Fish humps in two Colorado River fishes: a morphological response to cyprinid predation?

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Synopsis

Extant fishes endemic to the upper Colorado River of the American southwest include only cyprinids and catostomids. A curious attribute in species of both groups is the presence of a large nuchal hump. Largest cyprinid humps occur in humpback chub, *Gila cypha*, and largest catostomid humps occur in razorback sucker, *Xyrauchen texanus*. Several authors have suggested the humps confer a hydrodynamic advantage to life in fast flow, but this premise has not been confirmed with experimental work. To test the role of humps in Colorado River fishes, we subjected whole-body casts of preserved specimens with humps and with humps removed to controlled flows in an experimental tank. These tests confirmed that humps increased drag coefficients for *X. texanus* and *G. cypha* with no additional lift component. High energetic costs of locomotion and position-holding with a large hump, and the additional metabolic expense of forming large humps, suggest that the humps are not relict structures. Instead, we argue that these large humps represent convergent evolution prompted by predation from a cyprinid piscivore. Colorado pikeminnow, *Ptychocheilus lucius*, top piscivore in the Colorado River system, is the only native fish capable of consuming large *X. texanus* and *G. cypha*, and it also is sympatric with them. However, lack of jaw teeth and a relatively small jaw gape limit the maximum prey size that *P. lucius* can consume. Based on gape size, about 55% of *X. texanus* and 71% of *G. cypha* could be consumed by even the largest *P. lucius*. However, vulnerability would increase to 73 and 83% respectively if these species did not have humps. Coevolution tends to favor predator defense mechanisms in prey most vulnerable to such a voracious predator. Development of a large nuchal hump provides a deep body that is difficult or impossible for *P. lucius* to ingest.

Introduction

The Colorado River is home to an endemic fish fauna that has evolved over millions of years (Smith 1981, Minckley et al. 1986, Hoetker & Gobalet 1999). The upper mainstem Colorado River is unique in that its fishes are characterized by high endemism (i.e., 87%), and historically has been represented by seven large river species con-sisting of only cypriniform fishes (Jordan & Evermann 1896, Miller 1958, Carlson & Muth 1989). The top carnivore in this system is a large, voracious predator, the Colorado pikeminnow, *Ptychocheilus lucius*, largest North American minnow, which may have once reached nearly 1.8 m and 36 kg (Miller 1961). There are anecdotal reports of very large *P. lucius* from the historic Colorado River; however, fish larger than ca.

900 mm are exceedingly rare. The largest *P. lucius* captured in the multiagency Upper Colorado River Fishes Recovery Implementation Program was recorded at 1240 mm TL and only 7 of the more than 5000 *P. lucius* captured since the 1970s have exceeded 900 mm TL (C. McAda, US Fish & Wildlife Service, personal communication). The historical record is too scant to make valid statements about past fish sizes other than to speculate about maximum sizes that were probably attained (e.g., Miller 1961). Two other fish species of the Colorado River, the razorback sucker, *Xyrauchen texanus*, and the humpback chub, *Gila cypha*, have been described as 'bizarre' because they exhibit large nuchal processes that are located dorsally, posterior to the head. These pronounced humps look similar but are not homologous structures. The *X. texanus* hump is bony, formed mostly by enlarged neural and interneural bones (La Rivers 1962), while the *G. cypha* hump consists of a muscular mass (Miller 1946, Figure 1).

The function of these nuchal humps is unknown, though Miller (1946) speculated that the *G. cypha* hump provides a hydrodynamic advantage in swift currents. Miller reasoned that water flowing over the hump would produce a downward force on the fish, aiding the fish in maintaining position on the bottom. Flow at the benthic boundary layer is slower and would require less exertion to swim or maintain position in a river. Unfortunately, Miller (1946) was unable to observe *G. cypha* swimming in nature and little was known about its habitat use. La Rivers (1962) offered a similar explanation for *X. texanus*, hypothesizing that flowing water would push the sloping head downward while the bony keel provided increased stability in fast flows, thus steadying the fish against the bottom. However, La Rivers (1962) also was unable to test his hypothesis. Yet, their assumptions that nuchal humps are hydrodynamically advantageous adaptations to swift currents are often cited (e.g., Cole 1994, Sigler & Sigler 1996, Moyle & Cech 2004).

Additional information about the adaptations and life histories of Colorado River fishes gathered in the last 20 years has prompted us to reevaluate the function of large nuchal humps. It is now understood that humps in both species are formed later in life at a time when adult *G. cypha* predominantly occupy eddies and adult *X. texanus*
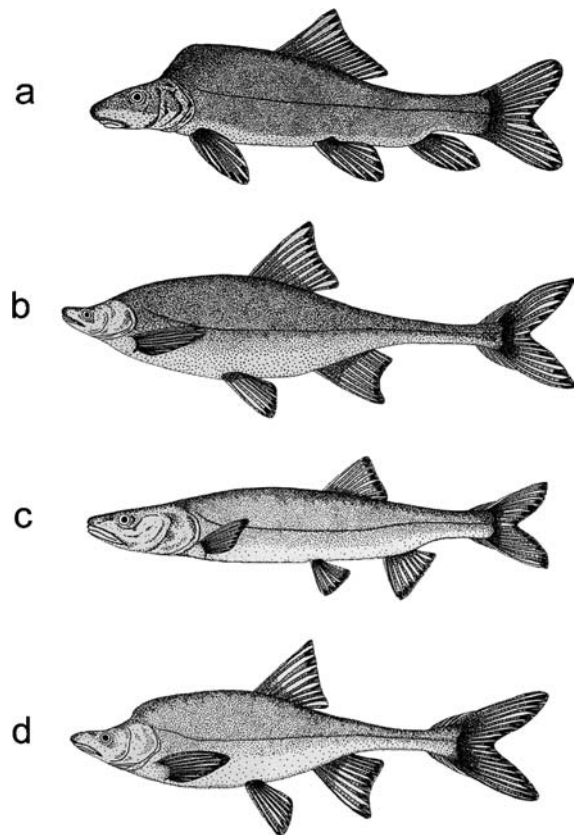

