

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 (Aleyev, 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.

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LITERATURE CITED

- ALEYEV, Y. G. 1977. Nekton. Junk, the Hague.
 BREDER, C. M., JR. 1926. The locomotion of fishes. *Zoologica* (N.Y.):4:159-256.
 BUDKER, P. 1971. The life of sharks. Weidenfeld and Nicolson, London.
 GRUBER, S. H., AND A. A. MYRBERG. 1977. Approaches to the study of the behavior of sharks. *Amer. Zool.* 17:471-486.
 HOUSSAY, F. 1912. *Forme, puissance et stabilité des poissons*. Herman, Paris.
 MAGNUSON, J. J. 1970. Hydrostatic equilibrium of *Euthynnus affinis*, a pelagic teleost without a gas bladder. *Copeia* 1970:56-85.
 THOMSON, K. S., AND D. E. SIMANEK. 1977. Body form and locomotion in sharks. *Amer. Zool.* 17:343-354.
 WEBB, P. W. 1975. Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Board Canada* 190:1-159.
 WEIHS, D. 1972. A hydrodynamical analysis of fish turning maneuvers. *Proc. R. Soc. Lond.* B182:59-72.

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VOLUNTARY SWIMMING SPEEDS OF TWO SPECIES OF LARGE CARCHARHINID 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

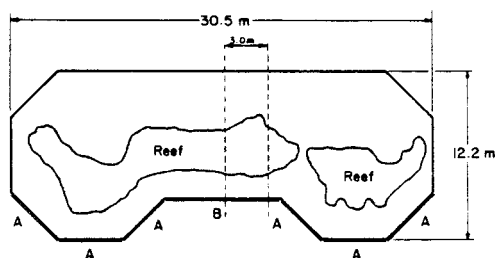


Fig. 1. Schematic description of aquarium. A indicates the smaller and B the larger viewing windows. The reef at all points is at least 3.0 m deep.

prey and oxygenating the gills, is a major fraction of the shark's energy budget. To understand and predict shark behavior, the swimming speed has to be known. In this note the voluntary swimming speeds of two species of sharks (*Carcharhinus leucas* and *Carcharhinus plumbeus*) are measured and compared to theoretical predictions based on energetical considerations (Weihs, 1977).

Observations on the swimming speed of bull (*C. leucas*) and sandbar sharks (*C. plumbeus*) were conducted in a 1.5 million liter enclosed aquarium, 30.5 m long, 12.2 m wide, and 4.7 meters deep at the deepest point. Six 2.4 m × 3.7 m and one 2.4 m × 7.3 m acrylic viewing panels allowed underwater observation. The pool is of elongated shape with a natural appearing concrete "rocky" reef occupying approximately 25% of the floor (Keyes, 1979) (Fig. 1). Viewing from the top was possible from all sides.

The tank contained two *C. leucas* (2.0 and 2.3 m total length [TL]) in addition to five *Negaprion brevirostris* (≈2 to 3 m TL), two *Negaprion acutidens* (≈1.5 to 2.0 m TL), four *C. plumbeus* (≈2 to 2.5 m TL) and seven *Ginglymostoma cirratum* (≈1.5 to 3.0 m TL). A population of the cleaner wrasse *Labroides dimidiatus* occupied the reef and functioned in removing parasites from the sharks. Total length of the sharks (the distance from the anterior margin of the snout to the most posterior point of the caudal fin) was converted to standard length (SL) following Bass et al. (1973).

A 3 m wide section of the rectangular part of the aquarium (Fig. 1) was marked by lines 6 mm wide, 0.5 m above the water surface so as not to interfere with the sharks' swimming. The 3 m section was chosen so the measurement error due to observer delays would be less than

5%, longer straight sections not being possible because of effects of the round parts of the tank. The swimming speed was obtained by measuring the time elapsed between the snout passing beneath the two marker strips. Only events including straight-line swimming perpendicular to the markers were recorded. Preliminary observations indicated that disturbances such as cleaning the tank, external construction noises, and encounters with other sharks during or just before the event, caused changes in their behavior. Measurements were carried out during both day and night (the difference being in lighting level, 4,000 W direct lighting during daytime and dim indirect lighting at night, as well as the absence of spectators at night). There was no significant difference between day and night swimming speed averages (the difference was less than ½ the standard error). The aquarium temperature was maintained at 26 ± 1 C. The sharks were fed in the early afternoon on Mondays, Wednesdays and Fridays. The only differences noted were just prior to, during and immediately after feeding. Only data collected more than 3 hours before and 6 hours after feeding were therefore used for the volitional speed analysis.

