A REVIEW OF OSMOREGULATION IN FRESHWATER AND MARINE ELASMOBRANCHS

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Introduction

Studies of osmoregulation in marine and particularly fresh water elasmobranchs have been intermittently reported in the literature over the last 80 years. Although there has been significant research on elasmobranch osmoregulation, no study exists uniting the previous work into a single comprehensive report. This study examines previous research in elasmobranch osmoregulation and presents the results in a single, comprehensive review, covering topics including body fluid (solute and solvent) volume and concentration variations, body fluid synthesis, retention and secretion, in different elasmobranch species, in different habitats, having varying nutritional states, and in different life history stages.

In elasmobranchs, blood and other body fluids are separated from the surrounding aqueous environment by permeable surfaces. Osmoregulation depends on the relationship between the solute to solvent concentrations of both the internal body fluids and the outside medium that surrounds the animal (Pang et al, 1977). Unless internal and external fluids have the same solute to solvent concentration, water will enter the body when its fluids contain a higher concentration of solute to solvent than does the water comprising the environment. In contrast, water will leave the body when the surrounding medium contains a higher concentration (Pang et al, 1977). Thus, marine animals face problems of dehydration and the elimination of excess salts while freshwater animals must conserve their salts and eliminate excess water (Pang et al, 1977).

Marine elasmobranchs have evolved the technique of reabsorbing and retaining urea and other body fluid solutes in their tissues so that serum osmolarity (solute/solvent concentration) remains just greater than that of the external seawater (Smith, 1931; Thorson, 1962; Poulsen, 1981). This greatly reduces their osmotic challenges so that they do not need to continuously drink seawater, as do teleosts. However, they still face the problem of a natural and continuous diffusion of salts into their bodies from the external seawater, where the concentration is higher. This is compensated for by salt excretion in the urine, by secretions of the rectal gland, and salt transfer at the gill epithelium (Haywood, 1973).

Fresh water elasmobranchs retain and synthesize less urea than that of their marine counterparts. Their body fluid solute concentrations are relatively low and urine is dilute and copious (Thorson et al, 1967; Thorson, 1970; Goldstein and Forster, 1971; Poulsen, 1981). This greatly reduces their osmotic problem of water retention. The freshwater stingrays of South America have abandoned retention of urea, they lack a functional rectal gland and they osmoregulate as much as do the freshwater teleosts (Thorson et al, 1967; Thorson, 1970; Goldstein and Forster, 1971; Thorson, 1976; Poulsen, 1981).

Review

Body Fluid comparison of freshwater and saltwater sharks

Marine elasmobranchs maintain serum osmolarity equal or slightly greater than that of their surrounding seawater environment and consequently suffer little or no osmotic loss of water (Pang et al, 1977; Poulsen, 1981). In dilute seawater or freshwater, elasmobranch serum osmolarity is reduced so that water does not continuously diffuse inward (Thorson et al, 1973).

Urea, TMAO, and other Ions:

In marine elasmobranchs, plasma osmolarity is high, in many cases higher than that of the surrounding seawater, largely because body fluid concentrations of organic nitrogenous compounds, such as urea and TMAO, are high. Bull sharks, *Carcharhinus leucas*, taken from marine waters have had mean serum urea levels of 356 mM/l and TMAO levels of 46.6 mM/l (Thorson, 1976; Thorson et al, 1973). Inorganic ions, both monovalent (sodium and chloride) and divalent (magnesium, sulfate and calcium), in marine elasmobranch body fluids are kept below seawater levels (Robertson 1975 and 1976). Holocephalans differ somewhat by having higher levels of sodium and chloride and lower levels of TMAO (Robertson, 1975 and 1976).

In freshwater elasmobranchs, plasma osmolarity is lower (but still higher than in teleosts) and body fluid concentrations of organic nitrogenous compounds such as urea and TMAO are relatively low (Smith, 1931; Thorson et al, 1973; Poulen, 1981). Thorson et al (1973) showed that *C. leucas* taken from fresh and estuarine waters had mean serum urea levels of 169 mM/l and TMAO levels of 13.2 mM/l respectively. Inorganic ions, both monovalent (sodium and chloride) and divalent (magnesium, sulfate, calcium), are kept at lower levels than those of marine elasmobranchs (Urist, 1962). Bull sharks that have moved into freshwater have urea levels about 40 % less than Bull sharks in the marine environment, magnesium levels about 37 % less and total sodium and chloride levels about 80 % less (Thorson et al, 1973).