Figure 1. Four endangered Colorado River fishes: (a) *Xyrauchen texanus*, (b) *Gila elegans*, (c) *Ptychocheilus lucius*, and (d) *Gila cypha*. Fish lengths are not to scale, however drawings were made from actual fish specimens courtesy of Jim Beard, U.S. Fish & Wildlife Service.

inhabit eddies, deep runs, and slack waters (reviewed by U.S. Fish & Wildlife Service 1990, 1998, unpublished observations). These are large, but quiet habitats where adaptations to fast flows are not required. Conversely, related native cyprinids (*Gila elegans* and *G. robusta*) and catostomids (*Catostomus latipinnis* and *C. discobolus*) that prefer fast flowing habitats do not have such large humps. Body shapes of these species suggest low pressure drag, which would be more adaptive to high mobility and fast flows (Webb 1984). Such body shapes tend to have the transitional point between laminar and turbulent flow located far back from the leading edge. In contrast, the transitional point in *G. cypha* and *X. texanus* occurs on the anterior leading portion of the body, a morphology not conducive to reducing drag (i.e., the

rate of removal of momentum from a flowing fluid; Webb 1975, Vogel 1994).

Reynolds numbers indicate the kinds of forces that have to be overcome by an object moving in a fluid. These numbers are a ratio of the inertial and viscous forces, which for fish are dependant on three factors: the swimming velocity of the fish, characteristic length of the fish (where shape is factored in), and viscosity of the water (Webb 1975, Denny 1988). Streams exhibit Reynolds number values of approximately 100 000, where neither viscous nor inertial forces dominate (Webb 1975, Vogel 1994, Lampert & Sommer 1997), and shapes of fishes that result in a hydrodynamic advantage may sometimes be difficult to predict. In most cases, stream fishes reduce structures that induce drag because increased drag also would increase energetic costs. Adult stream fishes are generally streamlined, with an exception in fishes that do not carry out sustained swimming (Webb 1984, Diana 1995).

In addition to drag, another hydrodynamic consideration for life in moving fluids is lift. Lift can be defined as any force that is normal to the direction of flow, in this case up (i.e., 'positive lift') and down (i.e., 'negative lift'; Denny 1988). The amount of lift generated by morphology depends on how much the flow is turned by the shape of the object. If flow above and below the shape are the same, no net lift results. However, if water pressure on the dorsal surface is less than that below, the result is a net upward force: in this case, the increased area of the leading edge deflects the water so that the streamlines are crowded together above the object. This crowding thus causes an increase in water velocity on the dorsal surface resulting in dynamic lift (Schlichting 1979, Denny 1988, Vogel 1994).

The 'nuchal hump hydrodynamic advantage hypothesis' attributed to Miller (1946) and La Rivers (1962) can be evaluated by determining the components of drag and lift produced by the humps. In this study we determine drag and lift components associated with large humps to evaluate whether the humps confer a benefit for life in fast flow. In addition, we explore an alternate hypothesis regarding the advantage of large humps by examining other factors exerting evolutionary pressures for hump development, such as a need for a morphological defense against predators.

Materials and methods

Drag and lift

Three of the fishes we studied, *G. cypha, G. elegans* and *X. texanus*, are endangered species protected by federal and state statutes, thus live or freshly sacrificed fishes could not be used in hydrodynamic tests. Instead, polyester resin casts of museum specimens were used to obtain information on how different body forms would be affected by water flow.

We made whole-body casts of each species from silicone rubber molds. We suspended fish specimens in a plexiglas molding box filled with GI-1000 RTV Silicone Rubber (Silicones, Inc.). We mixed the silicone rubber with a fixed amount of activator, placed it into a vacuum chamber, and rapidly degassed it before pouring it into the molding box. Once rubberized, we removed the mold from the Plexiglas® box, divided it into two halves, and retrieved the fish from the mold.

The cast-making procedure was as follows: the silicone rubber mold was placed back into the Plexiglas® box to maintain shape and we placed a brass mounting apparatus (used to connect the two-dimensional force beam to the fish cast) inside the mold. We then filled the mold with polyester resin mixed with 60 μm diameter glass microspheres (3M S60; Minnesota Mining and Manufacturing Company) to 40% of the total volume to add strength to the casts and to serve as filler. After a day of hardening time, we removed the casts with embedded mounting apparatuses from the molds and sanded them to remove any imperfections.

