

# SWIMMING KINEMATICS OF SHARKS<sup>1</sup>

P. W. WEBB<sup>2</sup> AND RAYMOND S. KEYES<sup>3</sup>

## ABSTRACT

Video-tape recordings were made of locomotor movements of six species of free-swimming sharks. The following kinematic parameters were measured, normalized where appropriate with total body length ( $L$ ): tail-beat frequency ( $f$ ), specific tail-beat amplitude ( $A/L$ ), specific wavelength of the propulsive wave ( $\lambda/L$ ), specific stride length ( $S/L$ ), and the rate of change of  $A/L$  with position along the body. These parameters were measured over a range of swimming speeds up to 3.9 m/s (4 L/s) for one species, the blacktip shark, *Carcharhinus melanopterus*. Data were obtained only over a narrow range of low swimming speeds for the other species, because they could not be induced to swim at high speeds. For the blacktip shark,  $f$  increased with speed, but  $A/L$ ,  $\lambda/L$ , and, hence,  $S/L$  all decreased as speed increased. Among the six species,  $\lambda/L$  and  $S/L$  tended to be larger for more fusiform species, while  $A/L$  and  $f$ , at a given speed, appeared to be lower. This implies swimming movements of more fusiform species generated more thrust per beat than elongate species and/or the swimming drag was lower. The pattern of amplitude changes along the body length of sharks was intermediate between that observed for elongate and fusiform teleosts.

Thrust and swimming efficiency can be improved when discrete fins interact, as between the dorsal and caudal fins of sharks. For this to occur, a phase difference of  $\geq 0.5\pi$  must occur between the vortex wake shed at the trailing edge of an anterior fin and the leading edge motion of a more posterior fin, which interacts with the upstream vortex sheet. The variations in swimming kinematics with speed, the differences among the species studied, and the conservative nature of body form in sharks probably function to increase thrust and efficiency by such interaction between median fins.

Most studies on fish locomotion have concentrated on bony fish, especially teleosts. As a result, modern ideas on fish locomotor functional-morphology are dominated by knowledge of only one of the major groups of fish. However, there are many unique features among cartilaginous fish that suggest they have exploited some different biomechanical possibilities. Sharks appear to swim like elongate teleosts, but in contrast they have discrete, often widely spaced median fins more typical of fusiform teleosts. Lighthill (1970) and Sparenberg and Wiersma (1975) have shown that this combination provides an opportunity for median fins to interact in such a way that thrust and Froude efficiency (the ratio of useful work to total work of the propellor system) are improved.

If shark locomotion were to utilize flow interactions between median fins to hydromechanical advantage, they would have to swim somewhat differently from teleosts. For example, teleosts

modulate tail-beat frequency with speed, but sharks might also have to vary other kinematic parameters, such as the length of the propulsive wave and tail-beat amplitude. Therefore, the following experiments were performed to determine how swimming kinematics and phase differences between fin motions varied with speed for six species of sharks. While difficulties were encountered in obtaining data over a wide range of speeds, the results suggest that sharks vary swimming kinematics to utilize interactions between median fins, as postulated by Lighthill (1970).

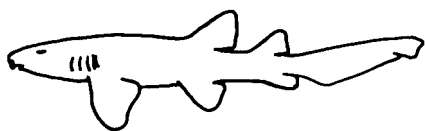
## METHODS

Observations were made on six species of free-swimming sharks (Fig. 1). Three species, the bull shark, *Carcharhinus leucas*; lemon shark, *Negaprion brevirostris*; and nurse shark, *Ginglymostoma cirratum*, were approximately 2-2.5 m in total length. They were contained in the public display at Sea World, San Diego, Calif., described by Weihs et al. (1981). Specimens of the other three species were smaller; Pacific blacktip shark, *Carcharhinus melanopterus* (total length,  $L = 0.97 \pm 0.5$  m;  $\bar{X} \pm 2SE$ ;  $N = 7$ ); bonnethead,

<sup>1</sup>Contribution No. 8104-SD from Sea World, San Diego, Calif.

<sup>2</sup>Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, Calif.; present address: School of Natural Resources, University of Michigan, Ann Arbor, MI 48109.

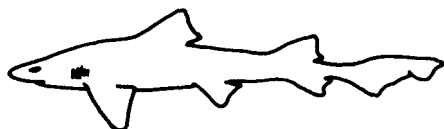
<sup>3</sup>Sea World, San Diego, CA 92109.



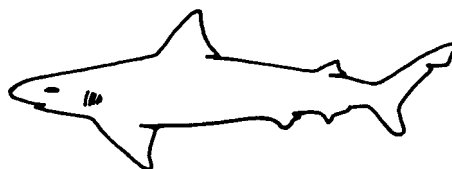
▲ *Ginglymostoma cirratum*  
nurse shark



■ *Sphyrna tiburo*  
bonnethead shark



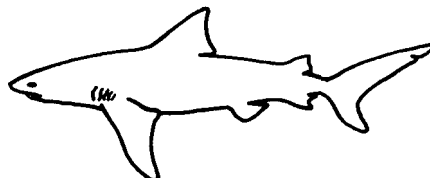
△ *Triakis semifasciata*  
leopard shark



● *Carcharhinus melanopterus*  
blacktip shark



□ *Negaprion brevirostris*  
lemon shark



○ *Carcharhinus leucas*  
bull shark

FIGURE 1.—Drawings (not to scale) showing the longitudinal body form of the six species of sharks for which swimming kinematic data were obtained. The symbols are used through most of the following figures.

