

In all organisms, shape is a real and distinctly biological phenomenon (Bookstein, 1978). Accurately quantified, shape in fishes is important for functional and ecological investigations. For example, Keast and Webb (1966) catalogued feeding and locomotory habits of individual lake fishes and related these to body form, described qualitatively. One could make better inferences of ecology and function from shape if specific aspects of form were isolated, quantified, and then related to function or ecology. Ecologists have also used morphological measurements of birds or lizards (Hespenheide, 1973) and more rarely fishes (Gatz, 1979a, b), as the basis for ecological generalizations about community structure. Such generalizations depend on measurements which accurately describe functionally important attributes of shape. The system I propose allows these attributes to be more easily isolated and consciously combined.

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DIVISION OF LABOR BETWEEN MEDIAN FINS IN SWIMMING DOLPHIN (PISCES: CORYPHAENIDAE).—Two primary components of the propulsive system of a fish are the muscle system and the body surfaces which react with the water to generate thrust. Both of these components show functional variations in relation to activity level. It is well known that the muscle system has two major components of red muscle, a low power, almost inexhaustible system functional at low speeds, and white muscle, a high power, rapidly fatiguing system that provides power at high activity levels (sprint speeds and acceleration). While some overlap in function exists at intermediate speeds, the major function of red and white muscle at different activity levels has led to the concept of a "division of labor" between the two systems (Bone, 1978).

Translation of muscle power into thrust power depends on the way the body moves and the distribution of dorso-ventral depth along the body length; as with muscle, optimum requirements vary with activity. Hydrodynamic theory (Lighthill, 1970; Weihs, 1972, 1973) and experimental observations (Webb, 1977) have shown that a deep tail and small anterior depth and area are optimal for steady (time independent) swimming. The opposite is true for turning and acceleration when body area should be maximized by large depth along the whole body length. In actinopterygians, body shape for these activities can be varied as fish can control the extension of their fins (Bone, 1971; Eaton et al., 1977; Wardle and Reid, 1977; Webb,

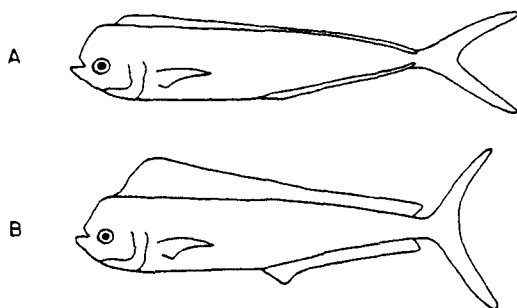


Fig. 1. Tracings from video tapes of dolphin fish showing the use of the median fins A) during steady swimming and B) during acceleration turns.

1977). Changes in the longitudinal distribution of depth and hence area can therefore act as a "variable propeller" optimizing thrust generation according to activity. A logical extension of this variable propeller would be specialization of different median fins for different activities, for which each fin could be more efficient than using a single multiple-function fin. Such specialization could be called a division of labor analogous to that of muscle specialization.

This note reports observations on the dolphin, *Coryphaena hippurus*, which has a lunate tail, usually associated with specialized steadily swimming species (Sharp and Dizon, 1978) and large collapsible dorsal and ventral fins, more appropriate for unsteady swimming (Weihs, 1972, 1973; Webb, 1977). The purpose of the observations was to test the hypothesis that these fins have discrete functions in different activities.

Observations were made in a rectangular tank, 12.7 m long, 4.2 m wide and 4.0 m deep. Water temperature was 22 C. The tank contained dolphin *Coryphaena hippurus*, yellowtail *Seriola dorsalis*, lookdown *Selene vomer*, blue and gold snapper *Lutjanus veridus*, and northern anchovy *Engraulis mordax*. Data were obtained for three dolphins (mean length,  $L = 1.09$  m). Supplemental observations were made on the yellowtails ( $L = 0.61$ ,  $N = 10$ ) because this species has a specialized lunate tail and lacks the ability to substantially alter the longitudinal distribution of depth.

