which allowed maintenance of $\dot{M}O_2$ and that which resulted in apparent failure of gas exchange was quite small. Even an actively swimming fish showing steady levels of $\dot{M}O_2$ during progressive mild hypoxia would suddenly stop swimming and appear moribund, with exaggerated buccal pumping movements, with a further decrease in P_{O_2} of only 5–10 mmHg. When returned immediately to air-saturated conditions, six of 10 fish quickly recovered, but four fish died (the last recorded P_{O_2} levels before death were 99, 80, 81, and 51 mmHg). In the six surviving fish, $\dot{M}O_2$ during an approximately 1-h recovery period after hypoxic exposure was not significantly different from the $\dot{M}O_2$ values before or during hypoxic exposure.

The value of $\dot{M}CO_2$, approximately 4 μmol $\cdot g^{-1} \cdot h^{-1}$ at a P_{O_2} of 150 mmHg, similarly showed no significant change ($P > 0.5$) with decreasing inspired P_{O_2} (fig. 8). As with $\dot{M}O_2$, values of $\dot{M}CO_2$ shortly after return to normoxia were not significantly different from values before or during hypoxic exposure. The average value of R (determined from the regression through the individual R values over an inspired P_{O_2} range from 150 down to 60) was between 0.6 and 1.0.

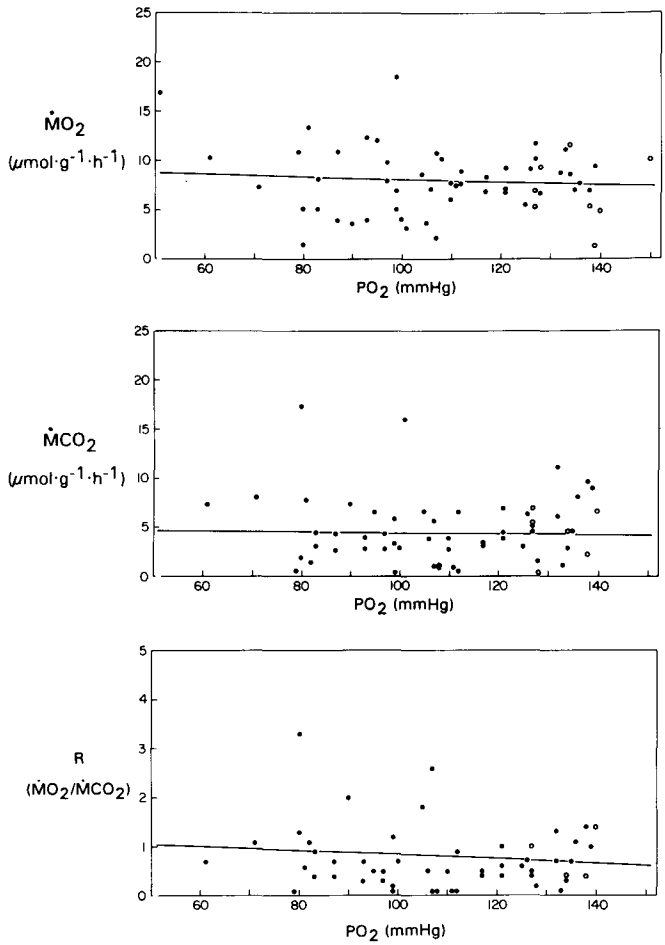

Fig. 8. A, $\dot{M}_{O_2}$ *as a function of ambient* P_{O_2} *in 10* Polyodon *in closed bottle respirometers. For* N = *51 specimens in an environment with decreasing* P_{O_2} *levels,* $r^2 = -0.09$ *(NS).* B, $\dot{M}_{CO_2}$ *as a function of ambient* P_{O_2} in *10* Polyodon *in closed bottle respirometers. For* N = *50 specimens in an environment with decreasing* P_{O_2} *levels,* $r^2 = -0.002$ *(NS).* C, R *as a function of ambient* P_{O_2} *in 10* Polyodon *in closed bottle respirometers. For* N = *50 specimens in an environment with decreasing* P_{O_2} *levels,* $r^2 = -0.14$ *(NS). Open circles are for six specimens returned to air-saturated water; see text for further explanation.*

Discussion

Rationale for Studying Juvenile Polyodon

Although adult specimens of *Polyodon* may achieve very large sizes (greater than 50 kg), our study of the physiology and anatomy of the respiratory

system in *Polyodon* focuses on young individuals. This is important for two reasons. First, young paddlefishes are more practical for laboratory work. Second, and more important, immature fishes are often neglected in physiological studies (although see Webb and Weihs 1986; Fuiman and Webb 1988). The bias toward studies of adults is unfortunate, especially since larval and juvenile fishes may show very different responses to environmental variables such as temperature and oxygen availability when compared with adults (Rombough 1988). Certainly, the morphology and physiology of a species is as likely to be shaped by selection acting on younger developmental stages as by selection on adults. No single stage can be expected to provide a "snapshot" of the overall physiological capacity of a species (see Burggren 1991*b*).