*Sphyrna tiburo* ( $L = 0.93 \pm 0.09$  m;  $N = 5$ ); and leopard shark, *Triakis semifasciata* ( $L = 0.98 \pm 0.11$  m;  $N = 5$ ). The three smaller species were part of a second public display in an outside pool at Sea World. This pool was approximately oval in shape, 9 m long, 5.5 m wide, and 0.3 m deep. Small individual sharks were also observed in a small rectangular tank, 2.5 m long, 1.2 m wide, and 0.3 m deep. This tank had a transparent bottom. The water temperature in all three facilities

was the same and constant at 24.5°C. Thomson and Simanek (1977) have shown that most sharks fall into one of four functional-morphology groups. Group 1 includes sharks with streamlined, fusiform, deep bodies; a narrow caudal peduncle with lateral flukes (streamlining); and a high aspect ratio tail. This group is represented by large pelagic species, such as *Lamna* which were unavailable for study. Group 2 is similar to group 1, but lacking the deep body and stream-

lined caudal peduncle. *Carcharhinus leucas*, *C. melanopterus*, and *S. tiburo* represent group 2. Group 3 includes sharks with a low aspect ratio tail, making a small angle to the horizontal, and a less fusiform body, represented by *G. cirratum*, *T. semifasciata*, and *N. brevirostris*. Group 4 incorporates the squaloid sharks, e.g., *Centrolepis*, which were not available.

Swimming movements were recorded on video tape. Recordings were made above the free surface of the public display facilities. Surface ripples were small compared with the images of the sharks and were therefore ignored. To avoid surface problems, observations in the rectangular tank were made from below through the transparent bottom. Surface ripples did not deleteriously affect measurement accuracy because no differences in data from the public facilities and the rectangular tank could be found.

Swimming records were obtained for as wide a range of speeds as possible. In most cases, normal variation in motor behavior due to the operation of the park was exploited. For the large sharks, observations were made before the display opened, during normal hours, and during feeding. Because of the possibility of injury leading to mortality, other invasive methods to induce higher speeds were not used. Similar procedures were employed for the smaller sharks. Underwater concussions, induced by dropping heavy objects (fluid-filled metal kegs), and visual stimuli were used to induce higher speeds in these sharks. Tactile stimuli were also employed to generate a range of speeds in the rectangular tank.

Video tape was analyzed "frame-by-frame," using manual advance to resolve movements to within 1/60 s (17 ms). Because a large length range was used, kinematic observations were normalized, for convenience, with respect to total length,  $L$ , measured from the tip of the nose to the tip of the tail. Specific swimming speed (speed/ $L$ ), specific amplitude (amplitude/ $L$ ), and tail-beat frequency ( $f$ ) were measured for periods of steady swimming of two or more tail beats. The speed of the propulsive wave ( $c$ ) was calculated from the backward displacement of wave crests, and specific wave-length ( $\lambda/L$ ) was calculated from  $c/Lf$ .

## RESULTS

Representative swimming movements for three of the species of sharks are illustrated in

Figure 2. The body was bent into a wave that travelled backwards over the body at a speed greater than the swimming speed. The amplitude increased caudally to reach maximum values at the trailing edge (the tip of the caudal fin). In general, the form of propulsive movements was similar to that of other fish, as originally described by Gray (1933).

Kinematic parameters varied among the six species and with swimming speed. In practice, it proved extremely difficult to induce the sharks to swim over a wide speed range. This is consistent with experiences of Johnson (1970) with the brown shark, *Carcharhinus plumbeus* (= *C. milberti*), and Brett and Blackburn (1978) with the spiny dogfish, *Squalus acanthias*. Hunter and Zweifel (1971) reported kinematic data for a single leopard shark, *Triakis henlei*, swimming in a water tunnel, but the speed range is not given. Only the blacktip sharks swam over a speed range large enough to permit examination of the relationships between kinematics and speed. Data for the other species was therefore simply averaged (Table 1). The sharks also did not swim at very low speeds.

Tail-beat frequency increased linearly with speed (Fig. 3A), as found for other species of sharks and for teleosts (see Johnson 1970; Hunter and Zweifel 1971; Webb 1975; Aleyev 1977). However, frequencies increased at a higher rate with speed than observed for other fish. Mean specific speeds and tail-beat frequencies varied among the six species of sharks. Compared with the slope of the blacktip shark relationship, more elongate species (e.g., nurse shark; group 3 of Thomson and Simanek 1977) tended to have higher tail-beat frequencies at a given specific speed than more fusiform fish (e.g., bull shark; group 2 of Thomson and Simanek 1977) (Fig. 3B; Table 1).

