OSMOTIC AND IONIC REGULATION IN THE GREEN STURGEON, ACIPENSER MEDIROSTRIS

by

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A THESIS

Presented to the Graduate School of the University of Oregon
in partial fulfillment of the requirements
for the degree of
Master of Science

August 1975

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INTRODUCTION

General History

The sturgeons (Acipenseridae) and paddlefish (Polyodontidae) are the only remaining living representatives of the early chondrostean fishes. These ancient fishes dominated the waters from the Devonian to the Permian and were apparently the forerunners of the now dominant teleosts (Lagler *et al.*, 1962). Modern day sturgeon and paddlefish can be traced back to Cretaceous times and retain many ancient features, including the heterocercal tail, spiracle, spiraled intestine, and heavily armored body. These fish have managed to successfully withstand a varying sea level, changing climatic conditions, and both habitat disruption and geographical isolation by uplifting of mountain ranges.

In the family Acipenseridae, there are four living genera. Only one genus, *Acipenser*, is present in North America. Of the 16 species of *Acipenser* now recognized, five occur in North America. *A. oxyrhynchus*, Mitchill, *A. brevirostris* LeSueur, and *A. fluvescens* Rafinesque, are present in eastern North America, while *A. transmontanus* Richardson and *A. medirostris* Ayres are found on the Pacific Coast (Vladykov and Greeley, 1963).

Life History

Both A. transmontanus and A. medirostris occur in the major rivers along the Pacific Coast from California to the Gulf of Alaska. A. medirostris is also found on the Asian coast from the Amui River to Taiwan. Although A. medirostris has never been of commercial importance, at the turn of the century A. transmontanus supported a large fishery in the Sacramento-San Joaquin River system, the Columbia River system, and the Fraser River system of Canada. Within a few years, the sturgeon population of all three rivers had drastically declined. Both commercial and sports fisheries were outlawed in California waters in 1915. A controlled sports fishery was reopened again in 1954 when the sturgeon population increased in abundance (Pycha, 1956). The Columbia River and Fraser River sturgeon fisheries have been regulated since the early 1900's (Bajkov, 1951; Semakula and Larkin, 1968). Populations in these rivers have also recovered, though they are still well below their historical numbers. However, life history studies show that only a sound management program can maintain the present levels of abundance.

Through examination of annual rings on the cross section of the sturgeon's first pectoral ray, one can obtain life history information just as scales reveal the same information on many teleosts. Sturgeon are long lived and slow growing, making them particularly

vulnerable to heavy fishing pressure. Reports of 80 year old sturgeon are not uncommon. A. transmontanus of the Fraser River are reported by Semakula and Larkin (1968) to reach a length of 20 inches in the first 5 years, then slow to an annual growth rate of approximately 2 inches. These fish may reach a length of 20 feet, and are documented to weigh over 1300 pounds. Acipenser medirostris will reach 7 feet in length, and weigh up to 300 pounds (Hart, 1973).

A peculiarity in the sturgeon's life history is its long immature stage, estimated at 11 or 12 years for the white sturgeon of the Columbia (Pycha, 1956). Even after maturity, spawning may occur only once every 4 to 9 years (Semakula and Larkin, 1968). Both A. transmontanus and A. medirostris are anadromous, normally spending part of each year in salt or estuarine waters, ascending the rivers to spawn in late winter or early spring (Miller, 1972).

Upriver migrations of Columbia River sturgeon are related to feeding as well as spawning habits. Bajkov (1951) noted the upriver movement of both mature and immature sturgeon in the spring to feed on the Eulachon, Thaleichthys pacificus. A. medirostris is generally not found above tidewater, and appears to be inclined to change river systems, often traveling great distances along the coast. A. transmontanus seems to confine itself more to one river system, usually being found in freshwater above the estuary (Miller, 1972).

Physiology

To date, research on the Pacific Coast sturgeon has been limited almost entirely to tagging programs and aging studies. Little information is available concerning their physiology. Research dealing with the physiology of these fish would be valuable for several reasons.

The need for physiological information to properly manage fish has become apparent in recent years as man manipulates rivers and streams. This information is essential for successful production of cultured fish stocks in hatcheries as well as making intelligent decisions in management of wild stocks. If the sturgeon is to become established as a major food fish in this country as it is in Europe, research should be done to increase our understanding of their physiological and behavioral needs. Such knowledge might prevent a reoccurrence of the drastic reduction in the sturgeon population caused by commercial fishing in the early 1900's.

The sturgeon's ability to adapt to the numerous environmental changes which occurred in the last 100 million years should make Acipenseridae a strong candidate for future research. Physiological studies would also appear warranted due to the unique life history of the sturgeon. The reasons for their long immature condition, sporadic spawning cycle, and ability to live well over a century should be explored to increase our understanding of fish physiology.

Due to the sturgeon's phylogeny, questions exist regarding whether these fish have developed the same osmoregulatory mechanisms to control their ionic and osmotic problems as the teleosts. When examining the literature for data concerning salt and water balance of fishes, it becomes evident that researchers have concentrated on the Cyclostomes, Chondrichthyes, and the Teleostei. Little attention has been paid to those Chondrostean and Holostean fishes which make up the remainder of the class Osteichthyes (Magnin, 1962; Grant et al., 1970; Potts and Rudy, 1972).

The sturgeon's movement from salt to brackish water and into freshwater causes osmoregulatory problems as in euryhaline teleosts. Holding the salt concentration of its body fluids well below that of sea water, these fish continually face the problem of water loss and salt accumulation. When these euryhaline fish enter the freshwater, osmotic and ionic gradients are reversed, as the salt concentration of the fish remains much higher than the surrounding media.

Large advances have been made in recent years in understanding the salt and water regulatory system of fishes. With the help of tracer elements and compounds, sites of exchange between important body salts and the environment have been established. The importance of the teleost's gill membrane in sodium and chloride uptake and removal is now widely accepted. Research is primarily concerned with the specific transport mechanisms occurring at the "chloride

cells" of the gill membrane. Researchers have gained a better understanding of fishes' water regulation through experiments utilizing drinking rates, water permeability, and urine catheterization.

The freshwater teleost must continually work to conserve body salts and extrude water. Permeability of water through the skin is low and the drinking rate is low in an effort to slow the movement of water into the body. Still, excess water is accumulated through the gills and oral membranes. To combat this problem, the freshwater teleost relies on kidneys with a well developed glomerular filtration system. Much of the solute is reabsorbed from the filtrate while moving through the tubules, leaving a dilute urine. Important body salts are still lost through the urine, however, as well as through gills and oral membranes. The high salt gradient is maintained in the body by ingesting food and salt absorbing cells at the gills (Maetz et al., 1964; Garcia-Romea and Motais, 1966; Motais and Maetz, 1969).

In the marine environment, the teleost must rid itself of excess salts and absorb water to avoid dehydration. Drinking rates of salt-water fishes have been found to be greater than their freshwater counterparts. Once the water has entered the gut it is absorbed into the body through the intestinal membrane, apparently following a gradient caused by the active uptake of Na^+ and Cl^- ions from the intestinal lumen. Thus, the Na^+ and Cl^- concentrations decrease as the salt-water moves down the intestine while K^+, Ca^{++}, Mg^{++} and SO_4^{--} show

an increase (Smith, 1932). The glomerular filtration system is of no use to the marine teleost, and the glomeruli are usually poorly developed or completely absent (Hickman, 1968).

Recent studies on salt and water flux in the urinary bladder have also revealed water reabsorption following Na^+ transport across the bladder wall of some teleosts (Hirano et al., 1972; Johnson et al., 1972; Utida et al., 1972). Urine production is low compared to the freshwater teleost, with osmolality of the urine approaching that of the serum. The divalent ions Mg^{++} and SO_4^{--} are concentrated for excretion in the urine while Na^+ and Cl^- are excreted through the gills.

Although the sites of ion movement have been located, the molecular mechanisms which accomplish the salt transfer are not yet thoroughly understood. Several theories have been presented to explain the transport mechanism of Na^+ and Cl^- in the gills.

Maetz (1964) found Na^+ and Cl^- to be pumped independently in the freshwater adapted goldfish Carassius. Na^+ influx appeared correlated to ammonia efflux, while Cl^- influx was considered to be associated with HCO_3^-. Trout gills also appear to have independent pathways for influx of Na^+ and Cl^- (Kirschner et al., 1970). Na^+ influx is not clearly linked with ammonia efflux as in Carassius, but instead appears coupled with H^+. In his review of salt transfer, Maetz (1971) discounted the theory of an obligatory exchange between

Na^+ and NH_4^+ and postulated the use of both NH_4^+ and H^+ in exchange for Na^+.

Chloride transport in trout was found to be stimulated by injections of $NaHCO_3$ and $(NH_4)HCO_3$ (Kirschner et al., 1972), although no apparent change was seen in chloride influx with the addition of the carbonic anhydrase inhibitor, acetazolamide. If a Cl^-/HCO_3^- exchange exists in the trout gill there is evidently sufficient HCO_3^- in the blood to accomplish the exchange.

In seawater fishes, two independent Na^+ and Cl^- pumps are again observed, resulting in the extrusion of these salts. Na^+ is thought to be exchanged with K^+, on the mucosal membrane of the chloride cell, being mediated by a Na^+-K^+activated ATPase (Epstein et al., 1967; Kamiya et al., 1969; Utida et al., 1970; Zaugg and McLain, 1970). This enzyme is reportedly higher in saltwater adapted fishes. However, electronmicrographs indicate the Na^+-K^+ activated ATPase is not located on the mucosal membrane as the theory suggests. Thus the function and importance of this enzyme in osmoregulatory control is presently unclear.

Diffusive flow along the electro-chemical gradient may be able to account for much of the Na^+ efflux. Kirschner (personal communication) observed an electro-potential shift from positive to negative (environment to blood) when rainbow trout are adapted from freshwater to saltwater which would eliminate the need for an active Na^+ transport mechanism.

Chloride is working against an electro-chemical gradient and is therefore thought to be actively excreted in the saltwater teleost. Maetz (1971) proposes a Cl^-/HCO_3^- exchange to move chloride from the blood to the "chloride cell." An electrogenic pump is then suggested for releasing chloride to the environment. Besides this active transport mechanism, Cl^- crosses through the branchial epithelium by diffusive flow and exchange diffusion.

Saltwater adapted teleosts show turnover rates of 30-50% of exchangeable internal Na^+ per hour (Maetz, 1969). Similar values have also been reported for Cl^- turnover rates in saltwater (Potts and Evans, 1967; Maetz, 1970). Upon entering freshwater, Na^+ and Cl^- outflux is reduced by about 90% (Mortais et al., 1966). This is accomplished through a large immediate drop, followed by a delayed secondary regulation which further reduces the Na^+ outflux. Ball (1969) believes the rapid drop in Na^+ efflux to be caused by a disruption of the exchange diffusion system. The secondary reduction in the Na^+ exchange rate is postulated to be under endocrine control.