We made casts from molds of different fish morphotypes to evaluate the hydrodynamics of each body plan. We made two different casts of each species morphotype using a cast most representative of a fully developed, mature adult. We used casts from the fish exhibiting enlarged nuchal humps (i.e., a 381 mm TL *G. cypha* and a 458 mm TL *X. texanus*) as the treatment group to measure drag and the direction of force resulting from the prominent nape. We later removed the humps on these fish models and retested the casts to assess performance without the humps. We compared lift and drag values for those casts with nuchal humps to the same casts with humps removed. We used

Student *t*-tests to determine if there was a significant difference between the control and treatment casts. In addition, we used casts of two species lacking humps, but closely related to each of the treatment fishes, to compare drag and force direction of nuchal humped and non-humped casts. The more streamlined catostomid was the flannelmouth sucker, *C. latipinnis*, and the more streamlined cyprinid was the roundtail chub, *Gila robusta*, 439 and 403 mm TL, respectively. We also determined drag coefficients of two well-known objects, a 324 mm TL rainbow trout, *Oncorhynchus mykiss*, and a 57.17 mm diameter sphere for comparison with other studies.

We compared humped vs. non-humped morphotypes by analysis of drag coefficients, which are widely used for comparing the hydrodynamic drag among fishes. The drag coefficient (C_D) is defined as

$$C_D = 2D/\rho SU^2$$

where D is the drag force, ρ is the fluid density, S is the reference area, and U is the velocity (Denny 1988, Alexander 1990, Vogel 1994). The drag coefficient is a dimensionless function of the Reynolds number that can be used to compare the effects of hydrodynamic drag on objects of different morphologies, including fishes (Webb 1975, Denny 1988, Alexander 1990). We compared drag coefficients of our fish casts with nuchal humps to those of more streamlined fishes and the casts with the nuchal humps removed to help evaluate the hydrodynamic role of nuchal humps of the Colorado River fishes. Such hydrodynamic comparisons have often been made between species, which may make it difficult to separate effects from other interspecific differences (Pettersson & Brönmark 1999). Hence, we tested both models of congenerics and models with humps removed.

We used two different methods for determining the surface area in this study: frontal area (the maximum projection of the body onto a plane normal to the direction of flow) and wetted area (the total surface exposed). We used the frontal area to calculate the drag coefficient of the sphere, and the wetted area to determine the drag coefficients of the fish casts. We calculated the reference area measurement in this manner to keep to convention and produce quantities that could be compared to values previously reported in the literature. Frontal surface area is considered easier to measure accurately, while wetted surface area is difficult to measure in complex shapes.

We tested drag and lift components of fish casts in an 18.3 m × 0.9 m × 0.6 m flow tank at the U.S. Bureau of Reclamation Hydraulics Laboratory in Lakewood, Colorado (Figure 2). Two 100 hp centrifugal pumps delivered water into a 950 000 l reservoir and then into the tank baffle through a 30 cm diameter pipe. A stone baffle within a screen helped to control the flow of water at the filling point, and 4.6 m below the baffle water also passed through an array of flow-straighteners consisting of 200 galvanized pipes (5.1 cm diameter and 51 cm long) stacked upon one another to fill the channel. We used a Sontek Adv-4 Doppler velocity probe to measure the flow rates, which reached 1.0 m s^{-1} in the flume.

We tested effects of lower velocities (i.e., 0.3 m s^{-1}) on the fish casts in a smaller flow tank at the University of Colorado at Boulder. Water flow was generated by a 0.5 hp electric motor which operated a propeller in a 15 cm PVC recirculating pipe. The water entered the flow tank through a pipe baffle to disperse flow into a larger upper end (0.3 m × 0.3 m × 0.64 m), which narrowed to a 0.3 m × 0.23 m × 0.64 m working section. The water entered the working section through a flow-straightener constructed of approximately 2000 drinking straws of 0.48 cm
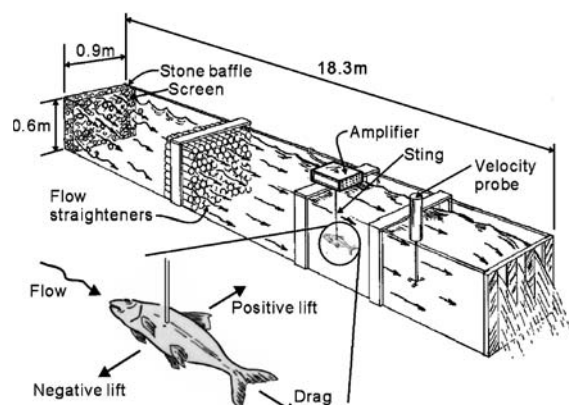

Figure 2. Experimental flume at the U.S. Bureau of Reclamation Hydraulics Laboratory in Lakewood, Colorado illustrating experimental design, including mounting and orientation of the fish casts along with various flow components.

diameter and 15.2 cm in length to reduce turbulence as water passed through the working section. Another 2000 straws filled the channel after the working section to counteract flow deflection induced by the exit pipe positioned on the side wall.