Specific amplitude of the blacktip shark decreased with increasing speed (Fig. 3C) and hence was inversely related to tail-beat frequency. Specific amplitudes varied from 0.06 to 0.21 among species, with the more fusiform sharks having lower values (Fig. 3D). With the exception of the bull shark, mean specific swimming speeds were greater for the more fusiform species. Thus, for the interspecific data, specific amplitude decreased with specific speed, similar to the intraspecific observations on blacktip sharks. Among teleosts, both tail-beat amplitude and frequency may increase together at very low speeds (Bainbridge 1958; Webb 1971, 1973). However, over most of the speed range, caudal

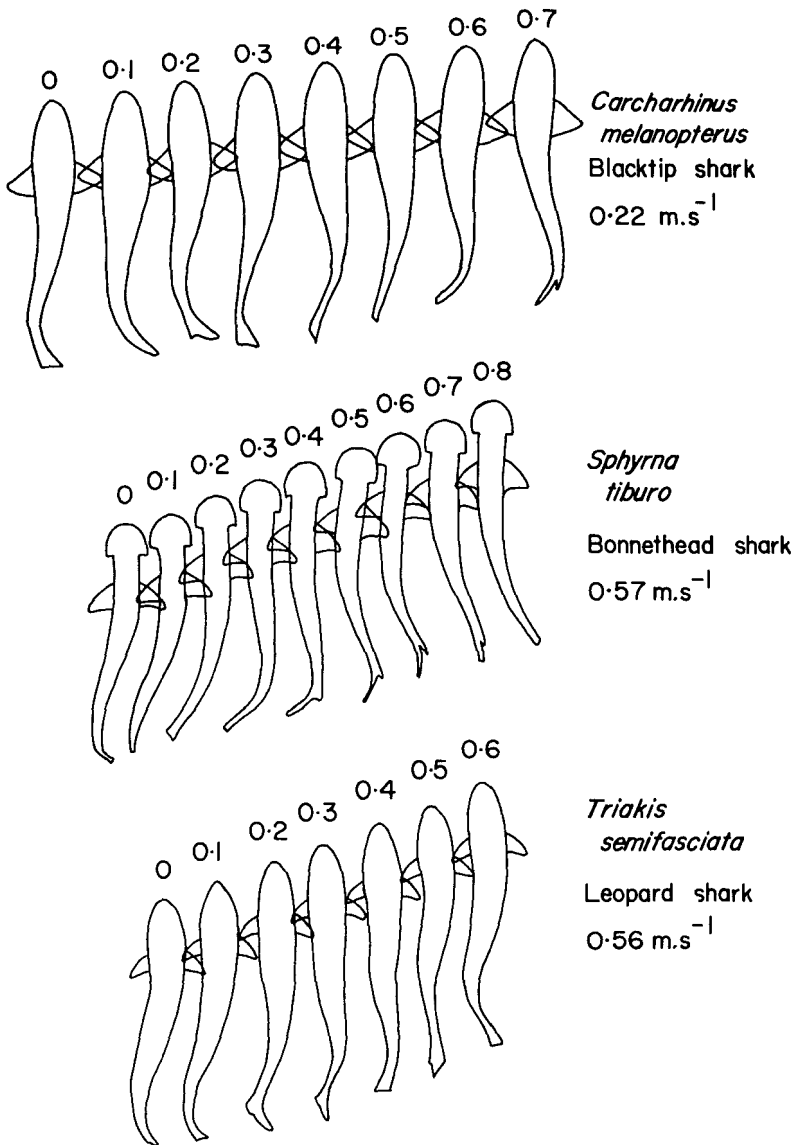


FIGURE 2.—Tracings from videotapes of three species of sharks swimming at three different speeds to show typical body movements. The times above each tracing are in seconds.

fin trailing edge amplitudes tend to be constant at about  $0.2 L$  (see Hunter and Zweifel 1971).

In those cases where specific amplitudes and tail-beat frequencies have been related, their product ( $fA/L$ ) is linearly related to speed. A similar relationship was calculated for this product using the relationships derived for *Triakis* by Hunter and Zweifel (1971) and was similar, but slightly curved for the blacktip shark (Fig. 3E). The product  $fA/L$  also increased with speed for the other species (Fig. 3F). The free-swimming sharks thus showed frequency and amplitude modulation with speed. This contrasts with

*Triakis henlei* in a water tunnel where only tail-beat frequency was modulated, perhaps due to the presence of walls in the water tunnel. The modulation of both tail-beat frequency and amplitude with swimming speed explains the differences in the kinematics-swimming speed relationships between teleosts and sharks. It appears that the shark propulsive system is more plastic than that of bony fish.

Because of the interrelationships between tail-beat frequency, specific amplitude, and specific swimming speed, stride length also varied inversely with swimming speed for the blacktip

TABLE 1.—Summary of mean kinematic parameters for six species of sharks. Data show mean values  $\pm 2SE$ . Sharks are ranked according to their morphology from the most elongate to most fusiform species. This morphology would be expected to be associated with more anguilliform and more carangiform swimming, respectively.