A growing body of evidence has revealed the importance of the endocrine system in osmoregulation in fishes. Prolactin promotes survival of hypophysectomized cyprinodonts in freshwater by conserving the internal Na^+ concentration (Burden, 1956). This has not been found in other taxonomic groups of teleosts (Chavin, 1956; Donaldson and McBride, 1967). Hypophysectomy of saltwater adapted teleosts

causes a reduction of Na^+ exchange, a decrease in salt excretion through the gills, and a reduction of salt and water absorption through the gut. Injection of ACTH and cortisol cause Na^+ turnover and flux rates in gill and gut to return to normal values. Prolactin shows no osmoregulatory control in the saltwater adapted teleost. Adrenalectomy is also followed by large reduction of gill Na^+ exchange and salt excretion. Normal levels are again brought about by injection of cortisol or ACTH. Cortisol is now believed to be needed for salt absorption in freshwater adapted fish as well as salt excretion in saltwater adapted fish (Maetz, 1969; Johnson, 1973).

Although cortisol injection has been shown to increase salt and water absorption through the gut, cortisol levels were found similar in both fresh and salt adapted eels (Gaitskell and Jones, 1970). Utida and Hirano (1972) found prolactin to inhibit water permeability while stimulating sodium absorption in the freshwater adapted eel intestine. Prolactin has, therefore, been postulated as an antagonistic mechanism to block the water reabsorption effect of cortisol in freshwater.

A number of other hormones have been considered in the osmoregulatory control of fishes, including somatotropin, aldosterone, vasotocin, isotocin, urotensin, acetylcholine, and adrenalin (Johnson, 1973). Data are not yet available to allow generalizations to be made on their effects.

The euryhaline teleost must be able to rapidly adjust its renal and extrarenal mechanisms of salt and water control when exposed to large changes in external salinity. Transport mechanisms at the gills must take on an absorptive rather than secretory function when the fish enters the river from the ocean. Renal adjustments must also be made to compensate for the influx of water the fish experiences in freshwater. As most teleosts are unable to accomplish this switch in osmoregulatory control, they are only able to survive a narrow range in salinity. Only the anadromous and catadromous fishes can do this with a degree of efficiency. During the summer of 1970, W. T. W. Potts and P. P. Rudy began preliminary observations on the osmoregularity abilities of the anadromous sturgeons of the Pacific Coast, A. medirostris and A. transmontanus (Potts and Rudy, 1972). Ion concentration values of serum and urine were obtained for fresh and saltwater adapted fish. However, due to the large size of the sturgeon, only a few individuals were examined. Results, especially those of urine analysis, were quite varied. Further osmoregulatory research on these chondrostean fishes is necessary to better understand the mechanisms involved with osmotic and ionic control in fishes. Such information may also prove valuable in studies of other diadromous species such as the salmonids. With more information available on the physiological needs of the sturgeon, chances of a successful management program will also increase. Research for this thesis

was thus undertaken to supplement and extend Potts and Rudy's initial study. Serum and urine ion concentrations of A. medirostris were obtained at saltwater, freshwater, and a salinity isosmotic with the serum. In addition, urine production rates were also established in order to gain an understanding of the sturgeon's ability to regulate its urine water loss with changes in environmental salinities.

MATERIALS AND METHODS

Field Collection

All but two of the A. medirostris used for the experiments were taken from the Umpqua River, approximately one-half mile below Reedsport, Oregon. A gill net was set for 20-30 minutes at late evening slack tides during June, July and August of 1973. According to Mr. Wilson Boye, a local shad fisherman who assisted in the capture operations, the green sturgeon begin a slow ascent of the river in March, reaching the tidal area around Reedsport by June. Several attempts were made in April to obtain sturgeon; however, these were unsuccessful. No further attempts were made until mid-June, when occasional sturgeon were picked up. Mid-July fishing proved to be the most productive, one set on July 10 capturing 15 sturgeon. During August, only an occasional sturgeon was again found, possibly due to the majority of the sturgeon moving above the sampling area.

All sturgeon captured in the Umpqua River were obtained in brackish water. Surface salinity varied from 18 $^{o}/_{oo}$ in June (high slack tide) to 12 $^{o}/_{oo}$ by mid-August (low slack tide). Water temperature increased from 17 ^{o} to 20 ^{o}C during this time period.

Although at times abundant, the sturgeon captured in the Umpqua were all quite large for use in the laboratory, varying from 3 to 5-1/2 feet total length. Therefore, one trip in late August was taken to the Rogue River where sturgeon were reported to be abundant, in hopes of obtaining smaller specimens. Two small green sturgeon (24 and 28 inches) were captured, using a gill net at Elephant Rock, approximately 2 miles from the mouth of the river. Seining and otter trawling were also tried but without success. These fish were taken during the night on a low slack tide. Temperature was 20°C and the water was fresh.

Sturgeon were transported to Oregon Institute of Marine Biology wrapped in sheets of wet burlap, where they were kept in circular fiberglass holding tanks containing approximately 900 liters of H_2O. A continuous flow of water plus additional aeration assured the fish of adequate oxygen. The fish were introduced to water of approximately the same salinity as they had been found in the river. Salinity was then changed at the rate of 5‰ /24 hours until the desired salinity was reached. Saltwater temperatures in the tanks were 14° to 16°C, while freshwater temperatures ranged from 17° to 19°C.

Experimental Design

The first sturgeon sampled, M-1,[1] was monitored at sea H_2O

[1] Number denotes order of capture and testing of specimens. M-1 through M-7 are Umpqua sturgeon; M-8 and M-9 are Rogue sturgeon.

and 12‰, which was thought to be close to isosmotic with the sturgeon's body fluid salt concentration. The drop in salinity from seawater to 12‰ occurred over an 8-hour period. M-3, the next sturgeon to be tested, was used only in saltwater. After gaining an understanding of the concentrations of ions in the serum and urine at each salinity from these two specimens, it was decided to continually monitor the next fish at each salinity, allowing 8 hours for each drop in salinity. This was done with M-4 and M-5.

In order to compare results from these abrupt, short term salinity changes with slow, long term acclimation, the remaining fish were acclimated for 3 to 4 days at a given salinity. They were then catheterized and monitored for 48 hours. If these fish were tested at more than one salinity, they were acclimated while free in the larger holding tanks, with a change of 5‰ /24 hours until the desired salinity was reached. Acclimation was then allowed for 3 to 4 days before catheterization was begun. As values were obtained throughout the course of the experiments, it became evident that 12‰ was slightly hyperosmotic to the serum osmolality. The intermediate salinity for the last two sturgeon was thus lowered to 9‰.

During the sampling period the sturgeon were confined to rectangular fiberglass troughs. Panels were inserted within the troughs to adjust the length and width, thereby restricting the fish's movements while the catheter was in place. Water of appropriate salinity

was continually run through the trough, along with an air supply to insure adequate oxygen.

Ion Measurements

Sodium, potassium, and calcium concentrations were measured by a Coleman 21 flame photometer. Chloride estimates were established by silver ion titration using a Buchler-Cotlove chloridometer. Sulfate values were obtained turbidometrically, SO_4^{--} being precipitated by a $BaCl_2$ gel (Berglund and Sorbo, 1960). Magnesium measurements involved formation of a thiazole yellow $Mg(OH)_2$ complex in alkaline solution (Sky-Peck, 1964). Both sulfate and magnesium were measured on a Coleman model 6/20 spectrophotometer. Total osmolality of samples was measured on a Hewlett Packard 302B vapor pressure osmometer.

Urine Sampling

Urine was collected for ion analysis and urine production rates by use of a size 8 French, Foley catheter. In A. medirostris the urethra is short, quickly opening into a large bilobed urinary bladder. The catheter was, therefore, inserted through the urinary opening only about 1 inch. The bulb was then filled with approximately 3 ml of water, causing a firm seal. This proved strong enough so no suture was required to hold the catheter in place.

The opposite end of the catheter was connected to a piece of latex tubing (50 cm in length, 3/8 inch I.D.). The tubing was brought through an opening at the side of the tank and inserted into a graduated cylinder, which allowed continual monitoring without additionally disturbing the fish. All urine collected for each 8-hour period after catheterization was pooled and ion concentrations determined for Na^{+}, K^{+}, Ca^{++}, Mg^{++}, SO_4^{--}, Cl^{-}, and total osmolality.

Blood Sampling

Blood samples were obtained in one of two ways. For all sturgeon except M-8 and M-9, an inside needle catheter (17 gauge needle, catheter tubing 24 inches in length) was inserted into the caudal vein, just posterior to the anal fin. The catheter tubing was secured with a suture and filled with dilute heparin solution to prevent clotting. The free end of the catheter was brought through an opening at the side of the tank, where blood samples could be drawn without disturbing the fish. Blood samples were obtained in the following manner. First, the heparin solution in the catheter tubing, plus 0.5 ml of blood were withdrawn with a syringe. This was discarded, and another syringe was used to obtain 2 to 3 ml of blood to be used for analysis. The catheter tubing was then refilled with the heparin solution. As the blood was slow to clot (10-15 min), no anticoagulant was used in the blood being analyzed. Blood was immediately

centrifuged at 2000 rpm for 10 minutes. After centrifugation, a clear supernatant remained. This often still contained fibrin, and had to be recentrifuged later to obtain the serum. On other occasions, the blood had already clotted after the first centrifugation and the clear supernatant was used without further spinning. Three to six blood samples were taken at each salinity during the time the sturgeon were being monitored for urine production.

The two small sturgeon were not catheterized in the caudal vein. Instead, a hypodermic syringe was inserted into the vein, and 2 to 3 ml of blood were removed. One blood sample was obtained for these fish at each salinity immediately after the urine production experiment.

RESULTS

Serum Ion Analysis

For those sturgeon which were cannulated in the caudal vein, three to six blood samples were drawn during the urine production monitoring period and serum ion concentrations measured. Ion and osmolality concentrations from all blood serum samples at each salinity were averaged (Tables II-V). Mean, standard deviation, standard error, and range are shown in graphs (Figures 1-7), along with ion and osmolality values of the urine for comparison. Serum concentrations found in this study are also listed with values from other species of Acipenser, Polyodon, and various teleosts in Table I.

A. medirostris's serum osmolality shows a marked decline as they are transferred from saltwater to freshwater (Figure 1). The majority of this drop can be attributed to a decrease in Na^{+} and Cl^{-} ions in the serum (Figures 2 and 4). A small decline was also noted in serum K^{+}, Ca^{++}, Mg^{++} or SO_4^{--} ions with the salinity change from seawater to freshwater.