A two-dimensional force beam was mounted on a bridge over the top of each flow tank. We fitted the fish casts to a round 0.635 cm diameter stainless steel rod (sting) that was 66 cm long. The sting was planed at 90° angles approximately 5.1 cm before mounting to the bridge and foil strain gauges were attached to each of the planed surfaces. We used standard force-measuring techniques in the construction of the force beam (Vogel 1994). Resistors in the foil strain gauges converted bending forces of the metal rod into voltage changes which were picked up in the amplifier circuit by strain gauges. We used a two channel half-bridge amplifier to gather both drag and lift voltage values together during the same trials. We sampled these values 50 times s^{-1} for a 30 s interval during each trial and recorded data with a Windaq Data Acquisition program. We tested casts of each species, species with humps removed, and the sphere in at least 10 trials per each velocity tested. We used a Dataq cast DI-220 analog-digital converter to transfer sampled voltage values from the amplifier to a computer.

Previous researchers measuring lift and drag components of fishes have attached force balances at the nose, abdomen, caudal, and dorsal regions, with each position having its own inherent hydrodynamic problems (Webb 1975). In preliminary studies, we compared lift values when the sting was mounted both dorsally and laterally, and found that attachment of the sting through the dorsum of the fish cast resulted in a small, but significant increased lift as an artifact of the sting. Therefore, we fixed the sting to the lateral surface of the casts, which were positioned on their side (Figure 2) and we calculated residual drag from the sting while determining drag and drag coefficients.

We quantified the dynamic fluid-induced forces on the fish casts by calibrating the force beam with a known force (weights). We determined drag exerted on the fish body forms at water velocities of 0.3 and 0.9 m s^{-1}. The casts were positioned at a zero degree angle of attack, 0.15 m from the bottom and midway between the sides in the 18.3 m flume, so that surface waves and frictional boundary layers with the flume would not affect drag and lift forces (Figure 2). The casts were also placed at a zero degree angle of attack, 0.1 m from the bottom and midway between the sides in the smaller flow tank.

Predation

Results of flow tests demonstrated that, as an adaptation, large nuchal humps were not advantageous to life in fast flowing water and so we sought a more plausible explanation. Because the hump produces the general effect of making the fish much larger in body depth, it might also make a fish less vulnerable to predation. The only native piscivore of concern for larger-size fish is *P. lucius*, and thus we hypothesized that the increased body size could have developed in response to *P. lucius* predation. This hypothesis was evaluated by measuring effective mouth gapes of the predator and obtaining body dimension measurements from prey species that possessed nuchal humps and those that did not. In this way we could contrast potential vulnerability to *P. lucius* predation.

We measured body depths in *G. cypha* and *X. texanus* as the linear distance from the base of the pectoral girdle to the dorsal nuchal ridge. In addition, we also measured body depths of *G. robusta* and *C. latipinnis* for comparison. We obtained data from preserved specimens in the Repository for Southwestern Species at the U.S.G.S. Biological Resources Division in Fort Collins, Colorado, and at the University of Colorado Museum. We also obtained body dimensions from live fish at the Dexter National Fish Hatchery at Dexter, New Mexico. We anesthetized live fish using 100 mg l^{-1} Finquel Tricaine Methanesulfonate (MS-222) in order to reduce the amount of stress on the fish and make it easier to obtain measurements.

We took body measurements from 719 individuals of prey species, including sizes that ranged from small juveniles to large adults. Measurements included: total length (mm), standard length (mm), dorsoventral body depth at nuchal hump region, and maximum dorsoventral depth. We took total length and standard length on a fish measuring board and we measured the body depths with a digital caliper.

We measured mouth gapes of *P. lucius* at the Dexter National Fish Hatchery, Dexter, New Mexico. We took measurements from 103 live specimens. We took total and standard lengths using a fish board. We determined weights with a spring scale. We measured mandibular arch width and maximum mouth gape (both laterally and dorsoventrally) using digital calipers. In addition, we took a measurement of the maximum pharyngeal opening with tong spreaders placed inside the pharynx. We used an inside dimension spring caliper to measure the pharyngeal opening on fish too small for the spreaders. Measurements of the mouth and pharyngeal cavity revealed that the dentary and maxillary bones of the *P. lucius* limited maximum sizes of prey that could be swallowed. Therefore, we calculated gape as the maximum distance between the maxillary and the dentary bones dorsoventrally in the mouth. We evaluated the relationship between mouth size (gape) of the predator and maximum dorsoventral body depth of the hump of the prey with regression analysis.

Results

Drag assessment

Drag coefficients using our apparatus and techniques were similar to that reported for a sphere ($C_D = 0.45$ *vs.* 0.47 reported by Vogel 1994) and *O. mykiss* ($C_D = 0.025$ vs. 0.022 reported by Webb 1975, Table 1). Also, drag coefficients demonstrated the importance of streamlining. The sphere (no streamlining) had the highest drag coefficient, and among the four Colorado River fishes that we tested, the catostomid and cyprinid without humps (i.e., *C. latipinnis* and *G. robusta*) had the lowest drag coefficient (Table 1). A comparison of C_D of the two humped forms from which humps were removed and sympatric forms were identical for *Gila* and almost identical for the catostimids (*X. texanus* = 0.24 and *C. latipinnis* = 0.25). When looking at the fish casts with humps vs. humps removed, there was a reduction in the drag force and therefore a reduction in the drag coefficient after the removal of the nuchal humps (Table 1; Figure 3; $p < 0.05$). Thus, the extra mass of the nuchal hump resulted in appreciable drag.