The dolphin and yellowtail were captured south of Cape San Lucas, Baja California, using baited hooks and line. At the time of the experiments, the fish had remained in the tank for 11 months. Fish were fed a submaximum

ration in three feedings per day. The diet was dead panaeid shrimp, smelt and squid. The fish swam continuously around the tank between feedings. During feeding, the fish swam discontinuously with numerous acceleration turns, combining a sudden rapid acceleration with a turn, to catch food items and to stay in the vicinity of the feeding area.

Video tape recordings were made of steady swimming activity between feedings and of unsteady swimming during feeding. In the former case, only steady swimming in the center of the tank was recorded midway between the ends. Video tape was analyzed using a stop-action recorder. Tape was advanced by hand to resolve events to within  $1/60$  sec (17 msec). The extension of the anterior median and caudal fins were recorded. Specific swimming speeds ( $L \cdot \text{sec}^{-1}$ ) were calculated for fish swimming normal to the camera. Turning radii were calculated from the geometry of the camera field and the known lengths of the fishes. The number of tail beats required to negotiate a  $180^\circ$  turn was recorded.

The lunate caudal fin was used for steady low-speed cruising by both dolphin and yellowtail and the long anterior median fins of the dolphin fish were fully furred (Fig. 1A). Dolphins swam in the sub-carangiform mode (more than one-half of a propulsive wave included along the body) and yellowtail swam in the carangiform mode (less than half a wavelength seen). Mean cruising speeds were  $0.72 \pm 0.03 L \cdot \text{sec}^{-1}$  ( $x \pm 2$  SE;  $N = 46$ ) for the dolphin and  $1.13 \pm 0.06 L \cdot \text{sec}^{-1}$  ( $N = 20$ ) for the yellowtail, similar to speeds of other fish in the wild (Beamish, 1978).

Unsteady swimming (acceleration turns) was observed during feeding. Dolphins fully extended their median fins immediately prior to a maneuver (Fig. 1A), furling them immediately on completion of the maneuver. They completed a  $180^\circ$  turn in one tail beat. This is comparable with non-lunate tail species, such as trout and goldfish with large fin areas (Weihs, 1972; Webb, 1976, 1977; Eaton et al., 1977). Yellowtail showed few turns and used three tail beats to negotiate a  $180^\circ$  turn. Specific turning radii (turning radius/length) were  $0.13 \pm 0.01 L$  for dolphin and  $0.23 \pm 0.06 L$  for yellowtail at mean speeds of  $1.48 \pm 0.16 L \cdot \text{sec}^{-1}$  ( $N = 27$ ) and  $2.27 \pm 0.34 L \cdot \text{sec}^{-1}$  ( $N = 12$ ), respectively. Higher speeds were probably prevented by limited space due to the presence of other fish competing for food. The minimum specific

turning radius of rainbow trout, *Salmo gairdneri*, an unspecialized non-lunate tail species, has been found to be independent of length with a mean value of 0.17 L (Webb, 1976). Specific turning radii are probably independent of size for other species so that values for fish of different lengths can be used as a basis for comparison. Howland (1974) has suggested that speed and turning radius of fish are inversely related as for rigid bodies. However, when fish flex their bodies to power a turn, the turning radius could be independent from speed or even decrease with increasing speed.

These observations show that dolphin fish use their median fins in distinct ways in steady and unsteady swimming activities consistent with a division of labor among median fins. During steady swimming, the lunate tail is employed alone, similar to specialized lunate-tail swimmers. This would maximize thrust (Lighthill, 1970) without a substantial drag penalty due to a large anterior area (Webb, 1973). However, the efficiency of the lunate tail is probably lower than that of specialized forms because dolphins continue to swim in the sub-carangiform mode rather than the more efficient carangiform mode (Lighthill, 1970). This is probably because the body width of dolphin fish is relatively small, promoting flexibility, while the reduced depth of the caudal peduncle (narrow necking) is not as well developed. Thus dolphins retain some kinematic features of steady swimming of non-lunate tail propulsion with some morphological features of specialized lunate-tail swimmers. Dolphins would be expected to be more efficient swimmers than the non-lunate tail species but less efficient than specialized lunate tail forms.