Urine Ion Analysis

Ion concentrations were determined for each 8-hour period after catheterization was started. The values from each 8-hour period at

TABLE I

BLOOD CHEMISTRY

mOsmol	Na^{+}*	K^{+}	Ca^{++}	Mg^{++}	SO_4^{--}	Cl^{-}	Comments	Reference	No. fish examined
Acipenser medirostris									
254.21 ± 12.42	140.93 ± 5.50	2.93 ± 0.30	2.97 ± 0.12	1.19 ± 1.12	4.85 ± 0.43	111.11 ± 3.70	Freshwater	Present Study	6
398.83 ± 14.61	206.78 ± 4.98	3.73 ± 0.17	3.72 ± 0.16	2.90 ± 0.39	6.67 ± 0.43	176.80 ± 3.70	Seawater	"	6
316.97 ± 7.59	139.00 ± 1.41	2.90 ± 0.07	2.75 - 0.04	1.15 ± 0.04	5.15 ± 0.04	117.75 ± 5.13	9‰	"	2
320.68 ± 10.51	161.99 ± 7.14	2.68 ± 0.20	1.88 ± 0.41	5.18 ± 0.19	1.88 ± 0.41	145.72 ± 3.44	12‰	"	3
---	120.71 ± 9.16	3.12 ± 0.77	2.31 ± 0.27	1.21 ± 0.25	2.80 ± 0.02	102.03 ± 8.94	Freshwater	Potts & Rudy, 1972	7
---	176.50 ± 14.18	2.07 ± 0.19	3.40 ± 0.58	1.61 ± 0.24	2.68 ± 0.09.	170.00 ± 8.65	Seawater	"	6
Acipenser transmontanus									
---	125.0	5.5	3.4	-	-	-	Freshwater	"	1
---	130.0	2.5	1.7	2.1	0.4	115.1	Seawater, males	Urist & Van de Putte, 1967	2
---	129.0	2.7	1.8	2.0	0.5	111.0	Freshwater	"	5
Acipenser oxyrhynchus									
---	150.6	2.67	1.9	0.9	-	112.9	Freshwater	Magnin, 1962	23
---	164.9	2.84	1.5	1.3	-	132.9	Brackish water	"	20
Acipenser sturio									
---	155.8	4.3	2.3	1.47	0.7	119.7	Freshwater	"	
---	163.6	4.65	2.1	1.57	0.5	126.4	Brackish water	"	
Polydon spathula									
258.1 ± 1.8	142.5 ± 0.3	3.79 ± 0.23	3.73 ± 0.56	2.94 ± 0.08	-	112.0 ± 11.5	Female, freshwater	Grant et al., 1970	3
260.2 ± 4.2	139.3 ± 2.2	3.57 ± 0.14	3.86 ± 0.10	2.30 ± 0.10	-	112.6 ± 1.4	Male, freshwater	"	8
Salmo gairdneri									
302.4 ± 1.5	163.4 ± 1.2	0.94 ± 0.09	6.53 ± 0.34	2.71 ± 0.15	-	124.1 ± 1.8	8 males, 2 females, freshwater	Grant & Mehrle, unpublished	10
Oncorhynchus tshawytscha									
---	159.0 ± 17.0	0.40 ± 0.10	5.80 ± 0.40	3.60 ± 0.20	-	112.0 ± 10.0	post-spawning males	Urist & Van de Putte, 1967	2
Micropterus salmonides									
---	164.3	2.9	-	-	-	113.6		Hunn, 1966	33

*Ion concentrations in mMoles per liter

± = standard error

TABLE II

A. MEDIROSTRIS ADAPTED TO FRESHWATER

Fish	mOsmolal	Na^+	K^+	Ca^{++}	Mg^{++}	SO_4^{--}	Cl^-
			Serum				
M-4	278.39	152.00	2.50	3.07	0.90	5.53	116.25
M-5	279.55	149.33	2.63	2.92	1.37	3.35	126.67
M-6	283.97	153.00	4.56	3.50	1.69	3.60	111.25
M-7	248.21	146.25	2.36	3.08	0.78	5.40	105.00
M-8	198.63	122.00	2.65	2.55	1.30	4.90	110.00
M-9	236.51	118.00	2.90	2.70	1.10	6.30	97.50
$\bar{x}$	254.21	140.93	2.93	2.97	1.19	4.85	111.11
S.D.	30.42	13.46	0.75	0.30	0.30	1.06	9.07
S.E.	12.42	5.50	0.30	0.12	0.12	0.43	3.70
			Urine				
M-4	33.69	1.63	9.18	0.70	3.31	3.11	2.52
M-5	23.76	2.77	3.38	0.53	1.29	1.53	0.87
M-6	143.10	20.63	14.88	1.61	3.01	5.35	0.33
M-7	30.63	2.70	7.12	0.48	0.63	2.85	0.16
M-8	30.07	4.46	2.56	0.40	0.53	2.41	0.50
M-9	21.75	7.59	5.52	0.47	0.98	3.62	4.34
$\bar{x}$	47.17	6.63	7.11	0.70	1.63	3.15	1.46
S.D.	43.10	6.54	4.12	0.42	1.12	1.18	1.53
S.E.	17.60	2.67	1.68	0.17	0.46	0.48	0.62

Ion concentrations in mMoles per liter

TABLE III

A. MEDIROSTRIS ADAPTED TO 9‰ SEAWATER

Fish	mOsmolal	Na^+	K^+	Ca^{++}	Mg^{++}	SO_4^{--}	Cl^-
			Serum				
M-8	306.24	141.00	2.80	2.80	1.10	5.10	125.00
M-9	327.70	137.00	3.00	2.70	1.20	5.20	110.50
$\bar{x}$	316.97	139.00	2.90	2.75	1.15	5.15	117.75
			Urine				
M-8	49.81	65.00	4.20	3.64	5.08	6.84	28.20
M-9	43.60	56.75	1.90	3.90	5.61	5.73	23.00
$\bar{x}$	46.71	60.88	3.05	3.77	5.35	6.29	25.60

Ion concentrations in mMoles per liter

TABLE IV

A. MEDIROSTRIS ADAPTED TO 12‰ SEAWATER

Fish	mOsmolal	Na^+	K^+	Ca^{++}	Mg^{++}	SO_4^{--}	Cl^-
			Serum				
M-1	344.00	144.50	2.20	2.80	5.45	2.80	152.50
M-4	299.55	170.80	2.82	1.08	5.42	1.05	138.00
M-5	318.49	170.66	3.02	1.80	4.73	1.80	146.67
$\bar{x}$	320.68	161.99	2.68	1.88	5.18	1.88	145.72
S.D.	18.21	12.37	0.35	0.72	0.33	0.72	5.97
S.E.	10.51	7.14	0.20	0.41	0.19	0.41	3.44
			Urine				
M-4	156.75	17.48	18.13	3.53	23.70	32.66	60.00
M-5	47.62	7.18	11.06	2.66	4.39	11.04	26.85
$\bar{x}$	102.19	12.33	14.60	3.10	14.05	21.85	43.43

Ion concentrations in mMoles per liter

TABLE V

A. MEDIROSTRIS ADAPTED TO SALTWATER

Fish	mOsmolal	Na^+	K^+	Ca^{++}	Mg^{++}	SO_4^{--}	Cl^-
			Serum				
M-1	378.31	194.67	2.98	3.70	1.94	5.56	182.50
M-3	398.76	227.33	3.67	4.23	2.40	8.13	191.67
M-4	389.93	217.33	4.00	4.07	2.30	6.80	183.30
M-5	343.47	207.33	3.97	3.83	3.43	5.53	178.33
M-8	457.41	200.00	4.25	3.20	2.50	7.00	182.50
M-9	425.07	194.00	3.50	3.30	4.80	7.00	142.50
$\bar{x}$	398.83	206.78	3.73	3.72	2.90	6.67	176.80
S. D.	35.79	12.19	0.42	0.38	0.96	0.90	15.85
S. E.	14.61	4.98	0.17	0.16	0.39	0.37	6.47
			Urine				
M-1	373.31	3.35	4.37	7.03	78.36	70.91	161.67
M-3	385.17	78.00	7.60	9.80	80.00	84.00	175.00
M-4	387.17	4.25	3.20	6.90	81.50	90.00	175.00
M-5	370.97	12.63	2.60	10.50	80.75	80.25	170.00
M-8	459.48	156.40	5.12	5.26	61.00	70.08	147.00
M-9	407.62	152.60	4.40	5.76	60.52	60.55	191.00
$\bar{x}$	396.95	67.87	4.55	7.54	73.69	76.00	169.95
S. D.	29.57	66.31	1.60	1.96	9.19	9.80	13.47
S. E.	12.08	27.08	0.65	0.80	3.75	4.00	5.50

Ion concentrations in mMoles per liter

each salinity were averaged for individual sturgeon (Tables II-V). The values for the first 8-hour period were not included in the average, in order to minimize the effects of initial handling while inserting the catheter. Figures 1-7 illustrate ion concentrations and total osmolality of the urine for each salinity. Mean, standard deviation, standard error, and range of ion values are shown for both urine and serum.

Sodium concentrations varied greatly in the saltwater adapted fish, not only between sturgeon, but for individual sturgeon at different times during the catheterization process. Values were often high during the first several sampling periods, then showed a marked decline (Table VI).

TABLE VI

SODIUM CONCENTRATIONS OF URINE IN SALTWATER ADAPTED A. MEDIROSTRIS

Sturgeon	Na^+ concentration (mM)		
	8 hours	16 hours	24 hours
M-1	35.0	4.5	2.0
M-3	190.0	133.0	23.0
M-6	51.0	36.0	14.0

Sturgeon M-4 showed a low Na^+ concentration (4.25 mM) in saltwater, but began excreting larger amounts of Na^+ at 12°/oo . A decrease then followed when subjected to freshwater. Although wide fluctuation in Na^+ concentrations in the urine were observed, urine

production rates and concentrations of other ions do not exhibit corresponding changes (Tables II-V).

Urine Production

Two sturgeon, M-4 and M-5, were monitored for urine production at seawater (32‰), 12‰, and freshwater. Catheterization continued as the salinity was dropped to each new salinity over an 8-hour period (Figures 8 and 9). M-8 and M-9 were checked for urine production at seawater, 9‰, and freshwater, but were acclimated to each salinity over several days prior to catheterization (Figures 10 and 11). Table VII indicates the rates obtained for all sturgeon examined for urine production. Because urine flow was occasionally inhibited during the catheterization, rates have been given for both the total time and for the time of continuous urine flow at each salinity. From examining Table VII and Figures 8 through 11, it is evident that A. medirostris is increasing urine production as the external medium drops from salt to freshwater.