An increase in area or wetted surface of the fish casts always resulted in increased drag, and drag force was greatest on fish with the largest frontal areas proportional to their length (Table 1). Drag coefficients obtained were consistent with published values (Table 1; Webb 1975, Vogel 1994), and diminished as fish became more streamlined (Table 1). There was a significant reduction ($p < 0.05$) in the drag force upon removal of the nuchal hump from the *X. texanus* and *G. cypha* casts (Figure 3, Table 1), as reflected by a 27% reduction in C_D for *X. texanus* and a 14% reduction for *G. cypha* (Table 1). However, drag forces seemed to be Reynolds number dependant because of the characteristic length, which takes into account the different shapes of the fish and were not

Table 1. Drag coefficients obtained from published sources and experimental results at water velocities of 0.3 m s^{-1} and their respective type of reference area.

| Objects	Drag coefficients	Reference area
Theoretical sphere	0.47[a]	Frontal area
Experimental sphere	0.45	Frontal area
O. mykiss	0.022[b]	Wetted area
O. mykiss	0.025	Wetted area
X. texanus	0.033	Wetted area
X. texanus (hump removed)	0.024	Wetted area
C. latipinnis	0.025	Wetted area
G. cypha	0.029	Wetted area
G. cypha (hump removed)	0.025	Wetted area
G. robusta	0.025	Wetted area

[a]Vogel (1994).
[b]Webb (1975).
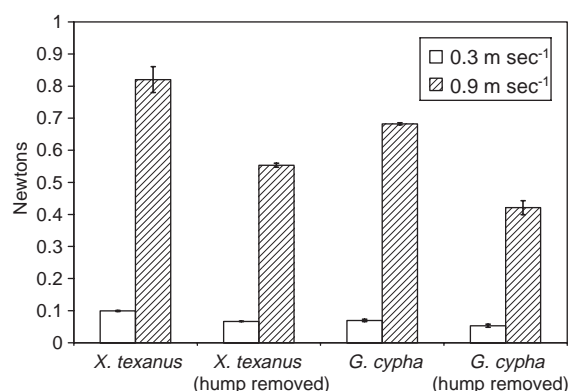
Figure 3. Drag (Newtons) exhibited by body casts of *X. texanus* and *G. cypha* in the experimental flume with water velocities of 0.3 and 0.9 m s^{-1}. Casts without hump are the same as those with hump except the hump has been removed by sanding.

Figure 4. Lift (Newtons) exhibited by body casts of *X. texanus* and *G. cypha* in the experimental flume with water velocities of 0.3 and 0.9 m s^{-1}. Casts without hump are the same as those with hump except the hump has been removed by sanding. Positive values indicate an upward force and negative values, a downward force.

exactly proportional to a velocity-squared relationship when fish casts with humps and humps removed were tested at velocities of 0.3 and 0.9 m s^{-1} (Figure 3).

Lift assessment

As expected, net lift varied greatly among the objects tested, and there was no lift on the sphere. A sphere is symmetrical; therefore the low pressure on one side is offset by the low pressure on the other side, thus, there should be no net force perpendicular to the flow (Denny 1988). Lift exhibited by the fish casts was dependent on species, but negative lift was unaffected by the presence of a hump. The nuchal process did not have an influence on the downward forces related to body design (negative lift), as indicated by the lift force values of *X. texanus* and *G. cypha* casts before and after removal of the hump, both tested at 0.3 and 0.9 m s^{-1} (Figure 4; $p > 0.05$). A slightly negative lift was produced by *X. texanus*; however, *G. cypha* produced a substantial positive lift, especially with higher water velocities (Figure 4). The different morphologies of *X. texanus* and *G. cypha* no doubt resulted in very different trends in lift performance. In part, this disparity can be explained by the noticeable asymmetry of *G. cypha*. A greater percentage of body volume is found above the dorsoventral mid-point between the leading edge of the rostrum and the tailing edge of the caudal
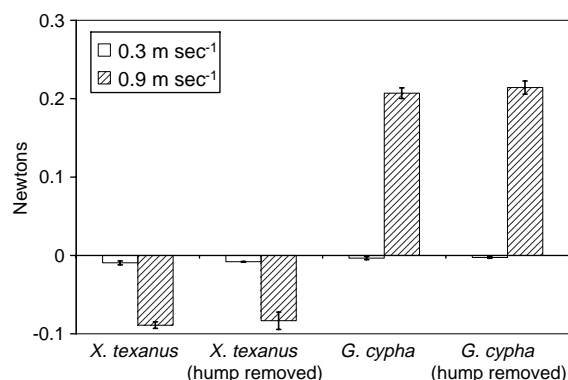
peduncle, thus producing positive lift due to lower pressure on the dorsal surface.

Prey morphology

Prey body depth at the nuchal hump was highly correlated with body total length for both *X. texanus* and *G. cypha* ($r^2 = 0.984$, n = 119, range = 67–559 mm TL; $r^2 = 0.986$, n = 224, range = 36.5–410 mm TL, respectively). A similar relationship also existed for fishes without nuchal humps, *C. latipinnis* and *G. robusta* ($r^2 = 0.985$, n = 148, range = 34–574 mm TL; $r^2 = 0.987$, n = 228, range = 39–447 mm TL, respectively; Figures 5 and 6). However, the slopes of the fishes without nuchal humps was less than that of the fishes with enlarged nuchal humps, demonstrating that fishes with nuchal humps increase in body depth much earlier in development (Figures 5 and 6).

