

DIRECT MEASUREMENT OF SWIMMING SPEEDS AND DEPTH OF BLUE MARLIN

By BARBARA A. BLOCK, DAVID BOOTH

The University of Chicago, Department of Organismal Biology, 1025 East 57th Street, Chicago, IL 60637, USA

AND FRANCIS G. CAREY

Woods Hole Oceanographic Institution, Department of Biology, Woods Hole, MA 02543, USA

Accepted 30 December 1991

Summary

Acoustic telemetry was used to monitor the swimming speed, depth and water temperature of three blue marlin (60 kg, 70 kg, 125 kg) and 165 h of continuous swimming speed data containing both sustained and burst swimming events were collected. Measurements of swimming speed show that, while blue marlin are capable of high speeds, they spend most of their time swimming slowly. The fastest sustained swimming speeds ($80\text{--}120\text{ cm s}^{-1}$) occurred during a 4–6 h recovery period immediately after tagging when marlin consistently swim at depths greater than 50 m. Short bursts of speeds up to 225 cm s^{-1} were usually associated with changes in depth. Slower swimming ($15\text{--}25\text{ cm s}^{-1}$) occurred when fish were within 10 m of the surface. These velocities are similar to direct measurements of swimming speeds of free-swimming sharks, seals and sea lions, indicating that many large aquatic vertebrates swim slowly to minimize energetic costs of transport.

Introduction

Blue marlin, *Makaira nigricans* (Lacépède), are members of the suborder Scombroidei, a group that contains many large, commercially important marine fish such as tunas, swordfish, marlin and spearfish. The genus *Makaira* includes the largest living teleosts with reported specimens weighing over 800 kg (Mather, 1976). Marlin are solitary pelagic fish that make yearly migrations of thousands of kilometers across ocean basins (Squire, 1985, 1987; Davie, 1990). The most notable long-distance return is that of a 58 kg black marlin, *Makaira indica*, released off Baja, California, and recaptured 10 000 km from the point of release off New Zealand by a Japanese longliner (Squire, 1985). They are highly adapted to a pelagic mode of life, having numerous morphological features that enhance locomotor performance. Body surfaces are characterized by extraordinary stream-

Key words: telemetry, speed, locomotion, blue marlin, *Makaira nigricans*.

lining, pectoral fins are swept back and have large surface areas for lift, while a high-aspect-ratio tail provides thrust. Many of their locomotory adaptations are thought to be related to the high burst speeds of these fish. The large size and pelagic habitat of blue marlin make them difficult to study. Only recently, with the rapid world-wide depletion of blue marlin stocks, has attention focused on the biology and conservation of this species. Laboratory-based research on blue marlin and other istiophorids (marlins, spearfish, sailfish) has rapidly increased in the past decade (for reviews, see Davie, 1990; Stroud, 1990) and has revealed numerous physiological and morphological specializations for a nomadic lifestyle in the open sea. However, because of the difficulties of studying free-ranging fish in the open ocean, there is little knowledge about what these fish do in the wild.

The powerful and acrobatic movements of blue marlin caught on hook and line have long captured the imagination of fishermen, and it is well established that they can explosively strike a bait trolled at high speeds (800 cm s^{-1} , F. Rice, personal communication) but no direct speed measurements have been made. Blue marlin are commonly assumed to be among the fastest of all fishes and swimming speeds as high as 2000 cm s^{-1} have been estimated (Walters, 1962; Davie, 1990). The power required to reach such velocities is extraordinarily high (Johnston and Salamonski, 1984; Hebrank *et al.* 1990). These bursts are thought to be powered by white muscle fibers, which constitute the bulk of the skeletal muscle mass.

By placing speedometers on blue marlin, we were able to obtain a continuous record of swimming speed and relate variations in speed to changes in depth and behavior. We present here the first direct measurements of swimming speed for blue marlin and show that, while capable of high speeds, they spend most of their time swimming slowly.

Materials and methods

Multiplexed acoustic transmitters capable of sending pulse-encoded data from depth, water temperature and speed sensors were attached to three blue marlin estimated to weigh 70, 60 and 125 kg. The three fish studied here (marlin 4, 5 and 6) were part of a larger study in which six marlin were tracked off the Kona coast of the island of Hawaii (Block *et al.* 1992).

Body length of marlin was difficult to estimate accurately because fish were continually in motion during the tagging procedure. Restraining them for accurate measurement would have led to unacceptable stress and injury. The length of the largest fish in our study (225 kg) was estimated as 1.8 m (lower jaw to fork length) from photographs taken during tagging. Masses of fish were estimated by the professional captains of sportfishing boats who are remarkably accurate with their estimates ($\pm 5\text{ kg}$). It should be noted that estimating body length from body mass is complicated by the inability to determine sex externally in blue marlin: there are considerable differences in the mass-length relationships of males and females.