Species	Specific swimming speed (U/L)	Tail-beat frequency (f; Hz)	Specific tail-beat amplitude (A/L)	fA/L	Specific stride length (S/L)	Specific wave-length ( $\lambda/L$ )	Phase difference (radians)	N
Nurse shark	0.34 $\pm 0.04$	0.67 $\pm 0.14$	0.21 $\pm 0.04$	0.15 $\pm 0.04$	0.51 $\pm 0.08$	—	—	12
Leopard shark	0.58 $\pm 0.15$	1.12 $\pm 0.30$	0.20 $\pm 0.04$	0.22 $\pm 0.08$	0.55 $\pm 0.10$	0.77 $\pm 0.14$	0.53 $\pm 0.18$	10
Lemon shark	0.47 $\pm 0.14$	0.95 $\pm 0.26$	0.18 $\pm 0.06$	0.16 $\pm 0.04$	0.58 $\pm 0.09$	—	—	6
Bonnethead shark	0.84 $\pm 0.11$	1.25 $\pm 0.14$	0.18 $\pm 0.02$	0.23 $\pm 0.04$	0.64 $\pm 0.03$	0.91 $\pm 0.06$	0.46 $\pm 0.08$	14
Blacktip shark	0.80 $\pm 0.10$	1.13 $\pm 0.14$	0.18 $\pm 0.02$	0.33 $\pm 0.12$	0.72 $\pm 0.03$	1.07 $\pm 0.09$	0.47 $\pm 0.05$	18
Bull shark	0.58 $\pm 0.09$	0.78 $\pm 0.21$	0.16 $\pm 0.03$	0.13 $\pm 0.05$	0.74 $\pm 0.14$	—	—	5

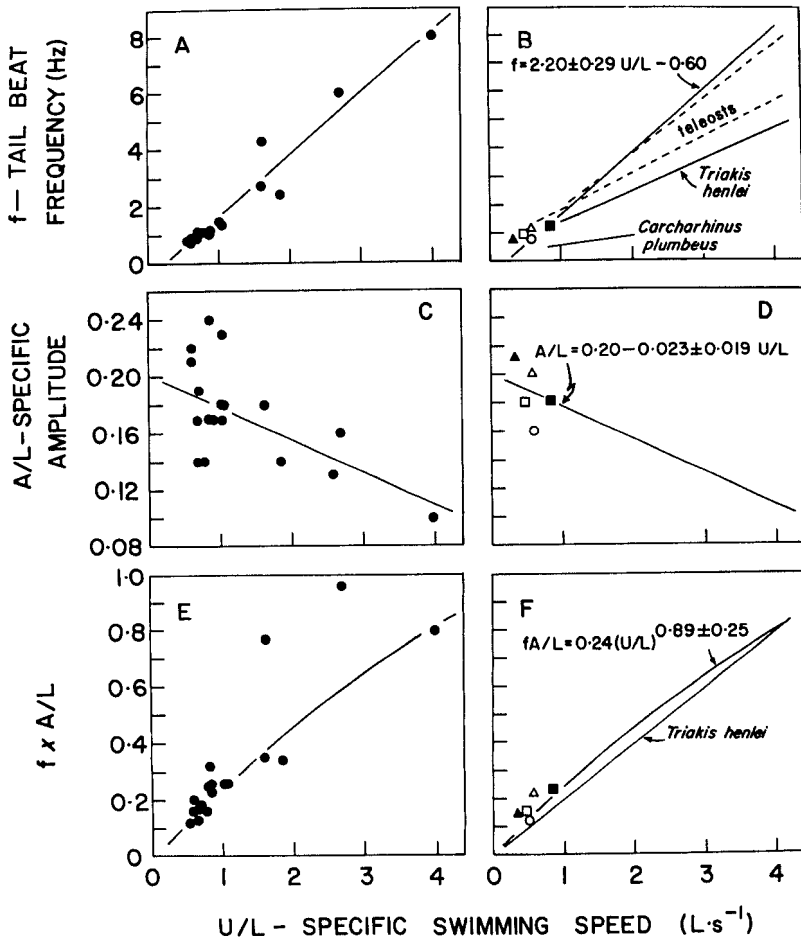


FIGURE 3.—Relationships between tail-beat frequency, f, specific amplitude, A/L, and their product, fA/L, as functions of specific swimming speed, U/L for various sharks. A, C, and E show data for blacktip sharks and best-fit functional regressions. These curves, and the pertinent equation, are shown with the mean values for the other species in B, D, and F. Values for the slope of the equations are the mean  $\pm 2SE$ . The key to symbols is in Figure 1. Other data are teleosts and *Triakis henlei* from Hunter and Zweifel (1971) and *Carcharhinus plumbeus* from Johnson (1970).

shark and among the six species (Fig. 4). Stride length is defined as the distance travelled per tail beat (Wardle 1975). In teleosts, specific stride length (stride length/ $L$ ) typically takes values of 0.6 to 0.8, and does not vary with speed (Wardle 1975). In blacktip sharks, specific stride lengths comparable with those of teleosts were seen only at low speeds and stride length was lower at higher speeds. Specific stride length was similar to the teleost values in the more fusiform sharks, but was lower in more elongate species, the lowest value of 0.51  $L$  being found for nurse sharks (Table 1, Fig. 4).