Predator mouth gape

The dorsoventral measurement of mouth gape in *P. lucius* determined the largest size prey that could be ingested. Predator mouth gape was correlated with total length ($r^2 = 0.911$, n = 103, range = 175–805 mm TL).

When predator mouth gapes and prey nuchal region depths were considered together it is evident
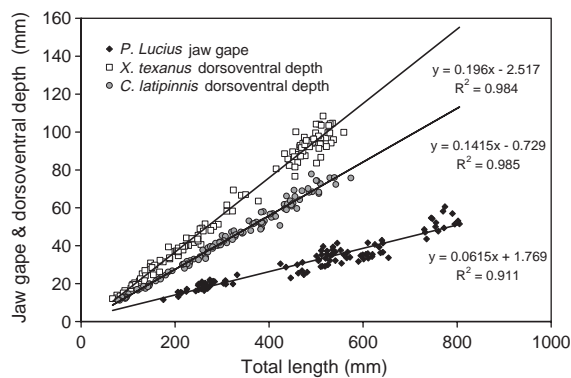
Figure 5. Jaw gape (dorsoventral dimension) of *P. lucius* and dorsoventral depth at nuchal region of *X. texanus* and *C. latipinnis*, as a function of total length. Individual fishes are represented as *P. lucius* (black diamonds), *X. texanus* (squares), and *C. latipinnis* (gray circles).
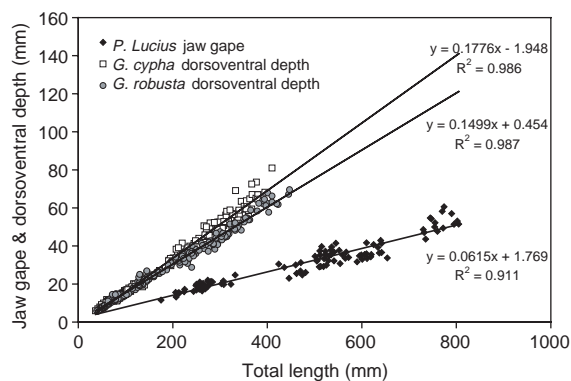

Figure 6. Jaw gape (dorsoventral dimension) of *P. lucius* and dorsoventral depth at nuchal region of *G. cypha* and *G. robusta*, as a function of total length. Individual fishes are represented as *P. lucius* (black diamonds), *G. cypha* (squares), and *G. robusta* (gray circles).

that *P. lucius* piscivory was limited to only the smaller sizes of fishes with enlarged humps (Figures 5 and 6). In addition, it appears that nuchal humps provide protection from *P. lucius* predation early in development (i.e., for small total length). For example, according to the data presented in Figures 5 and 6, about 73% of the total length range for *C. latipinnis* and 83% for that of *G. robusta* could be consumed by the largest *P. lucius* (i.e., 805 mm), with only the very large fish gaining protection, whereas, only 55% of the total length

range for *X. texanus* and 71% for that of *G. cypha* could be ingested by the largest *P. lucius* (Figures 5 and 6).

Discussion

A fair evaluation of the 'nuchal hump hydrodynamic advantage theory' required laboratory testing with the fish body casts, and the results were not surprising. Just as the wings of an airplane generate lift, a prominent hump on a fish also results in lift, which would make holding its position on the bottom more difficult. In addition, increased drag arises from frictional and pressure forces associated with a hump. Frictional forces for a given body can be reduced by maintaining laminar boundary layer conditions over as much of the body as possible. At moderate and high Reynolds numbers, any object from which flow separates will experience a relatively high drag. If the object is streamlined, fluid gradually decelerates in the rear with little separation occurring and the object is actually pushed forward by the wedge-like closure of the fluid behind it. Efficiency of a moving streamlined body through water depends on the positioning of the area of the body with the largest girth (shoulder). Fast-moving fishes, such as scombroids, have their shoulder situated far back on the body, which extends the influence of the favorable pressure gradient and encourages laminar boundary layer flow over most of the body (Webb 1975, Vogel 1994). A streamlined body usually has its maximum thickness at least 30% from its front (Denny 1988, Vogel 1994, Diana 1995). However, *G. cypha* and *X. texanus* have bodies in which the transitional point between laminar and turbulent flow is practically at the leading edge. The nuchal hump causes the shoulder to be very much anterior, which results in the immediate loss of a laminar boundary layer and an unfavorable pressure gradient. Therefore, these nuchal humps are a hindrance to the swimming ability of *G. cypha* and *X. texanus*.

We investigated whether enlarged nuchal humps might convey a hydrodynamic advantage for life in fast flowing water, and especially for facilitating position holding in stream flows. Thus, we were not concerned with measuring thrust power or complex fluid mechanics of these fishes, but rather

were merely interested in drag and lift components of fish body shapes with large nuchal humps. We believe that the casts (rigid-body analogy) we used were adequate for determining the role that protruding rigid structures (nuchal humps) have on drag and lift generated by fish that would be attempting to hold their position in flowing water. Thrust values were not sought after in this study; rather, we focused on dead-drag. The use of dead-drag is justified because we evaluated rigid structures and were not concerned with the action of the fleshy body or turbulence caused by fins and other structures (e.g., see Webb 1975).