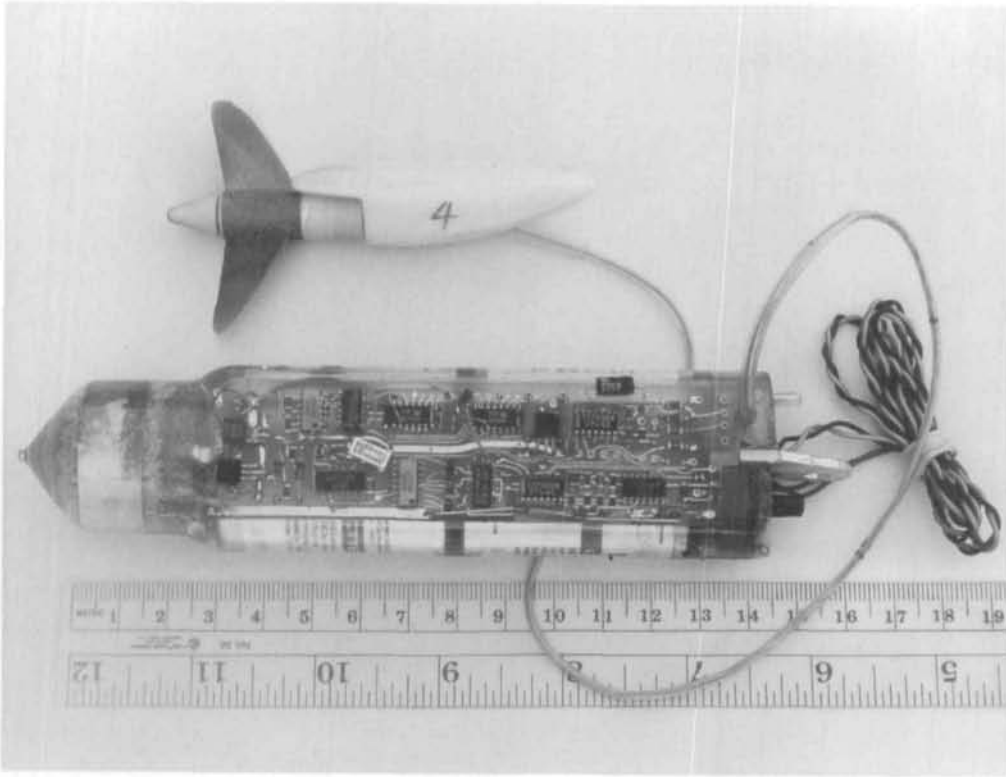


Fig. 1. Speedometer transmitter. The thermistor, pressure sensor and cable to the speed rotor are at the front (right) and the acoustic transducer on the rear (left). A small dart that holds the transmitter to the fish is attached to the aluminum eye. The roll of wire is removed before use.

Marlin estimated to be larger than 140 kg in Kona waters are assumed to be female (Hopper, 1990).

A transmitter with a speedometer is shown in Fig. 1. The multiplex transmitters were 18.0 cm long, 4.0 cm wide and 2.2 cm thick. They weighed 190 g in air and 78 g in sea water. The speed sensor was a 5 cm diameter, 10 cm pitch, plastic propeller (Octura Models 2050, Skokie, IL) containing a magnet which activated a magnetic reed switch. Circuitry in the transmitter divided the switch closures by 16 to give a pulse repetition rate for the speedometer between 0.5 and 2 Hz at the swim speeds we observed. The rotor was attached to a shaft mounted in a streamlined frontal piece cast from buoyant syntactic foam. A flexible 3 mm diameter 35 cm long cable ran from the transmitter to the rotor assembly, where it was attached asymmetrically to the lower side of the frontal piece. The asymmetric shape, and the buoyancy of the foam, caused the rotor assembly to plane away from the boundary layer surrounding the fish. The cable allowed the rotor to align with water flow regardless of the orientation of the transmitter. We observed this device on marlins 5 and 6 and in both cases the rotor was trailing above and behind the point

of attachment and aligned with the direction of flow. The speedometer, calibrated by towing in a flume at known velocities, had a linear response over a range of speeds from less than 20 cm s^{-1} to 210 cm s^{-1} , the maximum possible in our flume. Although the system could record faster speeds, such speeds were not encountered during experiments. The transmitter also contained a thermistor mounted on an aluminum stub to measure water temperature and a strain gauge pressure sensor (Keller PA-2-20) for depth. Data was time-multiplexed by the transmitter clock so that 32 s of information on speed, 24 s of depth and 8 s of water temperature data were broadcast in sequence over a continuously repeating 64 s cycle. A similar crystal clock on shipboard stayed synchronous with the transmitter clock and allowed the computer to identify the parameter currently being broadcast. The data collection system is described by Block *et al.* (1992). During data analysis, a mean was calculated for the parameters of interest for each data period within a 64 s cycle.