Data on specific wavelengths were only measured with sufficient accuracy for the three smaller species. Values ranged from 0.77 to 1.07  $L$ , and tended to be larger for the more fusiform species. Specific wavelength decreased with specific swimming speed in blacktip sharks (Fig. 5), contrasting with teleosts, where specific wavelength is usually independent of speed (Webb 1971, 1973; Wardle and Videler 1980).

Rates of change in amplitude were measured along the body length. In the sharks, there was an area along the body, about 0.2  $L$  from the nose, where both amplitude and its rate of change with body length were least (Fig. 6). Anterior to this area, rates of change in amplitude were negative where amplitude increased rostrally due to yawing of the nose. These patterns are similar to those of teleosts. The maximum rate of increase in amplitude in sharks occurred from 0.5 to 0.7  $L$ , and declined over more posterior portions of the body. This particular pattern has not been described in teleosts, which usually show an early rise in amplitude (e.g., eel) or sustain increasing rates of amplitude over the whole caudal region (e.g., fusiform teleosts). The area over which amplitude begins to increase in sharks is close to

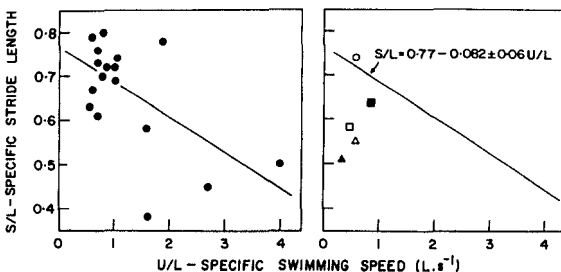


FIGURE 4.—The relationship between specific stride length,  $S/L$ , and specific swimming speed,  $U/L$  for several sharks. The key to symbols is in Figure 1.

the region of the trailing edge of the first dorsal fin (Thomson and Simanek 1977).

## DISCUSSION

The diversity of swimming kinematics in fish was originally described and classified by Breder

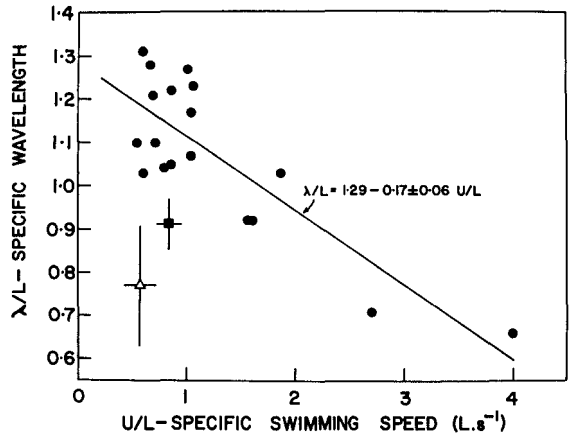


FIGURE 5.—The relationship between specific wavelength,  $\lambda/L$  and specific swimming speed,  $U/L$  for three species of shark. Vertical and horizontal bars are  $\pm 2SE$ . The functional regression was fitted only to data for the blacktip shark. The key to symbols is in Figure 1.

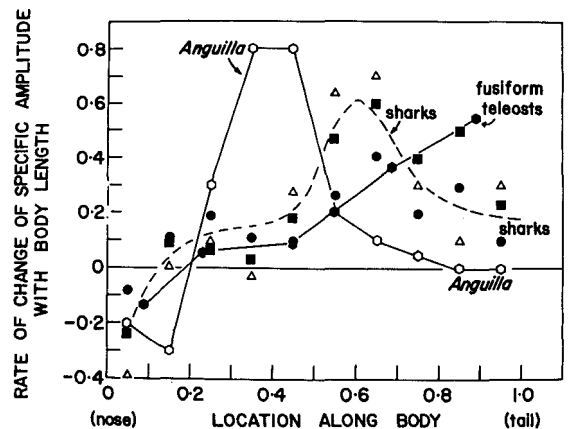


FIGURE 6.—The relationship between the rate of change of amplitude along the body length and the position along the body in some fishes. The data for fusiform teleosts (solid hexagons linked by solid lines) were taken from Bainbridge (1963) for dace, *Leuciscus leuciscus*, and bream, *Ambramsis brama*. Data for *Anguilla* (open hexagons linked by a solid line) were taken from Gray (1933). Data for the sharks (see key in Fig. 1) were taken from Figure 2; the dotted line was fitted by eye through the data for sharks.

(1926), and has been more recently updated by Lindsey (1978). The definition of common locomotor patterns, or modes (Lighthill 1975), for undulatory swimming movements of the body and caudal fin are based on the number of one-half wavelengths contained within the body length and the pattern of increasing amplitude along the body. The elongate eel, *Anguilla*, is definitive for the anguilliform mode where the body contains more than one-half wavelength within the body length, and often one or more complete waves. The lateral amplitude of body movements rises early and is large over most of the body length. Jacks, in the family Carangidae, are representative of the carangiform mode where the body length contains less than one-half wavelength, and lateral displacements increase rapidly over the posterior third or half of the body. Breder (1927) used the term "sub-carangiform mode" for fish with wave patterns of the anguilliform mode and amplitude changes similar to the carangiform mode. So far, detailed studies of fusiform teleosts have been on sub-carangiform swimmers.