Our use of rigid body casts instead of fresh specimens may be criticized. However, the main objective of this study was to evaluate whether a hydrodynamic advantage might be induced solely by large nuchal humps. Nuchal humps of *G. cypha* and *X. texanus* are rigid body structures of bone and hard muscle that have been thought to aid these fishes hydrodynamically while attempting to hold their position in a stream (Miller 1946, La Rivers 1962). Thus, we used rigid casts to evaluate the effect of humps on drag and lift in order to avoid turbulence and higher drag coefficients that would result as an artifact of body fluttering or due to fins that may cause spurious readings in fresh specimens (Webb 1975). Also, we did not address shape-specific effects of humped fishes of different sizes. No doubt, an evaluation of the allometric relationships between nuchal hump size and the drag and lift produced would provide useful information about the functional consequences of developing enlarged nuchal humps. However, determining these relationships was beyond the scope and budget of our study. This study is primarily concerned with determining whether large nuchal humps provide a hydrodynamic advantage (i.e., negative lift with marginal drag), and offering an alternate hypothesis of their usefulness.

The relatively high metabolic cost of swimming is indisputable and a direct reflection of the drag that must be overcome. For mobile organisms such as stream fishes, the cost of excessive drag is extreme, depending on habitats utilized. Fishes living in swift water must expend energy at a rate that is at least that of the product of drag and velocity (Vogel 1994). Our analysis of drag on the body casts of different fishes we studied produced results that are in agreement with habitat prefer-

ences obtained by empirical studies: *G. cypha* and *X. texanus* prefer slower habitats such as eddies, backwaters and slackwaters (Tyus 1987, Karp & Tyus 1990, Sigler & Sigler 1996). However, closely related forms utilize high velocity habitats. In the case of *G. cypha*, a congener, *G. robusta*, is more streamlined, has a much less pronounced nuchal hump, and does occur in swift currents. With respect to *X. texanus*, its close relative, *C. latipinnis*, also is more streamlined, lives in riffles and has no hump. For the hydrodynamic advantage theory to be correct, all other main channel fish species should have a large hump to benefit swimming performance in swift currents. Our findings show that Colorado River fishes with the most streamlined bodies are fishes that historically inhabited fast-flowing main river channels, whereas fishes with large humps are known to occupy eddies and slackwaters. In the case of *X. texanus*, a fish that has been occasionally observed feeding in shallow runs (Tyus 1987), enlarged pectoral fins may be an adaptation to compensate for lift created by the hump when the fish ventures into faster flows.

An apparently high energetic cost would be associated with hump growth and locomotion with the presence of a hump due to the drag that is produced (Pettersson & Brönmark 1999). Although it might be argued that humps are relict structures that once had some purpose that has been lost, logic dictates that some benefit must accrue. One possible explanation, in view of our findings that the humps do not aid swimming or produce 'negative' lift, might be sexual dimorphism as an aid in sexual selection. However, males and females of both species produce humps; thus, we discount sexual selection as the primary factor in hump formation. Humps of males do appear slightly larger, but we attribute such dimorphism to building on an already existing structure rather than developing the hump for this purpose de novo. This is supported by a regression of nuchal hump size vs. fish total lengths for fishes that we measured at Dexter National Fish Hatchery. In this case, no sexual dimorphism was evident, and a smooth transition occurred as hump size increased with fish growth ($r^2 = 0.984$ for *X. texanus*; Figure 5 and $r^2 = 0.986$ for *G. cypha*; Figure 6). An additional possibility is that enlarged nuchal humps are produced in these two species in response to predation.

Animals have a wide array of morphological structures that function to reduce predation and there are many cases in which morphologies have evolved to provide defense against some biotic selective agent (Havel 1987, Adler & Harvell 1990, Harvell 1990). Predator-induced morphological defenses are well known in aquatic invertebrates. For example, cladocerans and rotifers produce progeny with neckteeth or enlarged crests on their head in response to biotic cues from consumers (Havel & Dodson 1987, Stemberger & Gilbert 1987, Adler & Harvell 1990). Barnacles that come into contact with predatory gastropods early in their development are known to form asymmetrically, thus making it more difficult to open its opercular plates (Lively 1986, Adler & Harvell 1990).

A cyprinid fish, crucian carp, *Carassius carassius*, was the first vertebrate to be added to this long list of organisms with such adaptations (Brönmark & Miner 1992, Brönmark & Pettersson 1994, Nilsson et al. 1995). Brönmark & Miner (1992) discovered that *C. carassius* increased body depth in the presence of northern pike, *Esox lucius*, to reduce susceptibility to predation. Morphological change in *C. carassius* is so dramatic that effected individuals have been mistakenly identified as a separate species (Brönmark & Miner 1992, Brönmark & Pettersson 1994). This morphologic change reduces the ability of gape-limited piscivores, such as pike, which consume only prey they can swallow whole (Hambright 1991). In addition, prey are generally swallowed head first, and their dorsoventral body depth determines whether they can be ingested (Hambright 1991). Prey body depth also increases handling time for gape-limited piscivores, which provides a greater opportunity for prey to escape.

