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1976

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Reprinted from Science, November 9, 1962, Vol. 138, No. 3541, pages 688-690
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Partitioning of Body Fluids in the Lake Nicaragua Shark and Three Marine Sharks

Abstract. The relative volumes of major body fluids of freshwater and marine sharks are remarkably similar in spite of the differences in external medium and in osmotic pressure of body fluids. The small differences detected are in agreement with differences reported in comparisons of freshwater and marine teleosts: a slightly higher total water content and a smaller ratio of extracellular to intracellular fluids in freshwater forms.

Whereas there is a somewhat limited literature on the physiology of marine elasmobranchs, very little has been reported on the physiology of forms adapted to fresh water. Since the work of Homer Smith on freshwater elasmobranchs in the 1920's and early 1930's (1), the physiology of these animals has apparently been completely neglected. The ready availability of the Lake Nicaragua shark, *Carcharhinus nicaraguensis* (2), makes it a good subject for studies on the peculiar osmoregulatory phenomena encountered in elasmobranchs, yet, not a single reference is available on the physiology of this widely known freshwater selachian (2a). Most of the reports on the osmoregulation of elasmobranchs have concerned the urea retained in high concentrations, trimethylamine oxide, and the ionic concentration of body fluids. There are appreciable differences between marine and freshwater species in the concentrations of these solutes (1). It was thought that further clarification of the osmoregulation of elasmobranchs might be attained by comparing the body-water content and its apportionment among the various major fluid-containing compartments in marine and freshwater sharks.

The freshwater species of choice was *C. nicaraguensis* (family Carcharhinidae) because this is the only shark known to occur relatively permanently in a freshwater environment. Claims and counterclaims notwithstanding, it is not known whether these sharks remain in Lake Nicaragua throughout life or whether they move up and down the Rio San Juan between the lake and the Caribbean Sea (3). In any case, my work was carried on at Granada (4) at the northeast end of Lake Nicaragua, about 100 miles from the point where the river drains the lake. This, in turn, is well over 100 miles (by river channel) from the Caribbean. Therefore, sharks occurring at the

northeast end of the lake, even if relatively newly arrived from the sea, must be quite well adapted to the freshwater situation

The ideal marine species for comparison with the lake population would be *Carcharhinus leucas*, the closest relative of *C. nicaraguensis* if not the same species. To date comparison with *C. leucas* has not been possible, but specimens of the lemon shark, *Negaprion brevirostris* (also a member of the Carcharhinidae), and the nurse shark, *Ginglymostoma cirratum* (family Orectolobidae), were obtained at the Lerner Marine Laboratory, Bimini, Bahamas (5). In addition, data on the spiny dogfish, *Squalus acanthias* (family Squalidae), are available from previous work for comparison (6).

Details of the investigational methods used were reported in 1958 (6). In brief, the sharks were anesthetized with a narcotic known commercially as M.S. 222 (7). The total water content was determined by complete desiccation of representative portions of the animals at 105°C after other measure-

ments had been completed. The volume of plasma was measured by dye dilution (T-1824), the volume of extracellular fluid by sucrose dilution. The volume of whole blood was determined from the volume of plasma and the hematocrit reading. The value derived by subtracting the T-1824 space from the sucrose space was taken as an approximation of the volume of interstitial fluid, including lymph; the value for sucrose space was subtracted from that for total body water to arrive at an estimate for the volume of intracellular fluid. Admittedly these methods of measurement are crude, especially that for estimating the volume of intracellular fluid, but in the absence of better methods, they serve for purposes of comparison. Since in the time employed (3 or 4 hours) sucrose does not penetrate the minor compartments, such as those containing coelomic, ocular, and cerebrospinal fluid, these fluids are included in the volumes given for intracellular fluid rather than in those for extracellular fluid, where they belong. However, none of these fluids is plenti-

Table 1. Comparison of data on body characteristics and distribution of fluids in fresh-water Lake Nicaragua shark and in three species of marine sharks. All fluid volumes are expressed as mean percentage of body weight (italic type), followed in parentheses by the number of animals. Ranges are given in parentheses in the second line of each entry. Standard deviations (s.d.) are given for primary measurements of fluid parameters.

Parameter	Fresh-water Carcharhinidae, <i>Carcharhinus nicaraguensis</i>	Marine species			Combined marine sp.
		Carcharhinidae, <i>Negaprion brevirostris</i>	Orectolobidae, <i>Ginglymostoma cirratum</i>	Squalidae, <i>Squalus acanthias</i>	
Weight (kg)	48.07 (10) (27.7-57.2)	6.40 (9) (3.18-12.27)	16.03 (5) (11.36-22.70)	2.63 (33) (1.12-6.35)	
Length (in.)	74 (10) (63-81)	41 (9) (33.5-51.0)	56.3 (5) (53-61)	no data	
Pulse (beats/min)	12.2 (10) (8-18)	26 (9) (20-32)	22 (5) (16-24)	31 (14) (18-40)	
Hematocrit (% cells)	22.8 (10) (15-30) s.d., 4.46	21.5 (9) (18-25) s.d., 1.12	17.4 (5) (12-22) s.d., 2.93	18.2 (25) (14-24) s.d., 2.76	
Spec. grav., plasma	1.026 (3) (1.025-1.027)	1.027 (3) (1.025-1.028)	1.028 (3) (1.027-1.029)	no data	
Spec. grav., blood	1.044 (3) (1.043-1.045)	1.045 (3) (1.043-1.047)	1.046 (3) (1.044-1.048)	no data	
Plasma volume (T-1824 space)	5.1 (10) (4.3-6.8) s.d., .71	5.4 (9) (5.0-6.0) s.d., .34	5.7 (5) (4.7-6.6) s.d., .6	5.5 (24) (2.5-9.0) s.d., 1.4	5.53
Blood volume	6.8 (10) (5.4-9.1) s.d., 1.12	7.0 (9) (6.5-7.9) s.d., .42	6.8 (5) (5.8-7.6) s.d., .73	6.8 (24) (3.1-10.9) s.d., 1.79	6.86
Extracellular fluid (sucrose space)	19.7 (8) (17.1-21.8) s.d., 1.54	21.2 (8) (18.8-23.5) s.d., 1.34	21.9 (4) (17.8-24.5) s.d., 2.48	21.2 (3) (18.5-24.3) s.d., 2.38	21.43
Interstitial fluid (sucrose space minus plasma)	14.6	15.8	16.2	15.7	15.9
Total body water	72.1 (4) (71.0-73.1) s.d., .75	71.1 (6) (70.9-71.9) s.d., .34	71.7 (3) (71.2-72.1) s.d., .38	71.7 (16) (68.4-75.4) s.d., 1.9	71.5
Intracellular fluid (total water minus sucrose space)	52.4	49.9	49.8	50.5	50.06