TABLE VII

URINE PRODUCTION RATES

Sturgeon	Weight (kg)	Saltwater		12‰		9‰	Freshwater	
		RTT*	RCF**	RTT	RCF	RTT	RTT	RCF
M-1	13.6	4.2	4.2					
M-3	11.3	2.0	2.0					
M-4	9.1	0.6	2.5	4.5	9.8		9.6	12.8
M-5	9.9	0.6	1.6	9.7	11.3		28.7	28.7
M-6	19.1						16.6	
M-7	5.9						22.3	
M-8	0.79	4.0				29.9	56.3	
M-9	0.51	6.6				38.8	78.4	

*Urine production rate over total time period (ml/hr/kg sturgeon).

**Urine production rate over period of continuous flow.

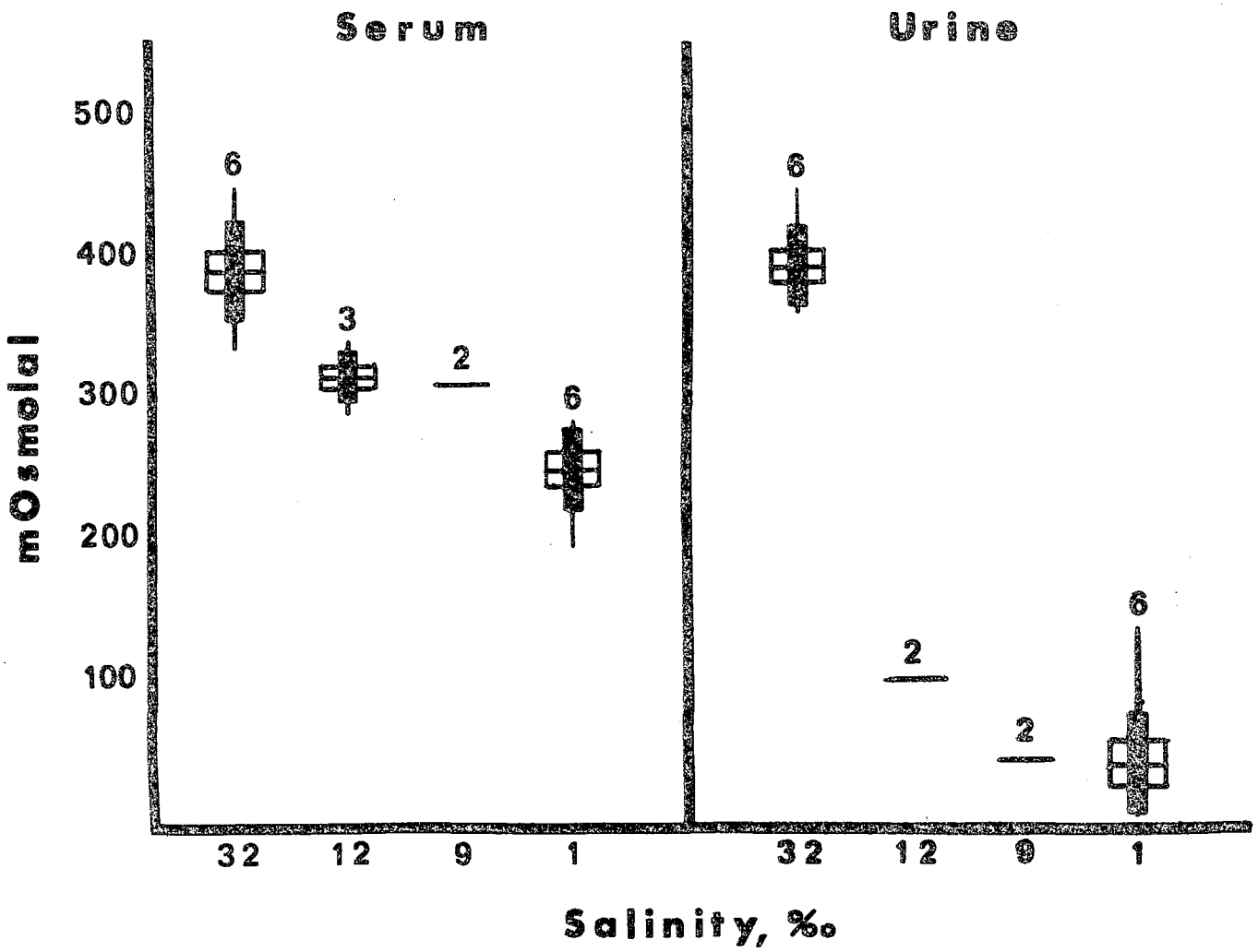

Figure 1. Environmental salinity vs. osmolality in A. medirostris serum and urine. Single horizontal line equals mean. Shaded bar equals standard deviation. Unshaded bar equals standard error. Single vertical line equals range. Number indicates sample size.

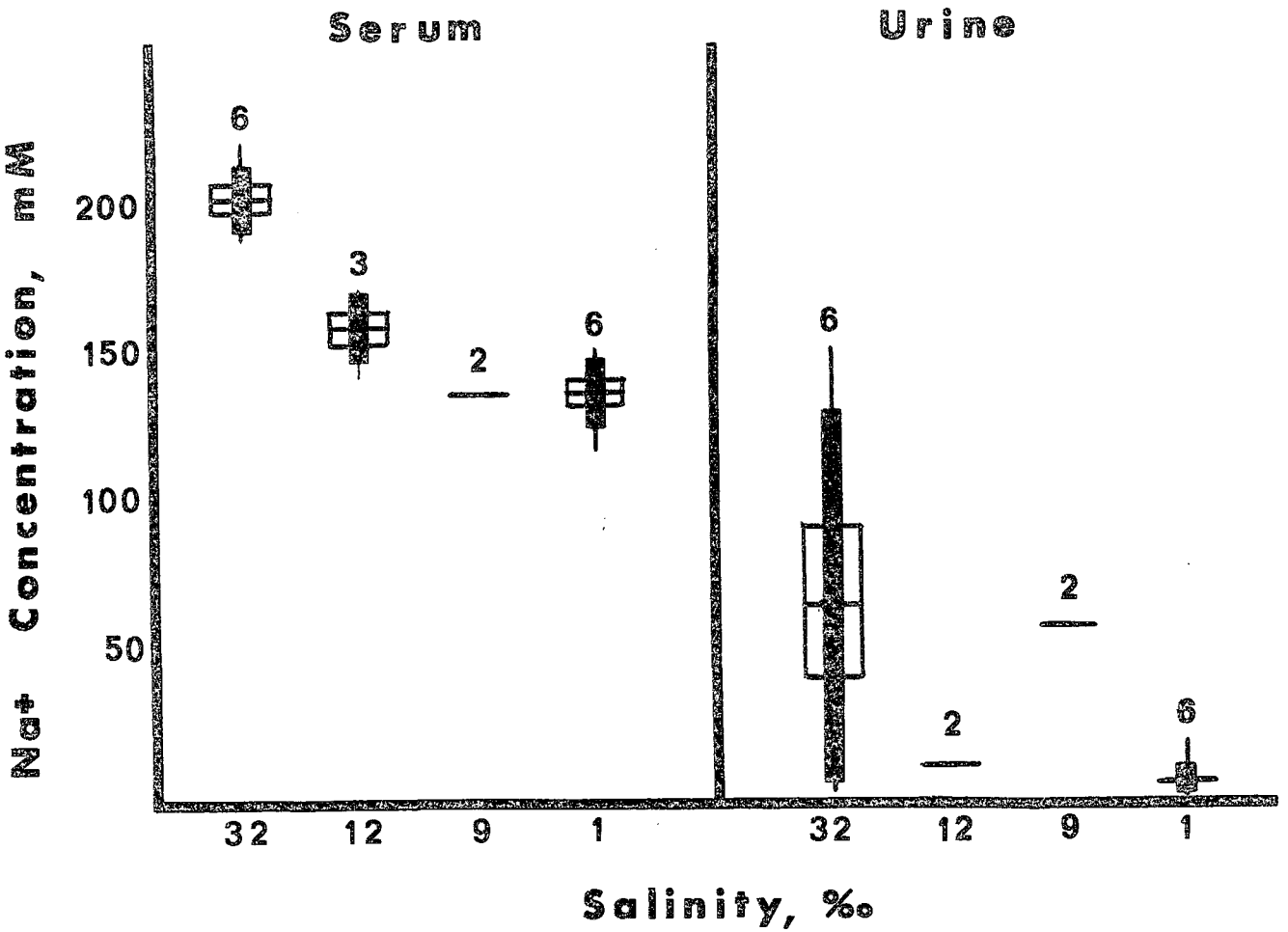

Figure 2. Environmental salinity vs. Na^+ concentration in A. medirostris serum and urine. Single horizontal line equals mean. Shaded bar equals standard deviation. Unshaded bar equals standard error. Single vertical line equals range. Number indicates sample size.