The major piscivore in the Colorado River System is *P. lucius*, which has exerted predation pressure over millions of years. If another cyprinid, *C. carassius* can increase dorsoventral body depth in just 12 weeks (Brönmark & Miner 1992, Nilsson et al. 1995), why could not *G. cypha* and *X. texanus* evolve similar adaptations through natural selection over thousands of years? *P. lucius* is gape-limited and thus piscivory would be restricted by increasing prey size. Thus, the relationship between body depth and piscivore mouth gape is important in selection of prey within the range of ingestible size (Gillen et al. 1981, Hambright 1991). Juvenile *G. cypha* and *X. texanus* are not associated with larger *P. lucius* until they leave their nursery grounds and then live sympatrically in pools and eddies with *P. lucius* (Tyus 1987, Karp & Tyus 1990, Tyus & Karp 1990). The timing of this change in habitat preference is synchronous with the enlargement of the nuchal processes in *X. texanus* (Minckley et al. 1991, Converse et al. 1998, R. Valdez, unpublished). Because *P. lucius* lacks jaw teeth, it has no way of wounding or holding partially consumed prey; thus, it must engulf its prey whole. Inefficiency in successfully consuming large-bodied prey could have resulted in an adaptive response in prey species most affected, which would be other fishes that occupy preferred habitats of *P. lucius*. For sympatric species, such as *G. cypha* and *X. texanus*, enlargement of the nuchal region could provide a means of attaining a body shape that would be difficult or impossible for *P. lucius* to ingest.

We offer an alternate hypothesis for the presence of large nuchal humps in *G. cypha* and *X. texanus*: the humps are in response to thousands of years of predation by a large, but gape-limited cyprinid. Humps would have developed in these two species and not others because they evolved in the same low velocity habitats foraged by adult *P. lucius*. These humps ostensibly allow the two prey species to reduce predation pressure at a smaller length and age, thus increasing their fitness. This is especially valuable in such long-lived species which can attain ages of 15–20 years and more.

Our findings show that based on gape size alone, *P. lucius* piscivory would be constrained by its relatively small gape and the presence of enlarged nuchal humps on its prey. Thus, gape limitations restricted predation to smaller sizes of the humped forms (Figures 5 and 6). Relating this to the present river system, the average size of adult *P. lucius* extant in four rivers was reported by Hawkins (1992) as 536 mm TL (modal range 500–550 mm, n = 2 176). Based on hump growth, *G. cypha* (>210 mm) and *X. texanus* (>220 mm) would be immune to predation from an average size *P. lucius*. Furthermore, young of both prey species occupy shallow shoreline areas, moving offshore to deeper water at 100–300 mm for *G. cypha* (Converse et al. 1998, R. Valdez, unpublished observations), and about 127–196 mm for

X. texanus (stocked fish; Minckley et al. 1991). Hump enlargement is already in progress in both species at these sizes, and *G. cypha* of 300 mm and *X. texanus* of greater than 200 mm would be approaching immunity from even the largest *P. lucius*. Populations of *G. cypha* attain sizes of 480 mm in nature and an average adult size of approximately 300 mm TL (Kaeding & Zimmerman 1983, Karp & Tyus 1990, R. Valdez, unpublished). Populations of *X. texanus* attain an average adult size of about 500 mm TL consisting of adults that range in size from 370 to 740 mm (Minckley 1983, Marsh & Minckley 1989), all of which would be immune from the largest *P. lucius* (e.g., 805 mm).

Further support for predator-mediated morphological change in both of these species is provided by other morphological adaptations linked with predator defense. The lack of, and reduction in size of scales, and the increased relative size of paired fins also are implicated. In *G. cypha*, scales are absent or greatly reduced in size and number on the dorsal and ventral surfaces. An almost scaleless, and thus, slippery fish can be very difficult for a predator with no jaw teeth to capture and manipulate for effective feeding. Increased maneuverability in more lacustrine-like habitats also would result from laterally flattening bodies, which facilitate complex evasive movements. While these adaptations to predation are constitutive in adult *G. cypha* and *X. texanus* (i.e., always present), it is possible that these morphological defense strategies may have been originally predator-induced during pre-adult habitat transitions where they become sympatric with *P. lucius*.

Native Colorado River fish populations have been extirpated from much of their historic habitats by reservoir inundation and altered flow regimes. Therefore, recovery efforts have been focused on physical habitat restoration. However, non-native predators such as northern pike, *Esox lucius*, largemouth bass, *Micropterus salmoides*, smallmouth bass, *Micropterus dolomieu*, and walleye, *Stizostedion vitreum*, have been introduced with devastating effects (e.g., see Minckley et al. 1991, Tyus 1998, Meretsky et al. 2000). If predation pressure has been the major selective force behind the evolution of enlarged nuchal humps instead of physical habitat constraints as previously reported, this suggests that these species may be especially sensitive to predation by non-native fishes. Hump formation, an interesting adaptation, which presumably resulted in long-life for breeding adults, may no longer provide an effective life strategy. As serious as physical habitat loss has been, biological, rather than physical changes may now play the major role in endangerment of these fishes. In this case, efforts to recover these fish will require increased emphasis on the biological attributes of habitat.

Acknowledgements

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