The sharks were observed to have preferred swimming patterns when undisturbed, making it easier to define "valid" measurements. These patterns, and their social significance, are being studied separately and will be described in due course. Social hierarchy was indicated, where individuals lower on the social order maneuvered to keep out of the more dominant individuals' trajectories. As a result of this "social behavior," only two individuals were seen to have undisturbed motion. These were Bull No. 2 (2.3 m TL) and Sandbar No. 1S (≈2.1 m TL). Bull No. 1 (2.0 m TL) also exhibited regular motion, but was somewhat influenced by the presence of Bull No. 2. Measurements of the speed of these three individuals were included in the final analysis.

Following preliminary observations on all individuals of the pelagic species available in the aquarium, 209 swimming sequences of Bull No. 2 were timed to examine uniformity, effects of outside disturbances, encounters and proximity to feeding time. Disturbed sequences, events where turning or non-level swimming occurred, and times measured close to feeding were deleted, leaving 88 measurements (Table 1). These results show the very narrow spread of speeds for Bull No. 2 and Sandbar No. 1S

TABLE 1. VOLUNTARY SWIMMING SPEEDS OF THE EXPERIMENTAL SHARKS.

Individual	Number of measurements	Average speed cm/sec	Standard error cm/sec	Highest measurement cm/sec	Lowest measurement cm/sec
<i>C. leucas</i> No. 2	88	62	±4	70	56
<i>C. leucas</i> No. 1	13	72	±6	83	68
<i>C. plumbeus</i> No. 1S	18	64	±2	67	60

and the somewhat elevated speed and greater variability of measurements of Bull No. 1. The latter may be a result of the presumed lower position of Bull No. 1 in the social hierarchy in relation to Bull No. 2.

Fig. 2 shows the average volitional speeds of the three sharks (including the standard error) as a function of their standard length (L). The full line on Fig. 2 is the theoretical prediction of the volitional swimming speeds as a function of standard length (Weihs, 1977). This prediction is based upon an energetic cost optimization. The hypothesis is that an undisturbed fish will swim at a speed at which it requires minimum energy per unit distance traversed, which occurs when the total metabolic rate is approximately double the standard rate. This predictive approach has proved successful for various freshwater and seawater species (Weihs, 1975; Gooding and Neill, 1980) such as trout and tuna and is shown here to describe elasmobranch behavior also. Some further evidence of an elasmobranch conforming to this behavior can be obtained from a recent study of *Squalus acanthias* by Brett and Blackburn (1978). They show the routine metabolism of the dogfish to be approximately twice that of the resting standard metabolism, which corresponds to the predicted ratio (Weihs, 1977). The observed swimming was irregular because of geometric limitations of the respirometer so that voluntary speeds were not obtained.

The theoretical prediction of voluntary swimming speeds of approximately 68 cm/sec for sharks at 2 m SL has been verified for *C. leucas* and *C. plumbeus*. Other species available at the Sea World San Diego aquarium, as well as other individuals of *C. plumbeus*, could not be examined quantitatively because of greater

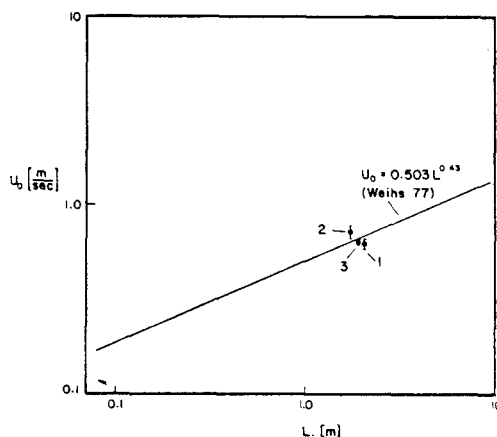


Fig. 2. Voluntary swimming speed, U_0 , versus standard length (L) of three individual sharks. (1) *C. leucas* No. 2, (2) *C. leucas* No. 1, (3) *C. plumbeus* (average and standard error of experimental data). Full line indicates theoretical prediction.

variability in their behavioral patterns. The speeds, when measured, however, also were close to the predicted values (60–75 cm/sec).

The close agreement between theory and experimental measurements at the Sea World facility indicates that these data will be typical of field results. These measurements also give further encouragement to the possibility of predicting behavioral patterns of these largely unknown and highly interesting animals by theoretical means.