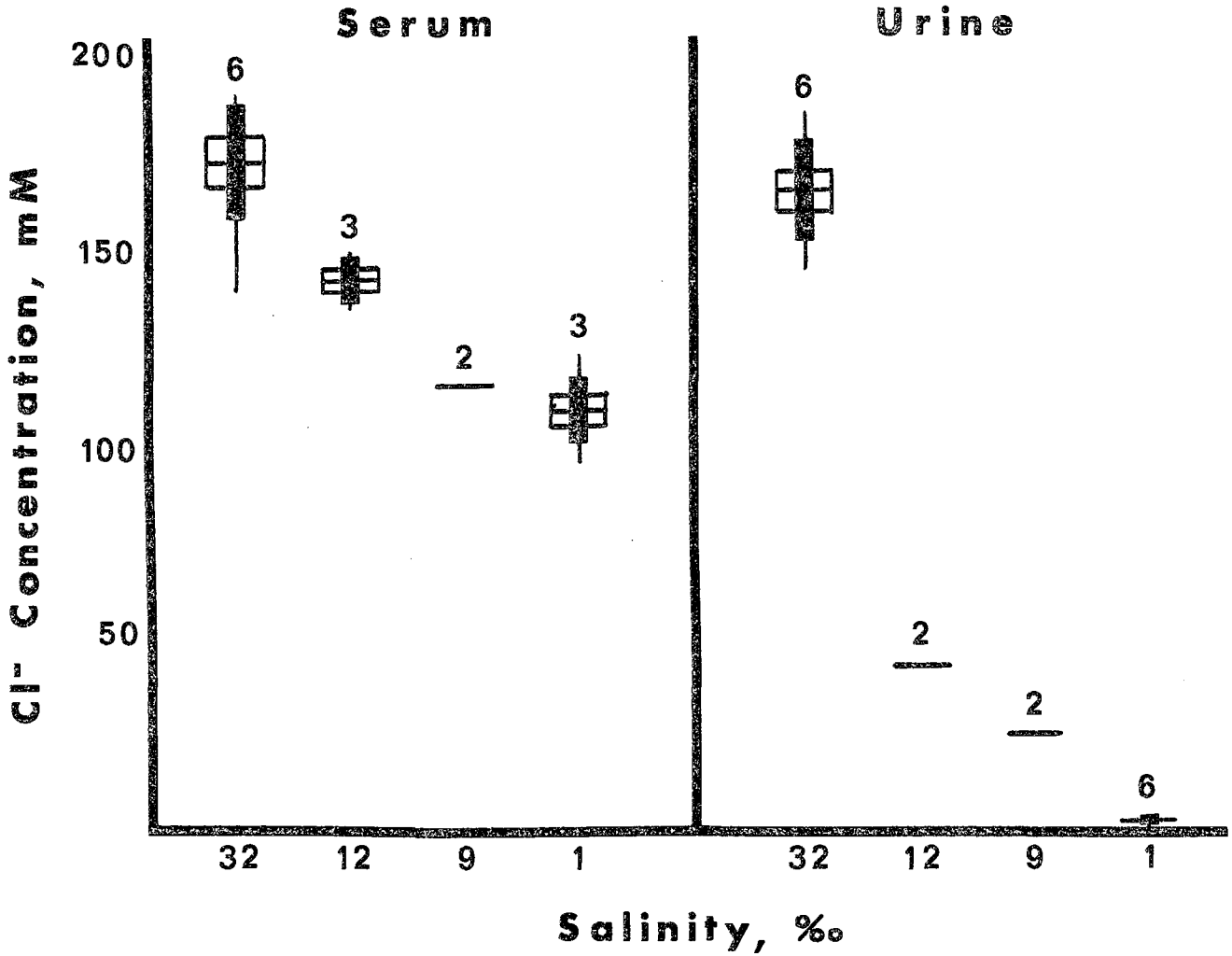

Figure 3. Environmental salinity vs. Cl^- concentration in A. medirostris serum and urine. Single horizontal line equals mean. Shaded bar equals standard deviation. Unshaded bar equals standard error. Single vertical line equals range. Number indicates sample size.

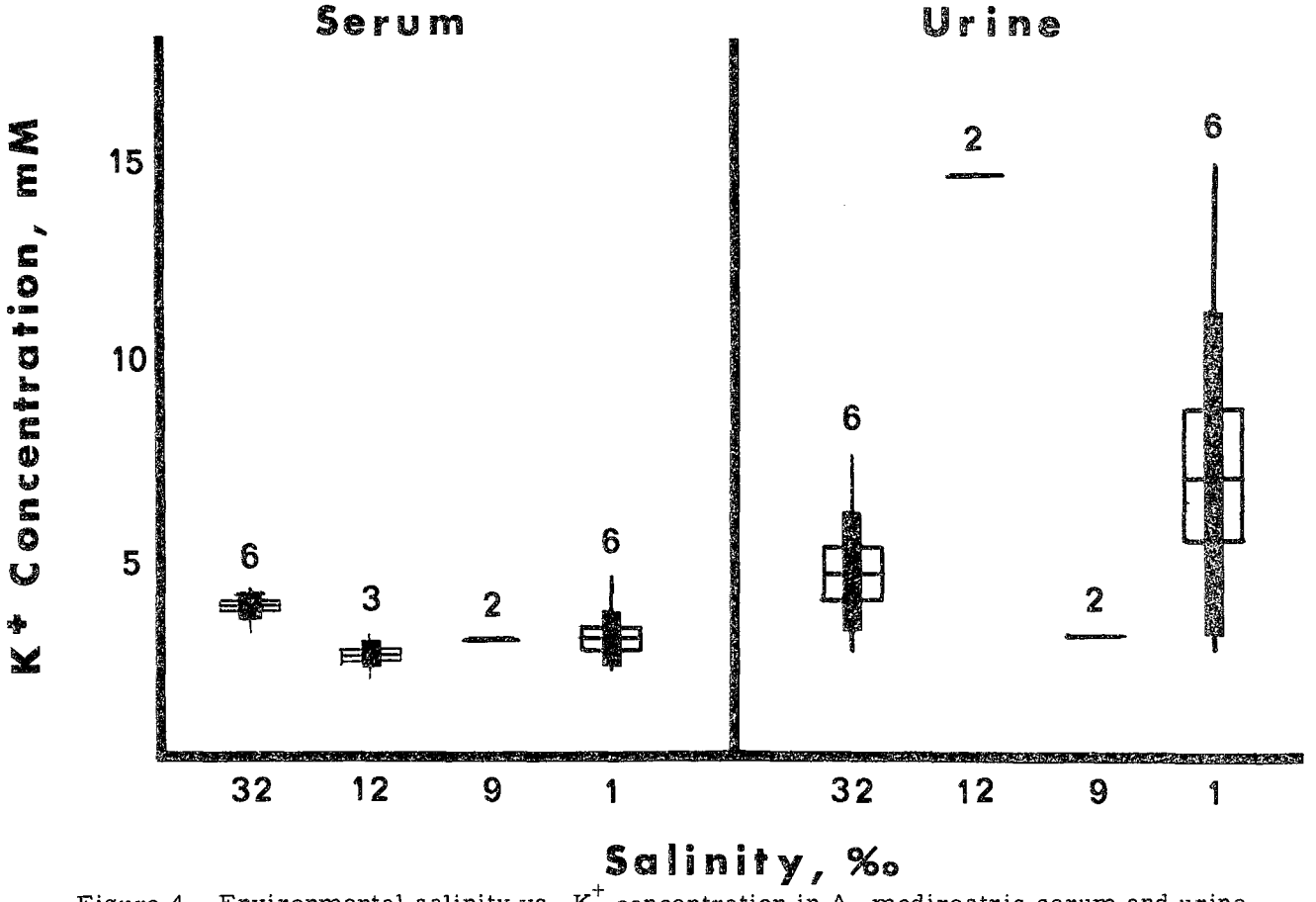

Figure 4. Environmental salinity vs. K^+ concentration in A. medirostris serum and urine. Single horizontal line equals mean. Shaded bar equals standard deviation. Unshaded bar equals standard error. Single vertical line equals range. Number indicates sample size.

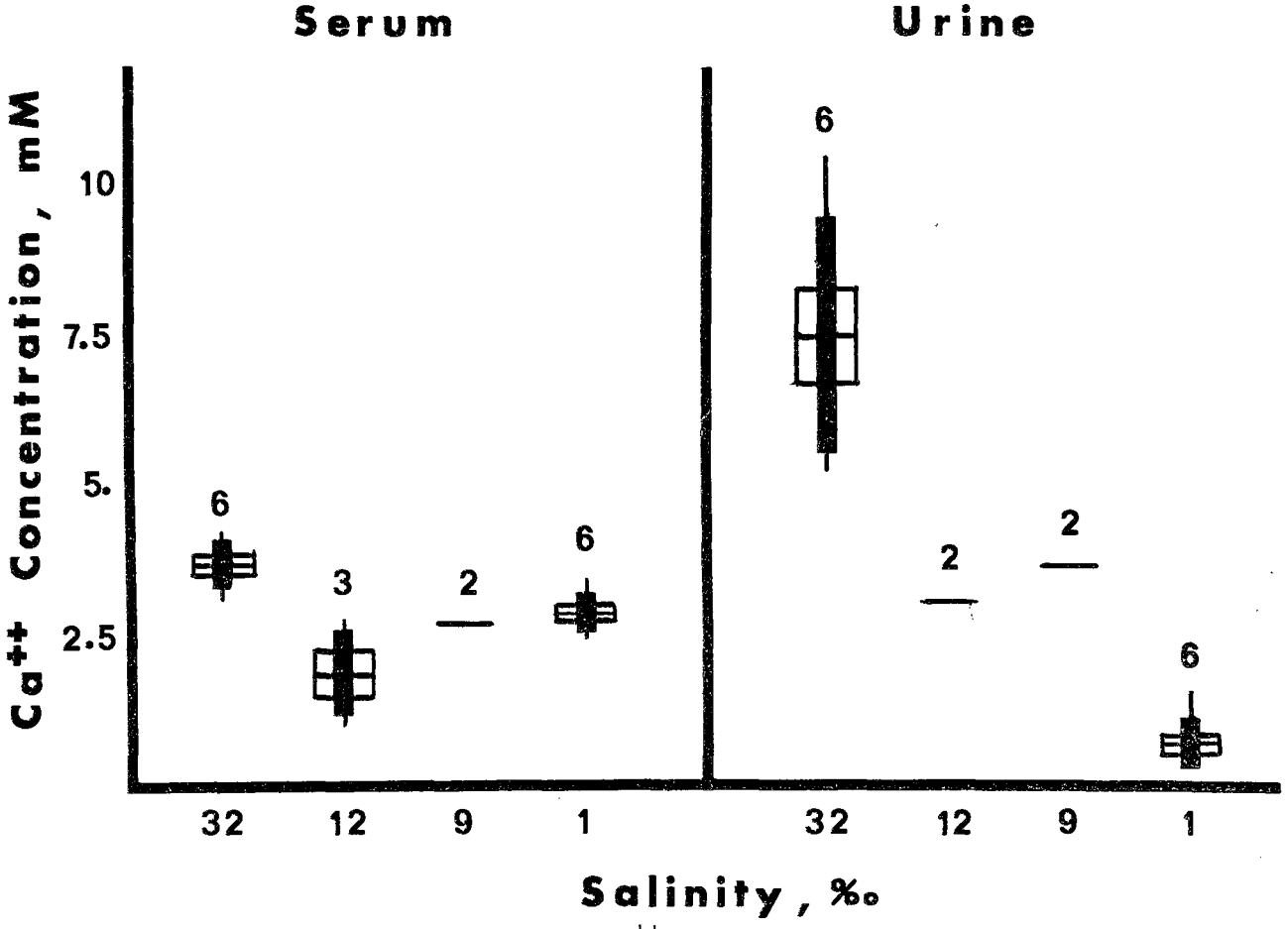

Figure 5. Environmental salinity vs. Ca^{++} concentration in A. medirostris serum and urine. Single horizontal line equals mean. Shaded bar equals standard deviation. Unshaded bar equals standard error. Single vertical line equals range. Number indicates sample size.