The six species of shark are also subcarangiform swimmers according to these definitions; the body contained more than one-half of a wave (Table 1, Fig. 5) and the amplitude of body movements increased predominantly over the posterior half of the body (Fig. 6). However, the maximum rate of increase in amplitude occurred over the third quarter of the body, intermediate between the situation for elongate and fusiform teleosts. Therefore, although the sharks swam in the subcarangiform mode, they were more eel-like than fusiform teleosts. This is consistent with the unaided visual impressions of shark swimming.

Among teleosts, trends in swimming kinematics from the anguilliform mode towards carangiform modes are associated with changes in body form from an elongate, flexible body to a more fusiform, less flexible body. This is coupled with a larger caudal fin depth increasingly separated from the body by a narrow caudal peduncle, a morphology defined as narrow necking (Lighthill 1975). The same trends are seen in the six species of sharks studied here (Fig. 1, Table 1). The more fusiform species were those with longer propulsive wavelengths and a larger tail depth swimming in a more carangiform mode than the elongate sharks. In terms of the classification of shark functional morphology by Thomson and Simanek (1977), group 1 is most carangi-

form and groups 3 and 4 are most anguilliform. Group 1 representatives were not studied here.

The two factors of increasing wavelength and caudal fin depth in the carangiform swimmers are known to increase thrust and Froude efficiency (Lighthill 1975). However, thrust is reduced by a decrease in tail-beat amplitude. Among the sharks, increasing wavelength and tail depth were found with smaller amplitudes. Thus, the more fusiform, more carangiform species show features that would both enhance and decrease performance. Stride length increased in these more fusiform sharks so that overall the larger wavelength and deeper caudal fins must generate more than enough thrust, perhaps more efficiently, to offset reduced amplitudes.

The details of kinematic movements appear very different for sharks compared with bony fish. In the teleosts that have been studied to date (see Hunter and Zweifel 1971; Aleyev 1977) tail-beat frequency is the major kinematic variable with speed, and over most of the range of swimming speeds, it is the only variable. In contrast, the blacktip shark modulated all three of the kinematic variables that influence thrust: tail-beat frequency, tail-beat amplitude, and the length of the propulsive wave. Teleosts vary one morphological parameter with speed that would also affect thrust. This is the depth of the caudal fin trailing edge (Bainbridge 1963; Webb 1971) to vary the mass of water accelerated by propulsive movements (see Alexander 1968; Lighthill 1975). The skeleton of shark fins is based on cartilaginous ceratotrichia, rather than bony rays, which cannot be individually controlled. As a result, shark fins lack the flexibility to substantially modify fin depth during swimming.

The differences in locomotor kinematics with speed of the sharks illustrated by the blacktip shark, compared with teleosts, may be related to hydrodynamic interactions between the median dorsal fins and the caudal fin. This interaction was first described by Lighthill (1970) and has been developed in detail using hydromechanical theory for inviscid fluids by Sparenberg and Wiersma (1975). A vortex sheet is shed by the trailing edge of any sharp fin or body edge. This vortex sheet travels downstream, but it also has a lateral velocity component determined by the motion of the trailing edge; i.e., the wake follows a sinusoidal path (see illustrations in Rosen 1959; Aleyev 1977). The vortex sheet carries momentum determined by the motions and dimensions of the body and fin at the fin trailing edge.

The momentum carried in the vortex sheet will contribute to instantaneous thrust, and if there is no downstream fin to influence the flow, this momentum will contribute to the mean thrust and power of the fish (Wu 1971; Newman and Wu 1973). However, when there is a downstream re-entrant fin (i.e., a second downstream median fin spanning the flow from the anterior fin) the vortex sheet will impinge on the leading edge of that fin. If the gap between the fins is small, there is little difference between the motion of the incident vortex sheet and the motion of the leading edge of the downstream fin. Then the mean strength of the vortex sheet shed by the downstream fin is determined by the motion of that fin, with no significant contribution from the upstream vortex sheet from the anterior fin, i.e., the upstream fin has no effect on the wake eventually shed by the fish. In this case, the interaction between median fins does not influence mean thrust.

Lighthill (1970) showed that a different situation can occur when the gap between median fins is large. Under these circumstances, there may be a large enough phase difference between the motion of the incident vortex sheet and the downstream fin, so that the momentum shed upstream is not annihilated by the second fin. Then, the work done by the anterior fin against the momentum shed by its trailing edge together with that due to an increased incident velocity at the downstream fin increase total power output and improve efficiency (Lighthill 1975:80-84; Sparenberg and Wiersma 1975).