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LITERATURE CITED

BASS, A. J., J. S. D'AUBREY AND N. KISTNASAMY. 1973. Sharks of the east coast of Southern Africa. I. The genus *Carcharhinus*. S. African Assoc. Mar. Biol. Res. Invest. Rep. 33.

BRETT, J. R., AND J. M. BLACKBURN. 1978. Metabolic rate and energy expenditure of the spiny dogfish *Squalus acanthias*. J. Fish. Res. Bd. Canada 35:816–821.

BUDKER, PAUL. 1971. The life of sharks (English version). Weidenfeld and Nicolson, London.

GOODING, R. M., AND W. H. NEILL. 1980. Respira-

- tion rates and low oxygen tolerance limits in skipjack tuna (*Katsuwonis pelamis*). (In Press)
- GRUBER, S. H., AND A. A. MYRBERG. 1977. Approaches to the study of the behavior of sharks. *Amer. Zool.* 17:471-486.
- KEYES, R. S. 1979. Description of live shark exhibit and research center, Sea World-San Diego. *Sea World San Diego Shark Res. Ctr. Rep.* 79-1.
- NELSON, D. R. 1977. On the field study of shark behavior. *Amer. Zool.* 17:501-507.
- WEIHS, D. 1977. Effects of size on sustained swimming speeds of aquatic organisms, p. 333-338. In: *Scale effects in animal locomotion*. T. J. Pedley (ed.). Academic Press.
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FORMULAE VARIATIONS OF PHARYNGEAL TOOTH COUNTS IN THE CYPRID GENUS *NOTROPIS*:—Identification of fishes in the Cyprinidae and Catostomidae is often based in part on the number and arrangement of pharyngeal teeth that occur on the fifth pair of ceratobranchials (Moore, 1988). However, few studies have been undertaken to examine the intraspecific variation that may occur in these counts which could lead to misidentification.

Variation in a number of fundamental characters in the genus *Notropis* was examined by Fowler (1910). Other studies on cyprinids are reviewed by Eastman and Underhill (1973); most species reported on have less than 20% variation from the expected count. Of the 42 additional cyprinid species examined by Eastman and Underhill (1973), only two deviated from the expected count more than 10% of the time.

Materials and methods.—Pharyngeal tooth counts from 100 individuals of the following eight species of the genus *Notropis* were examined: *N. albeolus*, Jordan, *N. analostanus* (Girard), *N. boops* Gilbert, *N. greenei* Hubbs and Ortenburger, *N. photogenis* (Cope), *N. scabriceps* (Cope), *N. whipplei* (Girard) and *N. zonatus* (Putnam).

Specimens were provided from the museum collection of the Appalachian Environmental Laboratory. When possible, specimens of each species examined were taken from the same collection to limit any deviations that could be attributed to geographic variation. Satinfish shiners (*N. analostanus*) were analyzed from collections within the same drainage taken during a 3-day period in 1976.

Arches were removed, carefully cleaned and inspected with the aid of watchmaker's forceps, an insect pin and a dissecting microscope. Counts (Hubbs and Lagler, 1964) for each individual fish were recorded in order to examine asymmetrical variability in formulae. Empty sockets were counted, however, care was taken not to count tooth crowns embedded within the mucosa of the arch that were destined to replace teeth already present. Any fish in which either arch broke along the tooth forming area upon removal was eliminated from the results.

Results and discussion.—Expected pharyngeal tooth formulae and observed counts for each species are presented in Table 1. All fish exhibited a most common tooth count with various numbers of deviant formulae. *N. photogenis*, with a most common formula of 2,4-4,2, had the most invariable count with only 3% of those examined possessing a different count. A mean deviation of 12.5% existed among the five species examined having this count. The remaining species (Table 1) most often possessed a 1,4-4,1 count with a mean deviation of 25%. *N. boops* was found to have counts varying from its usual 1,4-4,1 formula 36% of the time. The most consistent counts in this study were among fishes possessing the 2,4-4,2 expected formula.

Eastman and Underhill (1973) found a few instances of additions to the secondary row, but we did not. Additions and deletions to the primary row also occurred, the former occurring more frequently than the latter (Table 1). Eastman and Underhill (1973) suggested that additions improve the masticatory process and may be selected for. However, the limited number found in this study is probably more likely due to faulty tooth replacement (Evans and Deubler, 1955; Weisel, 1967), rather than an evolutionary trend.

Hubbs and Hubbs (1944) reported that variant asymmetrical tooth counts in western North American minnows tended to favor the left arch. Eastman and Underhill (1973) also noted this in tooth formulae in Minnesota cyprinids.