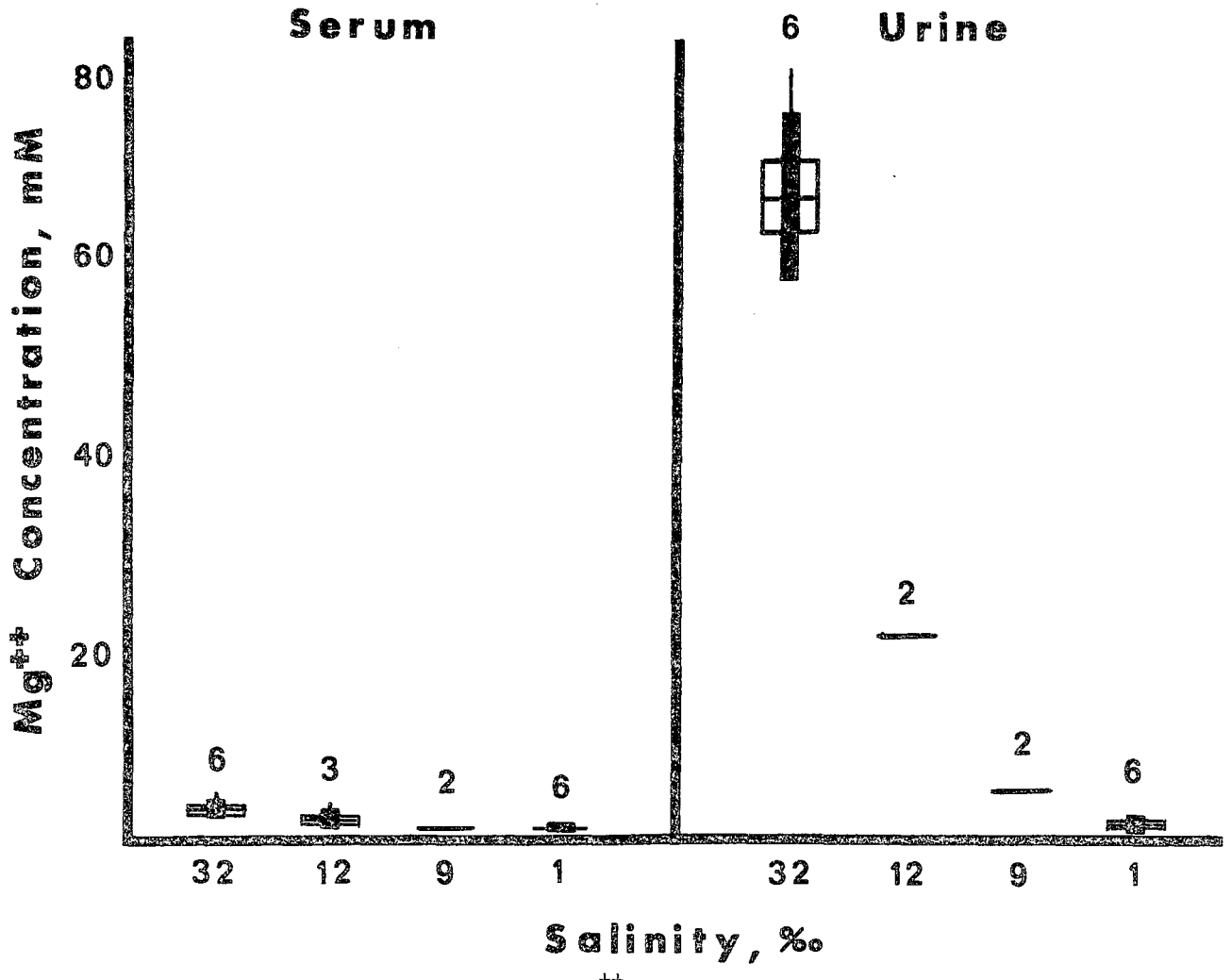

Figure 6. Environmental salinity vs. Mg^{++} concentration in A. medirostris serum and urine. Single horizontal line equals mean. Shaded bar equals standard deviation. Unshaded bar equals standard error. Single vertical line equals range. Number indicates sample size.

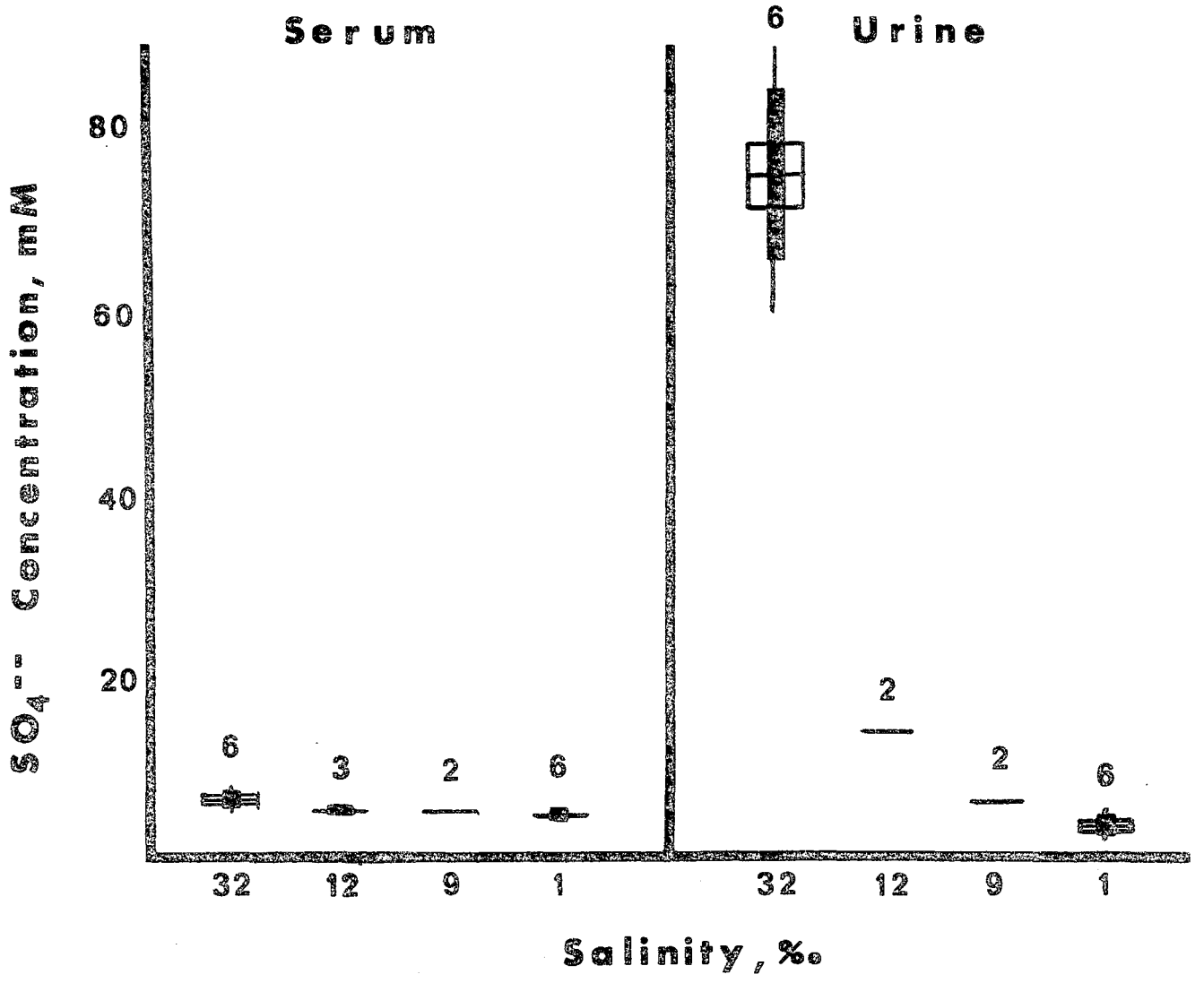

Figure 7. Environmental salinity vs. SO_4^{--} concentration in A. medirostris serum and urine. Single horizontal line equals mean. Shaded bar equals standard deviation. Unshaded bar equals standard error. Single vertical line equals range. Number indicates sample size.

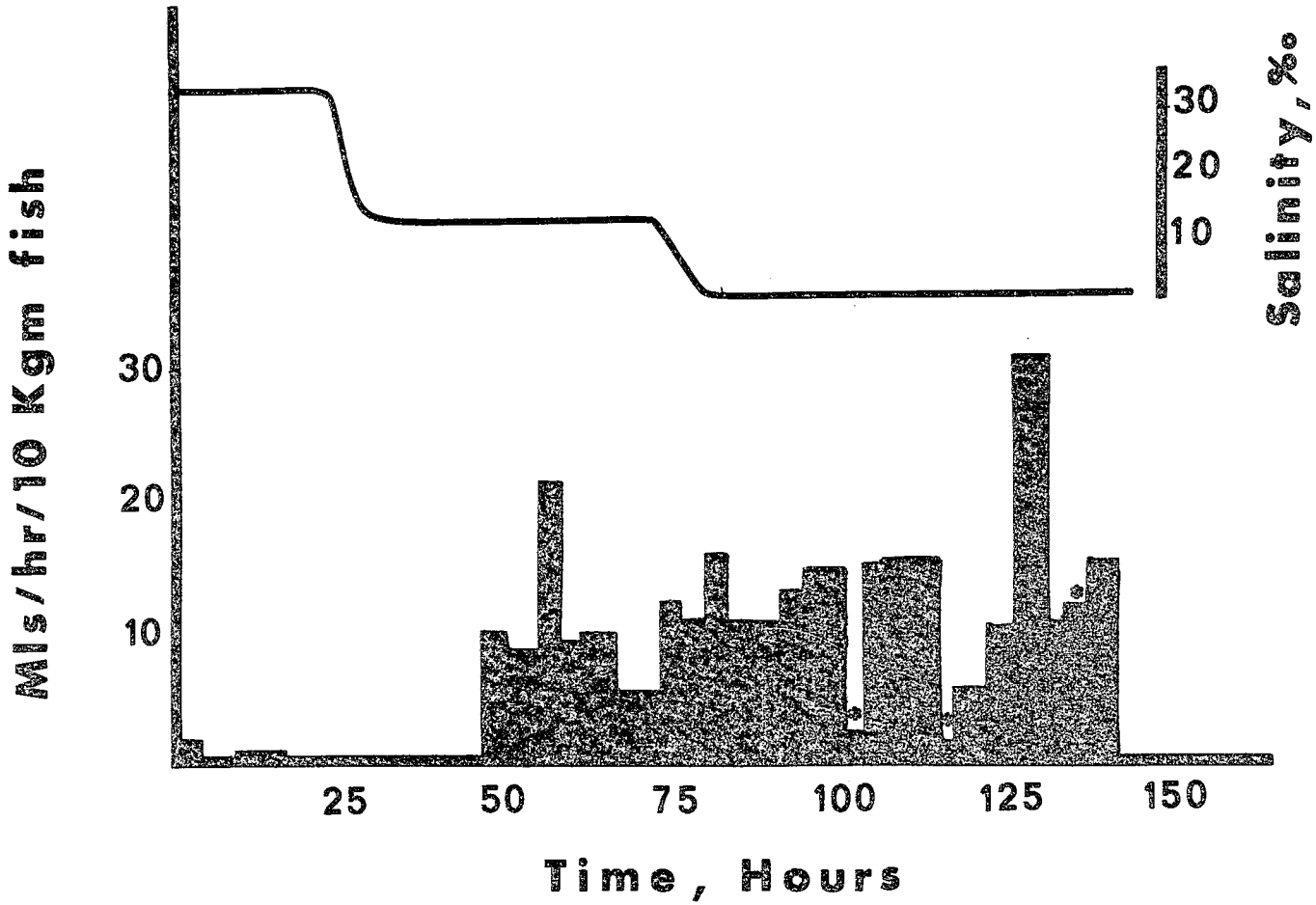

Figure 8. Environmental salinity vs. urine production in A. medirostris #4.