Results

The blue marlin were followed for periods of 25–120 h. Analysis of depth recordings from three marlin in the depth/speed study, as well as from three other fish fitted with depth/temperature transmitters, indicates a preference among blue marlin for the mixed layer, with the fish swimming predominantly above the thermocline (Figs 2 and 8). Figs 3–5 show continuous swimming speed records for three blue marlin. Similarities in their swimming behavior are apparent. Immediately after tagging, marlin 5 and 6 entered into a stereotypic recovery period lasting 4–6 h (Fig. 2; Holland *et al.* 1990), in which fish descended to 50–100 m and swam at elevated speeds ($80\text{--}100 \text{ cm s}^{-1}$). Swimming during this recovery period (Fig. 6) is presumed to be powered predominantly by aerobic red muscle fibers.

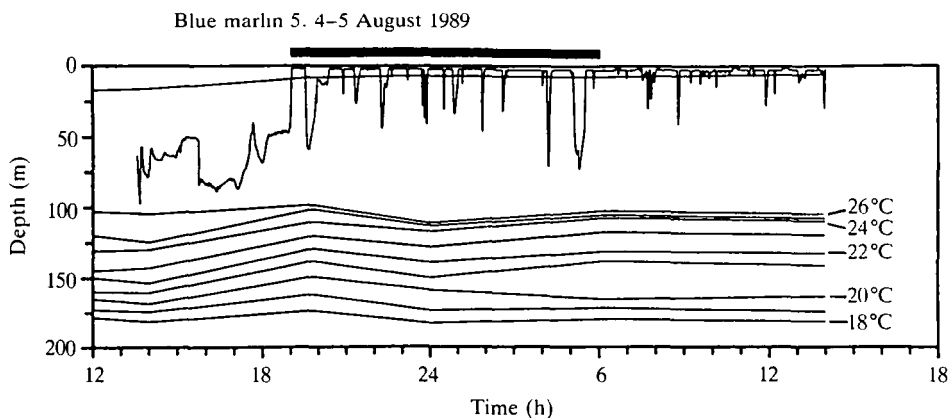


Fig. 2. Depth record of marlin 5 superimposed on a 1°C isotherm plot drawn from expendable bathythermograph casts. The dark bar indicates night. The recovery period lasted until sunset, 5.5 h after release.

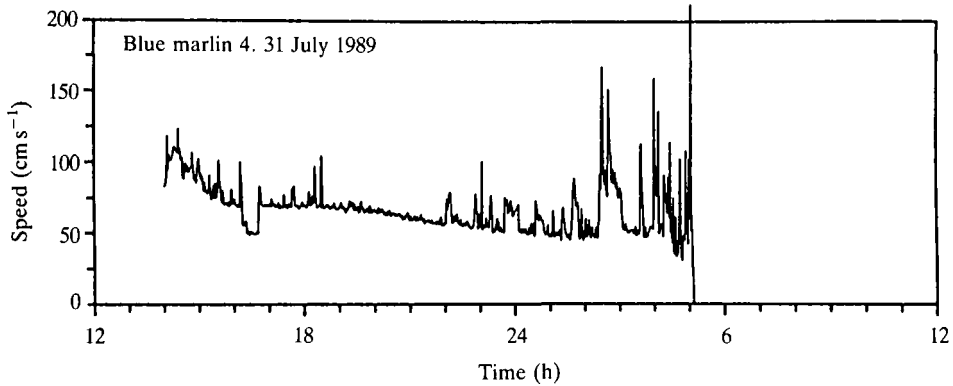


Fig. 3. Swimming speed record of marlin 4 off of Kona, Hawaii. Elevated swimming speeds are associated with periods at depth. The short rapid increases of speed are usually associated with rapid dives. This marlin was killed by a shark at 05:15 h.

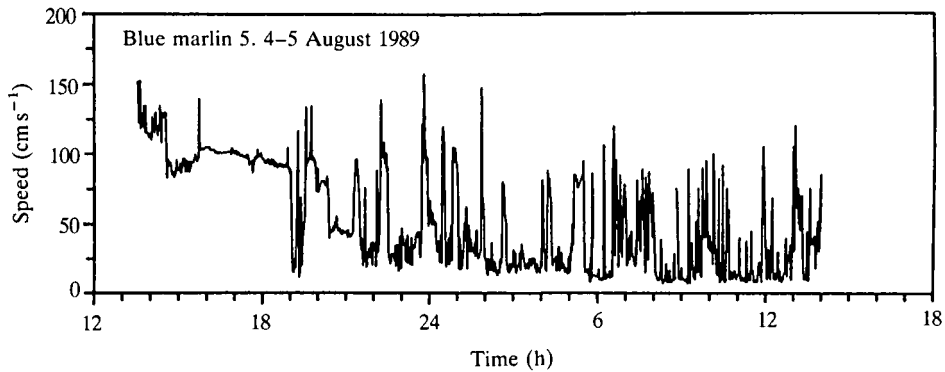


Fig. 4. Swimming speed record of marlin 5.