Bony fish generally (except the coelacanth) have a plasma osmolarity only about one-third that of seawater (Pang et al, 1977).

Urea –biosynthesis and retention

Urea levels, which in high concentrations have shown to be largely responsible for the high osmolarity found in marine elasmobranchs, result from the difference between the rate of biosynthesis and excretion of the compound. The South American freshwater ray, *Potamotrygon*, has low rates of urea biosynthesis and has also lost the ability to reabsorb urea in the kidneys (Goldstein and Forster, 1971).

Hematocrit

The differences in hematocrit (percentage by volume of red blood cells) between freshwater and saltwater elasmobranchs are not significant. Furthermore, the freshwater environment does not elicit dilution of the plasma in species that can normally move between salt and freshwater (Thorson, 1961; Thorson et al, 1973)

Water content

Although there is a significant difference in the concentrations of body fluid solutes between salt and freshwater elasmobranchs, including in euryhaline species that can move between the two mediums, there is no shift or difference in the total water content and in the distribution of water among the fluid containing body compartments (Thorson, 1962)

Serum pH (Hydrogen ion concentration)

The serum pHs of freshwater, estuarine and marine sharks broadly overlap and are not significantly different from one another (Thorson et al, 1973).

Osmoregulatory functions of the Kidneys

The high level of urea in marine elasmobranch blood is maintained by the kidneys. Renal tubules are capable of reabsorbing urea, insuring that this important osmoregulatory compound is not wasted (Pang et al, 1977). Elasmobranchs that are adapted to dilute seawater increase the renal excretion of urea, thus effectively lowering their plasma urea levels and osmolarity; however as branchial loss of urea remains largely unaffected, the renal mechanism is likely more significant (Pang et al, 1977). The obligate freshwater rays, *Potamotrygon*, have abandoned renal reabsorption of urea (Goldstein and Forster, 1971)

Osmoregulation by the Rectal Gland

Marine elasmobranchs face the problem of a natural and continuous diffusion of salts into the body from the external sea water, where the concentrations are higher (Haywood, 1973). The rectal gland of marine elasmobranchs functions as a salt secreting mechanism (Conte, 1969; Oguri, 1964; Haywood, 1975); however, disturbances produced by the cessation of its activity can eventually be compensated for internally by other means that are as yet unknown (Burger and Hess, 1960; Conte, 1969; Haywood, 1975).

Freshwater elasmobranchs do not face the problem of continuous diffusion of salts into the body and in fact, the rectal gland of Bull sharks moving from salt to freshwater becomes regressive (Oguri, 1964). No functional rectal gland in the freshwater rays, *Potamotrygon,* has been found (Goldstein and Forster, 1971).

Osmoregulation of the Gills

Branchial elimination of salts in elasmobranchs has generally been considered of little importance. However, to keep serum salt levels low, two-thirds of total sodium and chloride excretion in elasmobranchs may take place through the gills (Payan and Maetz, 1973; Pang et al, 1977).

Low permeability of elasmobranch gills to urea (working in tandem with kidney reabsorption) maintains high plasma urea levels (Pang et al, 1977).

Osmoregulation in developing elasmobranchs, neonates and juveniles

Thorson and Gerst (1972) showed that serum urea levels of the uterine pups of the euryhaline Bull shark resemble those of the mother, and change as she passes from fresh to saltwater and back accordingly. Neonatal or juvenile Bull sharks can live in either fresh or marine water at birth and juvenile Bull sharks caught in totally freshwater habitats had serum parameters (including urea) similar to those of adult Bull sharks in the same environment (Thorson et al, 1973).

Diet

While the external medium controls the actual composition of body fluids for euryhaline elasmobranch osmoregulation, the level at which regulation between these fluids and the external medium occurs is also affected by the availability of metabolic urea, which is directly related to the availability of food (Haywood, 1973).

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