Swimming Speed and Ventilatory Behavior

The juvenile specimens of *Polyodon* examined in this study had developed to the point of employing filter feeding. But irrespective of the presence of food in the water, they swam constantly at a mean speed of about 1.25 bls. Constant swimming (or positioning in a constant water stream) is normal in fishes such as bluefish, striped bass, tuna, mackerel, remoras, sharks, and shark suckers (see Steffensen 1985 and Roberts and Rowell 1988, for earlier literature). Many pelagic fishes exhibit varying degrees of ram gill ventilation, in which the work of gill ventilation is essentially transferred from the branchial muscles to the swimming muscles of the trunk (Jones and Randall 1978; Steffensen 1985; Roberts and Rowell 1988). Ram ventilation functions most effectively at high swimming speeds, when the hydrostatic pressure gradient from the mouth to the opercular cavity is largest. At lower swimming speeds, gill ventilation is achieved by branchial pumping.

In fishes such as the bluefish *Pomatomus saltatrix,* striped bass *Morone saxatilis,* and rainbow trout *Oncorhynchus mykiss* (Roberts 1975; Freadman 1981; Steffensen and Lomholt 1983), a well-defined transition swimming speed can be identified, at which point ram ventilation supplants gill ventilation by buccal pump. A similar transition from branchial pumping in stationary fish or at low swimming speeds to strictly ram ventilation at higher swimming speeds is evident in *Polyodon,* occurring at about 0.6–0.8 bls in the specimens studied. It is noteworthy that not only are the juvenile *Polyodon* studied here the smallest fish in which ram ventilation has been documented but also the speed at which ram ventilation occurs is far lower than that predicted from interspecific studies on a variety of other adult fishes that use ram ventilation (fig. 9). Jones and Randall (1978) suggest that small fish would never be able to swim fast enough to generate a water

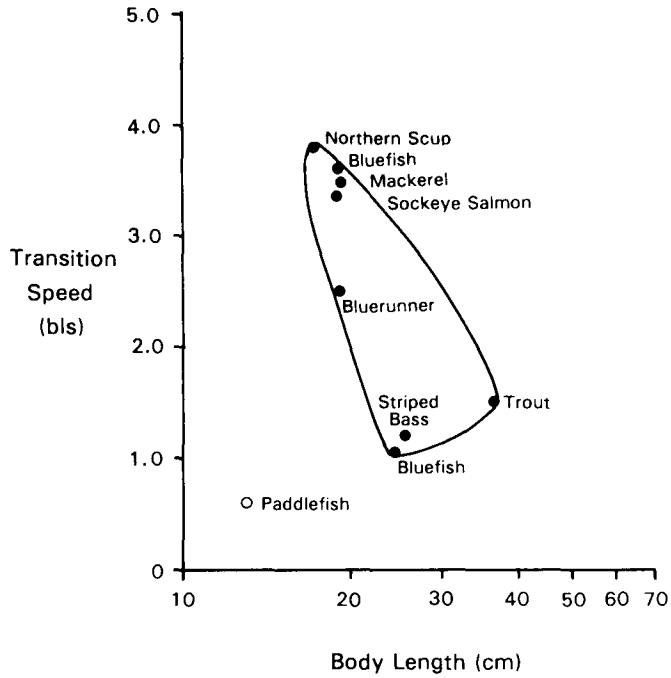

Fig. 9. Relationship between BL and the swimming velocity at which the transition is made from buccal gill ventilation to ram gill ventilation in marine and freshwater fishes. Data are obtained from Roberts (1975), Freadman (1981), and Steffensen and Lomholt (1983) and are encompassed by a line drawn by eye.

pressure at the mouth high enough to provide adequate ram ventilation. While their analysis may be widely applicable to normal fusiform fish, *Polyodon* is exceptional in that the huge gape of the mouth (fig. 2*A*) will no doubt present a lower resistance to water flow into the oral chamber. Of course, the gills themselves present the major resistance component during ram ventilation in any fish, and the lateral flattening of the gill arches in *Polyodon* reduces resistance to flow from the buccal to opercular chambers during either filter feeding or ram ventilation. In any event, highly effective ram ventilation occurs in *Polyodon,* and indeed buccal gill ventilation was only observed when the ability of juvenile fish was experimentally impaired by confinement in slowly moving or still water.