The phase difference in the motion of the trailing edge of one fin located at a position  $a_1$ , along the body, and the leading edge of a second more posterior fin at position  $a_2$ , is  $2\pi(a_2 - a_1)/\lambda$  where  $\lambda$  is the length of the propulsive wave. However, the vortex sheet travels downstream at the mean speed,  $U$ , of the fish, while the body undulation travels backwards at a speed  $c$ , greater than  $U$ . Therefore, the phase difference,  $\phi$ , in the motions of the vortex sheet shed by the anterior fin and the leading edge of a posterior fin is given by (Lighthill 1975, equation 28):

$$\phi = 2\pi \left( \frac{a_2 - a_1}{\lambda} \right) \left( \frac{c}{U} - 1 \right). \quad (1)$$

Sharks typically have three median fins, the first and second dorsal fins and the caudal fin. Thomson and Simanek (1977) have analyzed several morphological features of 56 species of

sharks and show that the second dorsal fin is characteristically small compared with the first dorsal fin, especially in pelagic species. In addition, the second dorsal fin would only be partly re-entrant to most of the vortex sheet shed by the upstream fin because of the posterior taper of the body. Therefore, it seems likely that the second dorsal fin has relatively little effect on the flow between the other two fins during steady cruising. Thomson and Simanek's observations also indicate that the caudal fin depth is typically greater than or equal to that of the trailing edge of the first dorsal fin, as required to maximize the interaction. Therefore,  $\phi$  was calculated for interactions between the first dorsal fin and the caudal fin of the blacktip, bonnethead, and leopard sharks (Table 2; Fig. 7).  $\phi$  was close to, or  $>0.5\pi$ , as required for the interaction hypothesized by Lighthill (1970). A single record for the dogfish, *Acanthias vulgaris*, in Gray (1933) also gives a value of  $\phi = 0.52\pi$  (Webb 1975). For

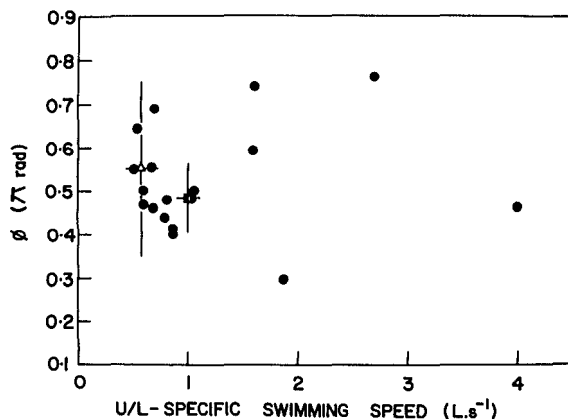


FIGURE 7.—The relationship between the phase difference  $\phi$  (see Equation (1)) and specific swimming speed for three species of sharks. Vertical and horizontal bars are  $\pm 2SE$ . The key to symbols is in Figure 1.

TABLE 2.—Separation,  $(a_2 - a_1)/L$ , between the trailing edge of the first dorsal fin ( $a_1$ ) and the mean position of the leading edge of the caudal fin ( $a_2$ ), and phase difference ( $\phi$ ) between their movements for three species of sharks.  $\phi$  was calculated from data in this table and in Figures 3 and 4 using Equation (1).

Species	$(a_2 - a_1)/L$	$\phi$ ( $\bar{X} \pm 2SE$ ) ( $\pi$ radians)
Leopard shark	0.48	$0.55 \pm 0.20$
Bonnethead shark	0.50	$0.48 \pm 0.08$
Blacktip shark	0.47	$0.51 \pm 0.05$



blacktip shark,  $\phi$  was of the order of  $0.5\pi$  over the range of swimming speeds studied.

In Equation (1),  $a_1$  and  $a_2$  are constants, and therefore,  $f$  or  $\lambda$  can be varied at any speed to keep  $\phi \geq 0.5\pi$ . However, such changes also affect thrust. For example, if  $\lambda$  varies with speed, compensatory changes in tail-beat frequency and/or tail-beat amplitude must occur to balance thrust and drag at a given speed. The blacktip shark modulated both. Therefore, the modulation of wavelength, amplitude, and frequency with speed can be explained in terms of mechanical advantages from an interaction between widely spaced median fins. It should also be noted that the early rate of increase of amplitude along the body in sharks, occurring near the first dorsal fin, might increase the strength of the vortex sheet. This could enhance thrust, perhaps more than would occur with patterns of increasing amplitude seen in fusiform teleosts.

Adaptive flow interactions between median fins as suggested by Lighthill (1970) apply to the established flow patterns of a steadily swimming fish. Therefore, the common body form and kinematic patterns of sharks appear to be adaptations for cruising. Some sharks, analogous in form to tuna (group 1 of Thomson and Simanek 1977), are obviously highly specialized for cruising (Lighthill 1975; Lindsey 1978), but the present observations suggest that other sharks are also specialized through the utilization of other principles, exploiting more anguilliform propulsion and a more elongate, flexible body. The distribution of the median fins along the body is very similar among sharks (Thomson and Simanek 1977). This suggests that such cruising adaptations are relatively common. Furthermore, sharks are frequently negatively buoyant, when continuous forward motion is important in swimming free from the bottom. This argues for the importance of cruising in the routine behavior of sharks, and hence the importance of any mechanisms to enhance thrust and efficiency in steady swimming.