During unsteady acceleration maneuvers, dolphins fully erect their median fins, the same as non-lunate tail species (Eaton et al., 1977; Webb, 1977). This would maximize thrust production for such activities (Weihs, 1972, 1973). However, the lunate tail has a relatively small area compared to non-lunate tails and this would be expected to reduce turning ability to some extent. In practice, the dolphin is able to turn in a smaller circle than trout, a non-lunate tail species. It is probable that the dolphin's thin body could offset possible disadvantages of the lunate tail in powered turns. Certainly the yellowtail, with a short thick body, had considerable difficulties in negotiating a turn.

The division of labor between the lunate tail for cruising and the median fins for accelera-

tion turns reflects the normal habits of the dolphin. Like other lunate tail species, the dolphin is migratory. Dolphins also forage in schools and take elusive pelagic prey similar to other lunate tail species (Kojima, 1961, 1965; Sharp and Dizon, 1978). However, dolphins are usually found in smaller schools and regularly forage under natural and artificial floating rafts of various materials where good maneuverability would be advantageous. Indeed the latter habits are the basis for a lucrative fishery (Kojima, 1965; Hunter and Mitchell, 1968).

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**DIEL BEHAVIOR OF THE TIGER SHARK, *GALEOCERDO CUVIER*, AT FRENCH FRIGATE SHOALS, HAWAIIAN ISLANDS.**—Adult tiger sharks, *Galeocerdo cuvier*, are among the largest aquatic predators in tropical and subtropical reef communities and are well known for their euryphagic diet (Ikehara, 1960, 1961; Tester, 1969; Fujimoto and Sakuda, 1972; Taylor and Naftel, 1978). However, the majority of information on the daily movement patterns of this shark comes from anecdotal field observations. For example, in Caribbean waters tiger sharks were considered nocturnal because they were rarely observed at the surface during the day but often captured on set lines (Randall, 1967) or encountered near fishing operations (Springer, 1943), at night. While tiger sharks inhabit the tropical waters of Florida throughout the year (Springer, 1963), some individuals migrate northward in the summer months along the western Atlantic coast as far as Woods Hole, Mass. (Big-

elow and Schroeder, 1948). Limited data from conventional tagging studies in Hawaiian waters indicate that tiger sharks may restrict movements within a geographic area for at least part of the year (Tester, 1969).

Much still remains to be learned of the diel activity patterns of tiger sharks. Herein, we present results of the first telemetric study on this predator and provide detailed data on the daily spatial requirements of a free-swimming adult tiger shark in its natural environment.

*Study area and methods.*—French Frigate Shoals is located in the center of the Hawaiian Archipelago, approximately 900 km northwest of Honolulu, Oahu (Fig. 1). The area was chosen because it offered a topography conducive to day and night operations of a small tracking boat and an abundance of sharks. In addition, it lies within the Hawaiian Island National Wildlife Refuge and presents a natural reef ecosystem relatively undisturbed by human activity. The shoal consists of a shallow reef on the north and east (windward) sides with a deeper leeward shelf (approximately 20-40 m deep) that extends westward to the reef drop-off. There are 13 small sand islands scattered on the reef and one basalt island, La Perouse Pinnacle, near the center of the shoal.

A high-power, long-range ultrasonic transmitter was developed to monitor the activity patterns of adult tiger sharks. Tags incorporated a modified version of the circuitry described by Ferrel et al. (1974), and transmitted at frequencies near 32 kHz. The cylindrical package was 25 cm long, 4 cm in diameter and weighed 440 g in air. Pulse intervals were controlled by a resistive depth sensor sensitive from 0 to 140 m and adjusted to rates ranging from 0.5 to 1.5 pulses/second, respectively. Signals were monitored with a tuneable ultrasonic receiver and a staff-mounted directional hydrophone. Absolute maximum range of the transmitter-hydrophone system under ideal conditions was approximately 4,000 m although transmission loss greatly reduced the audible signal at ranges greater than 2,000 m.

Transmitter signals were monitored from a 7-m tracking boat in which bearing and range estimates of the shark were recorded every 15 min. Bearings were taken with an oil-filled navigation compass based on the direction of the strongest audible signal. Accuracy of the bearing estimates was tested and found to be within  $\pm 7^\circ$ . Range estimates were based on the relative