in the treatment schedule may be necessary to produce optimum chromosome morphology.

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VARIATIONS BODY SECTION IN SHARKS—AN ADAPTATION FOR EFFI-CIENT SWIMMING.—Many species of sharks (mainly of the generalized group typified by the carcharhinids and the demersal group, as defined by Thomson and Simanek [1977]) and other pelagic, highly maneuverable fish species such as pike exhibit a curious distribution of body-mass in the longitudinal direction (Fig. 1). The head is compressed vertically to produce a horizontal wedge with rounded edges (roughly elliptical). At around one-quarter to onethird of the total body length the cross-section gradually changes into a rough ellipse with the long axis in the vertical direction (including the first dorsal fin). This configuration is typical of the central and rear part of the fish body, except when approaching the caudal peduncle where horizontal flattening occurs, again resulting in a horizontally elongated cross-section. Another change is observed immediately posterior to the peduncle where the caudal fin is highly elongated in the vertical direction.

The functions of these changes from horizontally elongated to vertically stretched body cross-sections have been speculated on for many years, and Houssay (1912) came up with an ingenious, but incorrect explanation. Due to the scarcity of information on sharks (Gruber and Myrberg, 1977), his reasoning is still widely accepted (Budker, 1971). It is, therefore, the purpose of this note to clarify the fallacy in Houssay's model, and to propose a different mechanism for these adaptations based on recent hydrodynamic analyses of fish locomotion.

Houssay suggested that the alternating elongation is physically equivalent to the shape of a jet of water issuing from an elliptical orifice. Standing waves which result in a periodic change in the shape of the jet are produced by alternating the direction of the long axis of the ellipse. This phenomenon is a result of an interaction of completely different mechanismssurface tension and inertia of the jet. Surface tension causes the elongated part of the section to move inwards, tending to form a circular section, while the liquid's inertia causes this motion to overshoot resulting in ellipticity in the perpendicular direction. This is therefore a purely dynamic effect of the interface of two fluids,



Fig. 1. A "typical" pelagic shark (Triakis acutipinnae) showing distribution of oval cross-sections along body.

with no relation at all to the shark's body, which is obviously not liquid. The problem of understanding the advantages of the observed crosssection shape distribution still remained unsolved, therefore.

The effort required for sideways motion of any section of the body is a function of the hydrodynamic resistance and inertia (virtual mass). Both the inertia and form drag are greatly reduced when an elongate section is moved parallel to the longer axis, as compared to moving it in the direction of its short axis, for the same section area.

The intertial effects, known as virtual, or added mass effects which dominate when motion is initiated, are proportional to the square of the largest dimension perpendicular to the direction of motion (Lighthill, 1969; Webb, 1975). Thus, the force required to overcome the inertial reaction to starting a cylinder with elliptical section with a 2:1 aspect ratio (for example) along its large axis (Fig. 2B) is four times smaller than that required to move the same section along its small axis (Fig. 2A). In addition, the hydrodynamic drag experienced after motion is already taking place is much smaller, when the ellipse is moving parallel to its long axis (Fig. 2B). (This is simply shown by moving an object such as your hand through water at constant speed in both orientations.) Here the numerical values of the drag ratio are much more difficult to obtain as they depend on Reynolds number, freestream turbulence and other factors, but these are not required for the present qualitative arguments.

Starting from the anterior parts, we notice

that turning maneuvers in fish (Weihs, 1972) start with a rapid motion of the head in the direction of turn. The turning radius is highly dependent on the rate at which this motion is performed. Thus, the decrease in vertical depth of the body section at the head enables a faster turn due to the decreased inertial effects and drag.

Sharks, as well as other species of fish with this body configuration, swim in the anguilliform mode (Breder, 1926). This requires lateral oscillations of the whole body as part of the swimming mode. Here an additional advantage of the vertical compression of the head comes in, as the drag due to side motions while swimming is reduced.

The same arguments, in reverse, hold for the central part of the body. In the turning process (Weihs, 1972), the reaction of the water on the outward motion of this part of the body produces the centripetal force bringing about the actual turning. Increasing the depth of sections in this part will therefore cause a larger reactive force, and therefore a swifter turn with smaller radius. Thus the change in direction of the body eccentricity causes the fish's effort to be applied in the correct place for efficient turning.

In straight line swimming, the lateral compression of the mid-body region helps minimize sideways excursions of this part of the body, which would cause flow separation and in turn increase the resistance to forward motion.

Thickening of the cross-section is again observed at the rear part of the body. This part



Fig. 2. Motion of an elliptical cylinder of 2:1 aspect ratio normal to (2A) and parallel to its large axis (2B).

of the body is moved sideways with an amplitude increasing to a peak at the caudal peduncle, as part of the anguilliform swimming mode. The larger amplitudes here are needed to drive the caudal fin which in turn provides a large part of the thrust required for swimming. These lateral excursions can therefore not be eliminated but their energetic cost can be reduced to increase efficiency. Again, this is achieved by producing a roughly elliptical section which moves in the direction of its large axis. To further decrease the drag on the peduncle region, some species have developed long appendages on the second dorsal and ventral fins (Fig. 1), or even series of finlets which serve as flow vanes, decreasing the shedding of vorticity and drag (Alevey, 1977). The horizontal flattening of the peduncle has an additional function (Magnuson, 1970) producing a part of the lift required to counteract negative buoyancy in some species. Finally, the caudal fin is elongated vertically to produce a large, high aspect-ratio hydrofoil propelling the fish by sideways motions. Another adaptation advantageous to rapid maneuvering is the "double tail" produced by the second dorsal and ventral fins, in front of the caudal fin.

In conclusion, the observed changes in body section shape, as a function of distance from the head, help reduce the effort required for maneuvering and cruising. This improvement is in addition to the lateral instability mentioned by Thomson and Simanek (1977) as aiding maneuverability. An increase in mouth ingestion area, and improved stereoscopic vision may well be additional beneficial results of this adaptation. Acknowledgments.—This note was written while I was NRC-NOAA Senior Research Associate at the NOAA Southwest Fisheries Center, La Jolla. I would like to thank J. R. Hunter and R. Lasker for their hospitality and Ken Raymond for assistance with the graphics.

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VOLUNTARY SWIMMING SPEEDS OF TWO SPECIES OF LARGE CARCHARHIN-ID SHARKS.—The elasmobranchs (sharks, skates and rays) have survived virtually unchanged for hundreds of millions of years, indicating an extremely successful adaptation. Very little information exists, however, on the behavior (Gruber and Myrberg, 1977) of the larger sharks, mainly because of the difficulties of observing these fish in the ocean (Nelson, 1977) and of keeping them under controlled conditions that simulate their life in the wild.

Most pelagic sharks are negatively buoyant (Budker, 1971) and must, for this reason, move continuously to counter their tendency to sink. This motion, which is also applied to seeking