Swimming Speed and Metabolic Rate

The preferred swimming speed of *Polyodon* is about 70%–80% of the maximum sustainable speed observed in the flow tank. These data correlate

well with the fact that $\dot{M}O_2$ at mean swimming speed in undisturbed fish was about 70% of maximum $\dot{M}O_2$ measured at the fastest sustainable swimming speed. It is difficult to make meaningful comparisons of metabolic rate with most other fishes, especially because most data are obtained under conditions of "rest" (i.e., minimal locomotor activity) rather than activity. The only time juvenile *Polyodon* are inactive is when physically restrained or in respiratory distress. Another potentially complicating factor is that differences in metabolic rate between species may be due to phylogenetic differences—that is, the metabolic rate of *Polyodon* may be different from a trout, for example, because of inherent differences between acipenseriforms and salmonids rather than because of differences in feeding habit. Thus, comparisons of physiological performance are best made between closely related species (Huey 1987; Burggren and Bemis 1990; Burggren 1991).

Unfortunately, there are very few data on swimming energetics in acipenseriforms. Juvenile white sturgeons (*Acipenser transmontanus*), swimming at their maximum sustainable speed of about 1.25 bls, have an $\dot{M}O_2$ at 22°C (calculated from data at 15°C with a Q_{10} of 2, body mass of 0.8–1.1 kg) of about 3.4 μmol $O_2 \cdot g^{-1} \cdot h^{-1}$ (Burggren 1978). Paddlefishes, swimming at only 85% of their maximum sustainable speed at 22°C, have an $\dot{M}O_2$ of 8 μmol $O_2 \cdot g^{-1} \cdot h^{-1}$ (fig. 7). For comparative purposes, highly active swimming fishes such as skipjack and albacore tuna have a metabolic rate at a normal cruising speed of 16–21 μmol $O_2 \cdot g^{-1} \cdot h^{-1}$ (Stevens 1972; Graham and Laurs 1982), which is about twice that of paddlefishes. To place these data in context, none of the pelagic marine fishes are as small as the paddlefish studied here, but neither do they routinely cruise at 75% of their maximum sustainable swimming speed.

Although swimming efficiency varies greatly among fishes, about 70%–80% of total $\dot{M}O_2$ is required for locomotion when juvenile (2–10 g) sockeye salmon (*Oncorhynchus nerka*) swim at 75% of their maximum sustainable speed (Brett 1965). These data are calculated from the factoral increase of $\dot{M}O_2$ during swimming over that measured in stationary fish. Similar calculations are not really possible for *Polyodon,* which is an obligate swimmer and becomes highly distressed when prevented from swimming. Nonetheless, by swimming at 75% of their maximum sustainable speed, juvenile *Polyodon* are clearly expending considerable amounts of their total energy budget on locomotion. In return, however, they simultaneously achieve gill ventilation, which would otherwise require the expenditure of considerable additional metabolic energy by the muscles powering buccal pumping. Nor does *Polyodon* need to expend any additional energy on locomotion for

foraging, since they can filter feed even as they swim to ram ventilate their gills.

Metabolism during Hypoxic Exposure and Recovery

Polyodon is an O_2 regulator from an inspired P_{O_2} of 150 down to about 90 mmHg. Almost all other fish that have been examined similarly regulate $\dot{M}_{O_2}$ to some critical P_{O_2}, below which $\dot{M}_{O_2}$ falls sharply (for discussion see Burggren and Roberts 1991). *Polyodon* is unusual, however, in that the critical P_{O_2} is also very close to the lethal P_{O_2}, since every paddlefish examined in closed respirometers went from a condition of active, normal appearing swimming to one of complete loss of equilibrium with a further decline in P_{O_2} of only 5–10 mmHg. In the six (of 10) fish that survived following immediate return to a P_{O_2} of 150 mmHg, none showed any evidence of a payback of an O_2 debt in the next hour, as would be evident by elevated $\dot{M}_{O_2}$ in the recovery period. This suggests that *Polyodon* is a highly aerobic fish with limited capability for anaerobic metabolism. In this respect it is interesting to note that the white sturgeon *A. transmontanus,* the closest relative of *Polyodon* for which similar experiments have been performed, also shows little or no O_2 debt repayment after hypoxic exposure (Burggren and Randall 1978). Unlike *Polyodon,* however, *Acipenser* is an O_2 conformer, reducing $\dot{M}_{O_2}$ with virtually the first decline in P_{O_2} below air saturation.