ful in the species of sharks studied, and in no case would they normally account for as much as 0.5 percent of the body weight.

Examination of the data in Table 1 discloses a high degree of consistency for the three marine species with respect to the values for volume of fluid, even though the three species represent three quite divergent families. Indeed, they represent two suborders, the family Squalidae belonging to the suborder Squaloidea and the families Orectolobidae and Carcharhinidae, to the suborder Galeoidea (8). More remarkable than the uniformity among taxonomic groups is the similarity between findings for the marine species and the freshwater *Carcharhinus nicaraguensis*. It has long been known that marine elasmobranchs retain sufficient urea to bring the internal osmotic pressure up to, or slightly above, the pressure of the external medium. On movement into fresh water the internal osmotic pressure drops, due to a reduction of salts and especially of urea, but the body fluids are still greatly hypertonic relative to the external medium (1). Consequently, the maintenance of water balance would appear to be a more acute problem in the freshwater environment. With the drop in the concentration of solutes in the body fluids of freshwater elasmobranchs, one might look for marked shifts in the total water content and in the distribution of water among the fluid-containing compartments. However, no such shifts are clearly evident. The fresh-

water shark has a slightly higher water content than the marine species, and the relative volumes of intracellular and extracellular fluid are a little higher and a little lower, respectively, in the freshwater species. The latter difference is reflected in the volumes of plasma and interstitial fluid, both subcompartments of the extracellular fluid. The differences in pulse rate appear to be related to the size of the animals. With the exception of the values for whole blood, where differences in the hematocrit reading influence the figures, these small differences in compartment volumes prevail for all measurements, whether the freshwater shark is being compared with individual species of marine sharks or with averages for all marine species. That these are valid differences cannot be positively stated, but they are in close agreement with similarly slight differences observed between freshwater and marine teleost fishes (9). It would appear that in elasmobranchs as well as in teleosts the body-water content and the apportionment of the body water are maintained within fairly close limits, whether in a marine or a freshwater environment and in spite of differences in osmotic pressure of the body fluids. But the small differences that are evident suggest that marine sharks as well as marine teleosts function with a slightly larger fraction of the total water in the circulating or mediating compartments, and with a smaller fraction of intracellular or protoplasmic water, than their freshwater counterparts (10).

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References and Notes

1. H. W. Smith, *Biol. Rev. Cambridge Phil. Soc.* 11, 49 (1936).
2. H. B. Bigelow and W. C. Schroeder, *Copeia* 1961, 359 (1961). In their paper, the authors propose that the features formerly used to separate *Carcharhinus leucas* and *C. nicaraguensis* are not valid and that the latter name should be placed in synonymy with *C. leucas*.
- 2a. Since this report was submitted, two papers have appeared, one by me [*Am. Zoologist* 2, 452 (1962)] and one by M. R. Urist [*Science* 137, 984 (1962)].
3. A tagging program is being planned to determine the extent of movement of sharks both up and down the Rio San Juan between the Caribbean Sea and Lake Nicaragua, as well as within the lake itself.
4. The work on *C. nicaraguensis* was done in July and August 1960, at Colegio Centro America, Granada, Nicaragua. I thank the Rev. José V. Aranguren, at that time rector of the school, for his generous provision of living accommodations, laboratory space and facilities, and transportation, and the many members of the staff and student body who aided me in every phase of my work.
5. The work on *N. brevirostris* and *G. cirratum* was completed in April 1962. I am deeply indebted to Dr. James A. Oliver (director of the American Museum of Natural History), to Dr. Robert F. Mathewson (resident director of the Lerner Marine Laboratory), and to other staff-members and investigators at the Lerner Marine Laboratory who helped make completion of the work possible.
6. T. B. Thorson, *Physiol. Zool.* 31, 16 (1958).
7. P. W. Gilbert and F. G. Wood, Jr., *Science* 126, 212 (1957).
8. H. B. Bigelow and W. C. Schroeder, *Fishes of the Western North Atlantic* (Sears Foundation for Marine Research, Yale University, New Haven, Conn., 1948), pt. 1, chap. 3.
9. T. B. Thorson, *Science* 130, 99 (1959); *Biol. Bull.* 120, 238 (1961).
10. This paper is study No. 345 from the Department of Zoology and Physiology, University of Nebraska. This research was supported by the U.S. Public Health Service (grant No. H-3134) and by the University Research Council of the University of Nebraska. I wish to acknowledge my appreciation for the stimulating interest and enthusiasm for research on sharks of Robert C. Dorion of Guatemala City.

6 August 1962