Comparative observations on teleosts also suggest that in general, sharks are specialized in cruising. Experimental studies have shown that optimal design for transient swimming patterns (angular and linear acceleration) differs from, and is largely exclusive of, that for steady swimming such as cruising (see review by Webb in press). In teleosts, optimal morphological features for steady swimming include a small area anterior to a deep high aspect ratio tail propel-

ling a fairly rigid body. For maximum acceleration, depth (and hence area) should be large over the whole length of a flexible body. Bony fish can achieve some compromise because of their flexible fins, but in general design for unsteady acceleration activity appears most important (Webb 1982). Compromises are excluded for sharks because they do not have collapsible fins. In addition, the separation of the median fins reduces the area of the body available to generate large forces for acceleration. Some sharks, e.g., the horn shark, *Heterodontus francisci*, have somewhat enlarged median fins that suggest a greater importance of acceleration. In general, a more posterior location of the first dorsal fin is associated with larger area fins, as in *Ginglymostoma cirratum* that could similarly improve acceleration. In this case the more posterior location of the first dorsal fin may be at the cost of reducing  $\phi$  below  $0.5\pi$ . However, the body and fin form typical of sharks (Thomson and Simanek 1977) probably provides for poor acceleration performance.

In conclusion, sharks appear to have exploited their different structural capacities to specialize for cruising when swimming.

## ACKNOWLEDGMENTS

This work was completed while P. W. Webb was an NRC/NOAA Research Associate on leave from the University of Michigan. I am indebted to R. Lasker and J. R. Hunter for their hospitality. The authors thank Sea World for providing specimens and facilities.

## LITERATURE CITED

- ALEXANDER, R. MCN.  
1968. Animal mechanics. Univ. Washington Press, Seattle, 346 p.
- ALEYEV, Y. G.  
1977. Nekton. Junk, The Hague, 435 p.
- BAINBRIDGE, R.  
1958. The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat. J. Exp. Biol. 35:109-133.  
1963. Caudal fin and body movement in the propulsion of some fish. J. Exp. Biol. 40:23-56.
- BREder, C. M., JR.  
1926. The locomotion of fishes. Zoologica (N.Y.) 4:159-297.
- BRETT, J. R., AND J. M. BLACKBURN.  
1978. Metabolic rate and energy expenditure of the spiny dogfish, *Squalus acanthias*. J. Fish. Res. Board Can. 35:816-821.

- GRAY, J.  
1933. Studies in animal locomotion. I. The movement of fish with special reference to the eel. *J. Exp. Biol.* 10: 88-104.
- HUNTER, J. R., AND J. R. ZWEIFEL.  
1971. Swimming speed, tail beat frequency, tail beat amplitude, and size in jack mackerel, *Trachurus symmetricus*, and other fishes. *Fish. Bull.*, U.S. 69:253-266.
- JOHNSON, C. S.  
1970. Some hydrodynamic measurements on sharks. *Nav. Underwater Cent. Tech. Rep.* 189, 13 p.
- LIGHTHILL, M. J.  
1970. Aquatic animal propulsion of high hydromechanical efficiency. *J. Fluid Mech.* 44:265-301.  
1975. *Mathematical biofluidynamics*. SIAM, Phila., 281 p.
- LINDSEY, C. C.  
1978. Form, function, and locomotory habits in fish. *In* W. S. Hoar and D. J. Randall (editors), *Fish physiology*, vol. VII, p. 1-100. Acad. Press, N.Y.
- NEWMAN, J. N., AND T. Y. WU.  
1973. A generalized slender-body theory for fish-like forms. *J. Fluid Mech.* 57:673-693.
- ROSEN, M. W.  
1959. Water flow about a swimming fish. U.S. Navy Ordinance Test Stat. Tech. Publ. 2289, 96 p.
- SPARENBERG, J. A., AND A. K. WIERSMA.  
1975. On the efficiency increasing interaction of thrust producing lifting surfaces. *In* T. Y.-T. Wu, C. J. Brokaw, and C. Brennen (editors), *Swimming and flying in nature*, vol. 2, p. 891-917. Plenum Press, N.Y.
- THOMSON, K. S., AND D. E. SIMANEK.  
1977. Body form and locomotion in sharks. *Am. Zool.* 17:343-354.
- WARDLE, C. S.  
1975. Limit of fish swimming speed. *Nature (Lond.)* 255:725-727.
- WARDLE, C. S., AND J. J. VIDELER.  
1980. How do fish break the speed limit? *Nature (Lond.)* 284:445-447.
- WEBB, P. W.  
1971. The swimming energetics of trout. 1. Thrust and power output at cruising speeds. *J. Exp. Biol.* 55:489-520.  
1973. Effects of partial caudal-fin amputation on the kinematics and metabolic rate of underyearling sockeye salmon (*Oncorhynchus nerka*) at steady swimming speeds. *J. Exp. Biol.* 59:565-581.  
1975. Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Board Can.* 190, 158 p.  
1982. Locomotor patterns in the evolution of actinopterygian fishes. *Am. Zool.* 22:329-342.
- WEIHS, D., R. S. KEYES, AND D. M. STALLS.  
1981. Voluntary swimming speeds of two species of large carcharhinid sharks. *Copeia* 1981:219-222.
- WU, T. Y.  
1971. Hydrodynamics of swimming fishes and cetaceans. *Adv. Appl. Math.* 11:1-63.