*Catheter unplugged and reinserted

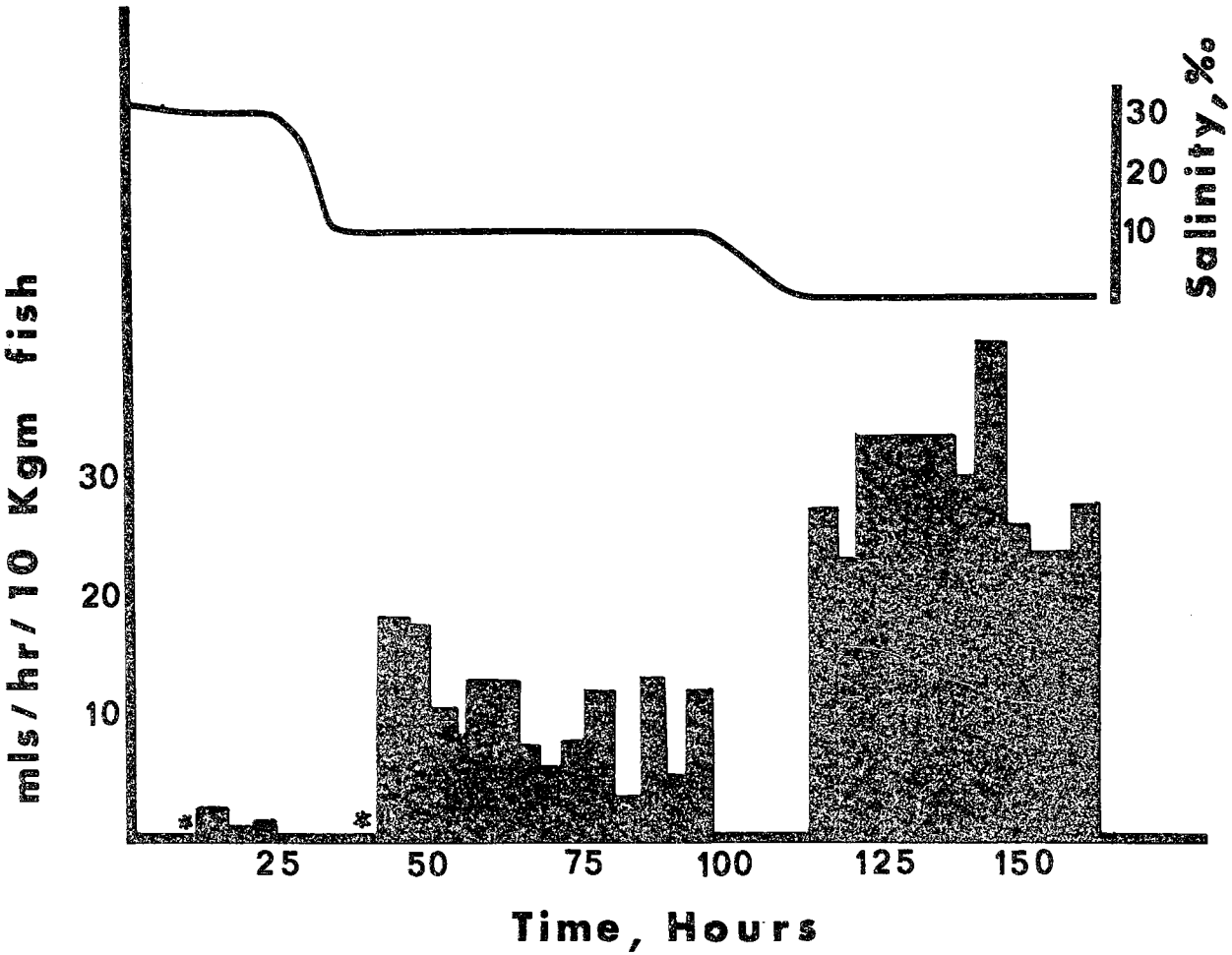

Figure 9. Environmental salinity vs. urine production in A. medirostris #5.

*Catheter unplugged and reinserted

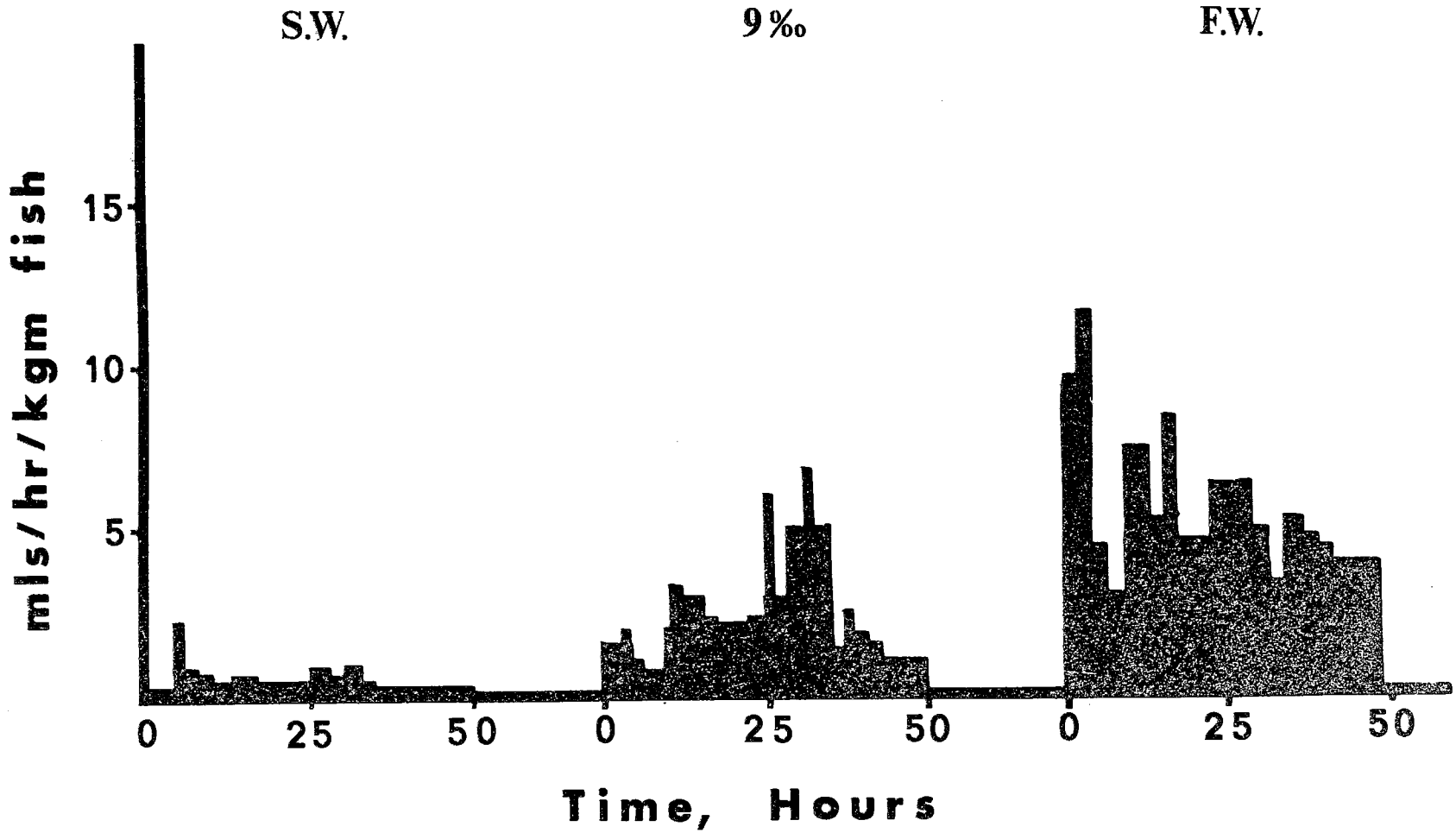

Figure 10. Environmental salinity vs. urine production in A. medirostris #8.