The failure of juvenile *Polyodon* to cope with moderate hypoxic exposure would appear to relate to the fact that the paddlefish must swim continually, and at relatively high speeds, to ram ventilate its gills. As inspired O_2 falls, increased rates of gill ventilation (the response normally shown by fish exposed to hypoxia; see Burggren and Roberts 1991) can only be achieved in *Polyodon* by increasing swimming speed. Since swimming speed is already close to maximum when air saturation is high, there is little latitude for increasing ventilation. Moreover, the increased speed of swimming itself consumes more O_2. Certainly, *Polyodon* can increase the rate of buccal pumping movements, but the fact that paddlefish not permitted to swim become highly distressed and even lose equilibrium suggests that these movements may be inadequate to maintain sufficient gas exchange. Thus, we would predict that juvenile *Polyodon* require relatively well-oxygenated water. As body mass increases, $\dot{M}_{O_2}$ generally decreases in fish and other organisms. Consequently, large adult *Polyodon* may not be as restricted by low environmental P_{O_2} as are juveniles. These predictions are in accord with at least some points in the general life history of paddlefishes: although the adults tend to be fishes of big rivers, they spawn far upstream on gravel

bars, which is one of the reasons why early stages of *Polyodon* were so late in being discovered (Purkett 1961).

Evolution of Ram Ventilation and Filter Feeding in Polyodon

Several anatomical features of the head of *Polyodon* may prove to be specializations related to ram ventilation. Perhaps the best example of this concerns the virtual absence of well-developed oral and opercular valves. Buccal and opercular valves are also absent in the other living polyodontid, the Chinese paddlefish *Psephurus gladius.* These valves are present in such outgroup forms as *Polypterus* (Lauder 1980) and are quite likely plesiomorphic for actinopterygians so that we regard their absence in polyodontids as a derived condition. These features warrant a broader phylogenetic survey among actinopterygians.

Another point concerns the size and function of the spiracle. The spiracle, although well developed in *Polypterus,* appears to play only a minor role in respiration (Brainerd, Liem, and Samper 1989). Sturgeons of the subfamily Acipenserinae also have large spiracles, and in these fish the spiracle has a demonstrated respiratory function (e.g., *A. transmontanus;* Burggren 1978). Although scaphirhynchine sturgeons lack the spiracle as adults, this is clearly a derived character based on recent ontogenetic information (Findeis 1990). Both living genera of paddlefishes (*Psephurus* and *Polyodon*) have minute spiracles; thus, it is probable that spiracle reduction is a derived character at some level within Polyodontidae. The spiracle is an insignificant site for either intake or outflow of water in Polyodontids. Thus, water taken into the oral cavity has only one exit over the gill epithelium.

In the context of a recent phylogenetic study of polyodontids (Grande and Bemis 1991, p. 100), it is interesting to note that filter feeding is a derived feature within this clade: *Polyodon* is the most derived genus in Polyodontidae and is the only one to employ filter feeding (the other fossil and Recent genera are piscivorous). Also, many of the forms outgroup to *Polyodon,* including *Psephurus* as well as some sturgeons, swim more or less continuously, and use ram ventilation. These points suggest two things. First, the evolution of ram ventilation in acipenseriforms almost certainly preceded the evolution of filter feeding in *Polyodon.* Second, ram ventilation in plesiomorphic acipenseriforms would seem to provide an ideal "preadaptation" for the subsequent origin of filter feeding in *Polyodon.* Although it is of course impossible to test such ideas of "preadaptation," evidence supporting this idea might be found by making comparable studies of filter feeding and ram ventilation in other clades of fishes.

Summary

Juvenile paddlefishes are highly aerobic and rely extensively on ram ventilation. Many points in their anatomy and physiology suggest that they are specialized for this respiratory mode. Although ram ventilation requires great expenditure of energy, the combination of ram ventilation and filter feeding is predicted to conserve energy that would otherwise have been needed for buccal pumping and foraging. To aid in understanding the possible link between ram ventilation and filter feeding, it will be important for future studies to examine ram ventilation in other filter-feeding fishes.

Acknowledgments

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