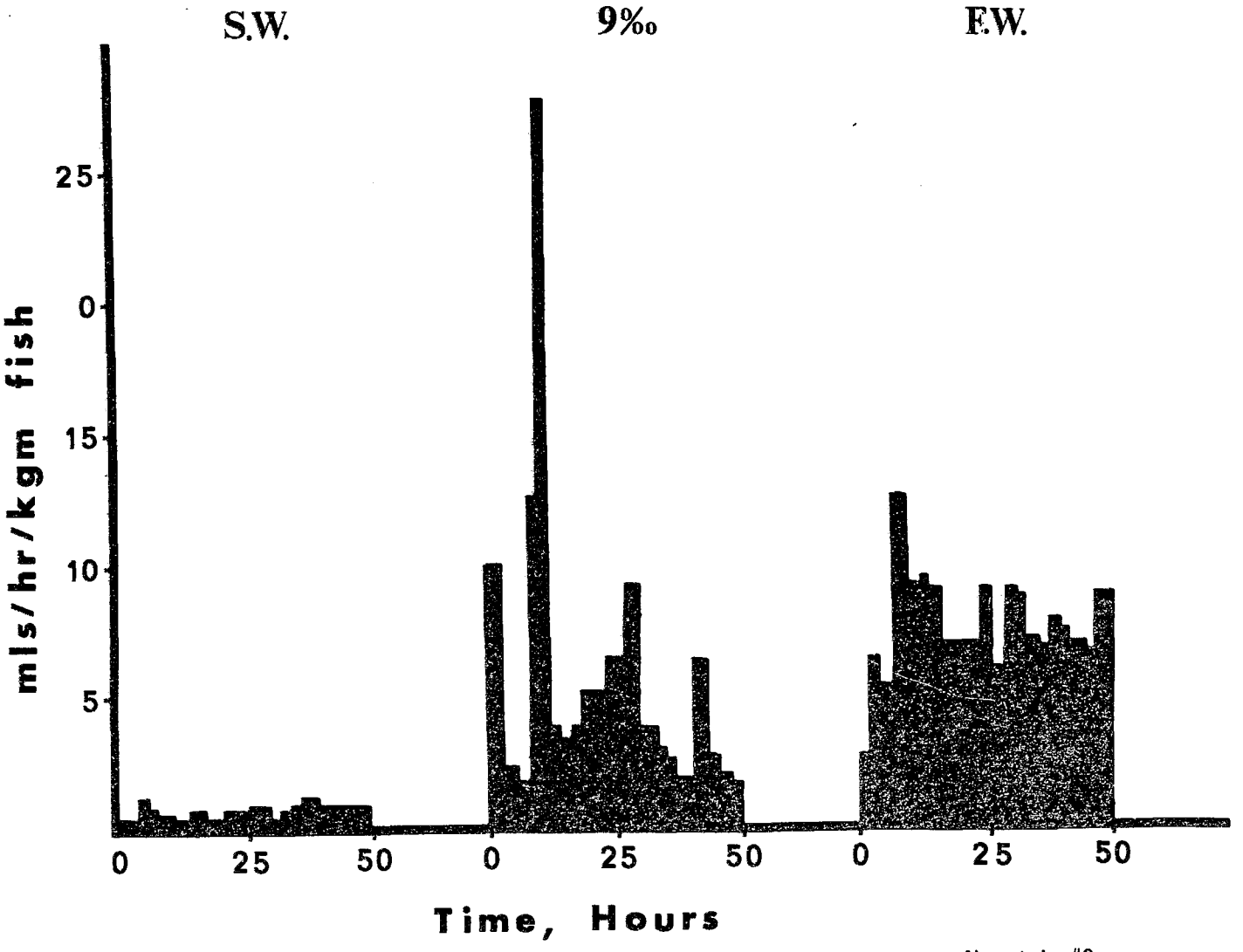

Figure 11. Environmental salinity vs. urine production in A. medirostris #9.

DISCUSSION

Ions and Osmolality of Serum

Ionic values of the blood of A. medirostris confirmed previous blood chemistry data for other Acipenseridae species. These values are also close to those given for a variety of teleostian fishes. Ion concentrations for both fresh and saltwater adapted A. medirostris appear similar to the values found by Potts and Rudy. Sulfate, however, is consistently higher (6.67 mM vs. 2.68 in saltwater and 4.85 mM vs. 2.8 in freshwater). These SO_4^{--} concentrations are also larger than have been reported for other species of sturgeons. The reason for these high sulfate values remains unknown.

Sodium concentrations of serum for freshwater adapted A. medirostris are close to those values previously reported for other species of sturgeon. However, unlike the white sturgeon, A. transmontanus, which increase their Na^+ concentration only slightly when subjected to seawater (Urist and Van de Putte, 1967), A. medirostris shows a considerable rise (140.93 mM to 206.78 mM). Potts and Rudy also found this large rise in serum Na^+, although their averages at both salinities remained lower (120.71 mM in freshwater and 176.50 mM Na^+ in saltwater adapted A. medirostris).

This notable increase in ion concentration is also evident in serum chloride values in A. medirostris, which rise from an average 111.11 mM in freshwater adapted fish to 176.80 mM in fish adapted to saltwater. Again, such a large rise is lacking in Cl^- values reported from Urist and Van de Putte's examination of A. transmontanus.

As A. oxyrhynchus and A. sturio move from fresh to brackish water, a rise is seen in the ion concentrations of the serum (Magnin, 1962). As these fish were not examined in saltwater, it is not known how high the ionic concentrations will rise in the two species. However, it appears that the ion concentrations of the serum are showing an increase, much like those of A. medirostris. This rise in ion concentrations of the serum is seen in most other euryhaline fishes also (Parry, 1966).

While all values of total serum osmolality are quite high in seawater, M-8 and M-9 are seen to be extremely large (457.07 mosmol and 425.07 mosmol, respectively). These two small sturgeon were also seen to have high urine concentrations, primarily caused by large concentrations of Na^+. As serum and urine values were comparable to the larger fish at lower salinities, it would appear smaller sturgeon are having difficulty osmoregulating at full strength seawater.

It is unfortunate that total osmolality was obtained for only one other species of sturgeon (A. sturio) that has previously been

examined (Magnin, 1962). These fish were examined only at freshwater and brackish water of unknown concentration.[2] No values for saltwater adapted sturgeon were made. It is, thus, hard to compare total osmolality fluctuation with salinity changes for the different species of sturgeon.

Ions and Osmolality of Urine

A. medirostris produces an isotonic urine when adapted to saltwater (Figure 1). At lower salinities, the urine becomes hypo-osmotic to the blood. From the fish examined, it seems evident that sturgeons, like the teleosts, are relying on an increased urine flow in dilute salinities to rid themselves of excess water.

Reports of urine ionic concentrations of other sturgeon are notably lacking in the literature. Potts and Rudy (1971) sampled five saltwater adapted A. medirostris for urine analysis. Na^+ concentration also varied greatly in these fish, ranging from 5 mM to 40 mM, with an average of 14.2 mM. Magnin (1962) reports ionic concentrations in urine for nine freshwater adapted and six brackish water*

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[2] When examining Magnin's values in Hoar and Randall's Fish Physiology, the concentrations for brackish water adapted individuals are mistakenly reported as saltwater adapted. As these fish were taken from estuarine waters, the salinity of the brackish water adapted sturgeon fluctuated considerably. Acipenser oxyrhynchus was reported found at approximately 15 gr%. No measurements were given for A. sturio, as salinities at capture sights were quite varied.

adapted A. sturio. Values are again found to fluctuate considerably, especially for sturgeon in the higher salinity (10.78 mM Na^+ to 61.4 mM Na^+).

Values from these authors were not monitored over an extended period of time; therefore, it is unknown if individual sturgeon showed fluctuations as seen in the present study. Mg^{++}, SO_4^{--} and Cl^- concentrations in urine of saltwater adapted A. medirostris were found to be much higher than previously reported by Potts and Rudy (Table VIII). While Potts and Rudy recorded an average Cl^- concentration of only 92.9 mM in saltwater adapted sturgeon, they found values as high as 167 mM. Due to the improved collecting device used and the consistency of the values, the higher values would appear more valid. As the saltwater teleost uses the urine to dispose of its excess divalent ions, chiefly Mg^{++} and SO_4^{--}, it is quite reasonable to suspect the sturgeon also use this route to eliminate these ions.

TABLE VIII

AVERAGE ION VALUES OF URINE IN SALTWATER ADAPTED A. MEDIROSTRIS (mM/l)

	Mg^{++}	SO_4^{--}	Cl^-
Potts & Rudy	22.90	9.70	92.90
Johnson	80.15	80.46	176.75

Measurements of ionic concentrations of the urine proved more variable than those for the blood chemistry. Two explanations might be considered. The first deals with the mechanical problem of obtaining the urine from the catheter. Although the Foley catheter appeared to seal firmly in the urethra, the collecting tube may have extended into one of the lobes of the bladder. If this occurred, there would be some possibility of blockage of urine in the other lobe of the bladder. On several occasions the catheters became clogged and urine remained in the bladder for some time before being expelled. Recent studies on the salt reabsorption abilities of the urinary bladder (Hirano et al., 1972; Johnson et al., 1972; Utida et al., 1972) indicate that some teleosts exhibit a Na^+ pump across the urinary bladder membrane. Johnson and coworkers speculated that saltwater adapted Platichthys stellatus used the Na^+ pump to create a concentration gradient in order to reabsorb water.

Hirano et al. surveyed 17 different species of fishes in their study of the osmoregulatory properties of the urinary bladder. Their findings showed a large variation in the use of the urinary bladder for osmotic and ionic regulation by different species. Marine fishes showed a considerable range in their water permeability properties. Stenohaline freshwater fishes showed little water permeability, the sodium reabsorption varying with the species. Bladders of euryhaline fishes of

saltwater origin decreased in water permeability when moved from saltwater to freshwater. Euryhaline fishes of freshwater origin, however, proved to be largely impermeable.

If Acipenser has developed such a reabsorption mechanism in its bladder, urine ionic concentrations obtained through catheterization may not reflect the fish's normal discharge. Because the catheter caused a continuous flow of urine, there would be little time for any reabsorption to take place. If the catheter becomes clogged, urine may have a chance to remain in the bladder long enough for some ion reabsorption to occur, thus causing fluctuation in ion concentration when the urine is later expelled.

The possibility of variation in urine production rates and fluctuations in ion concentrations of the urine being caused by handling stress must always be considered when working with fish. This "laboratory diuresis" may be caused by changes in internal hormonal concentrations as well as mechanical changes in permeability due to loss of mucus, scales, and scratches. High urine production rates and high salt concentrations are characteristic symptoms of this condition (Forster and Berglund, 1956).

When examining Table II, it is readily apparent that there is considerable variation in the amount of urine produced for the different sturgeon, especially at the lower salinities. Both M-8 and M-9 show urine production considerably higher than the other sturgeon.

This can in part be explained by the great size difference in these two fish from the other sturgeon. Being 10 to 20 times smaller in weight, M-8 and M-9 will have a much greater surface to volume ratio, thus creating a larger osmotic problem than in the other fish.

Developmental aspects of ion regulation are almost completely unknown. Magnin (1962) indicates A. oxyrhynchus and A. sturio juveniles cannot tolerate saltwater until the fourth to sixth year. Euryhalinity appeared to be a function of age in these fish rather than size. No data have been published on how soon the Pacific Coast sturgeon journey to the sea after spawning. Dees (1961) reports that sturgeon (not indicating species) spend 1 to 3 years in the rivers in which they were hatched, entering marine or estuarine waters by the time they have reached 3 feet in length. In this respect, the osmoregulatory abilities of the two small sturgeon obtained from the Rogue River are extremely interesting. Both fish showed high salt concentrations in serum and urine when subjected to seawater.

Although the ages of the two small Acipenser medirostris are unknown, it might be estimated at 4 to 5 years by the length vs. age graph for A. transmontanus. If the maturation of osmoregulatory abilities in the A. medirostris follows that of its European counterparts, the values observed when these small sturgeon were placed in saltwater might result from being physiologically unprepared to tolerate a high external salt concentration. A more thorough

examination of salinity tolerance, using sturgeon of varying age groups needs to be completed before definite conclusions can be made.

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Typed by Mary Jo Stratton