When in near-surface waters (<10 m), marlin always display much slower swimming speeds (<25 cm s⁻¹). Because blue marlin spend over 50 % of their time in the top 10 m of the water column (Holland *et al.* 1990; Block *et al.* 1992), most of the time these fish were travelling at low speeds.

The frequency distributions of swimming speeds for the cumulative track time of all three blue marlin are shown in Fig. 7. The most striking result is the relatively slow speeds at which marlin normally swim. For over 97 % of the time, swimming speed was less than 120 cm s⁻¹ (0.7 BL s⁻¹ for marlin 6, where BL is body length), and the maximum speed we observed was less than 225 cm s⁻¹. Typically, long periods of swimming at speeds of less than 30 cm s⁻¹ were punctuated by short increases in speed up to 225 cm s⁻¹. Periods of elevated speed were often correlated with movement of the fish to greater depths (see Figs 8 and 9).

The following is a brief description of the track of each fish tagged with a speedometer. Marlin 4, 70 kg, (Fig. 3) was exhausted after capture on hook and

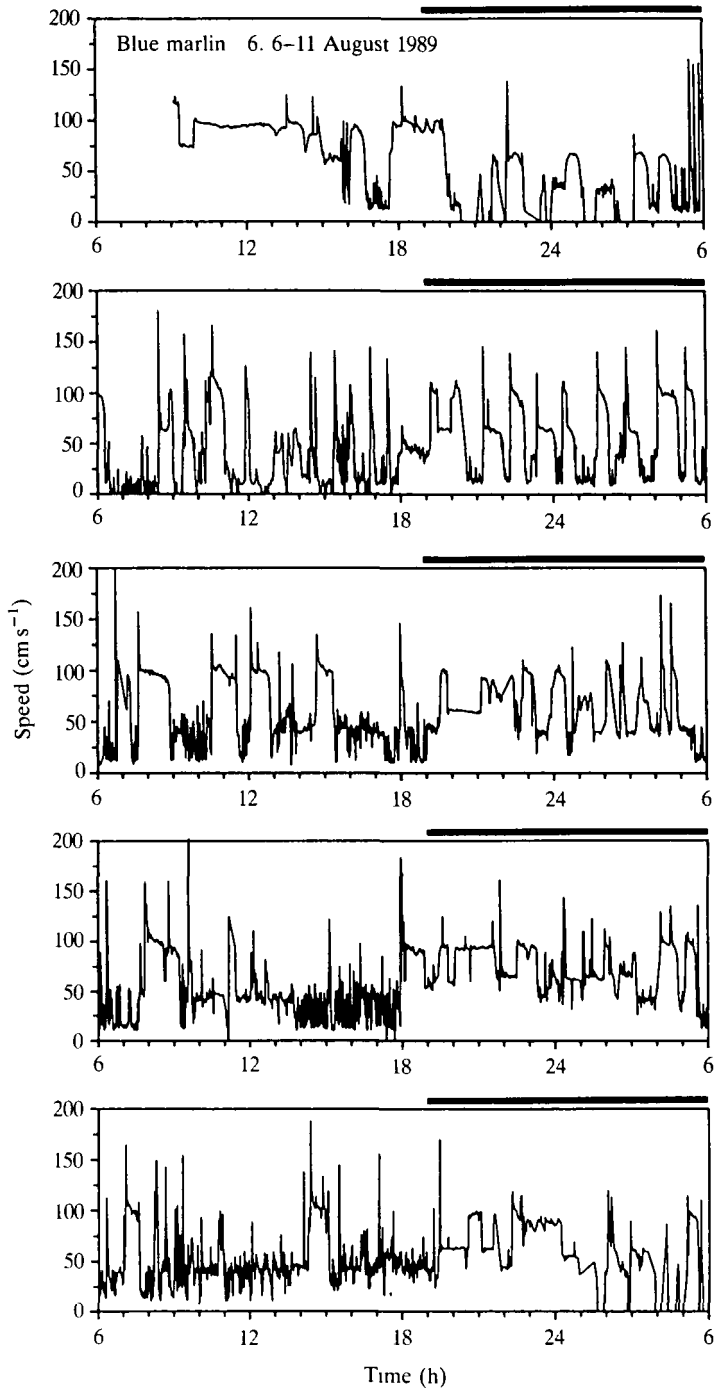


Fig. 5. Five-day swimming speed record of marlin 6. Dark bars indicate night. This fish showed a diel record with slow periods of swimming at the surface during the day and periods of faster swimming during the night. Days three, four and five show clear differences between the average daytime and nighttime speed.

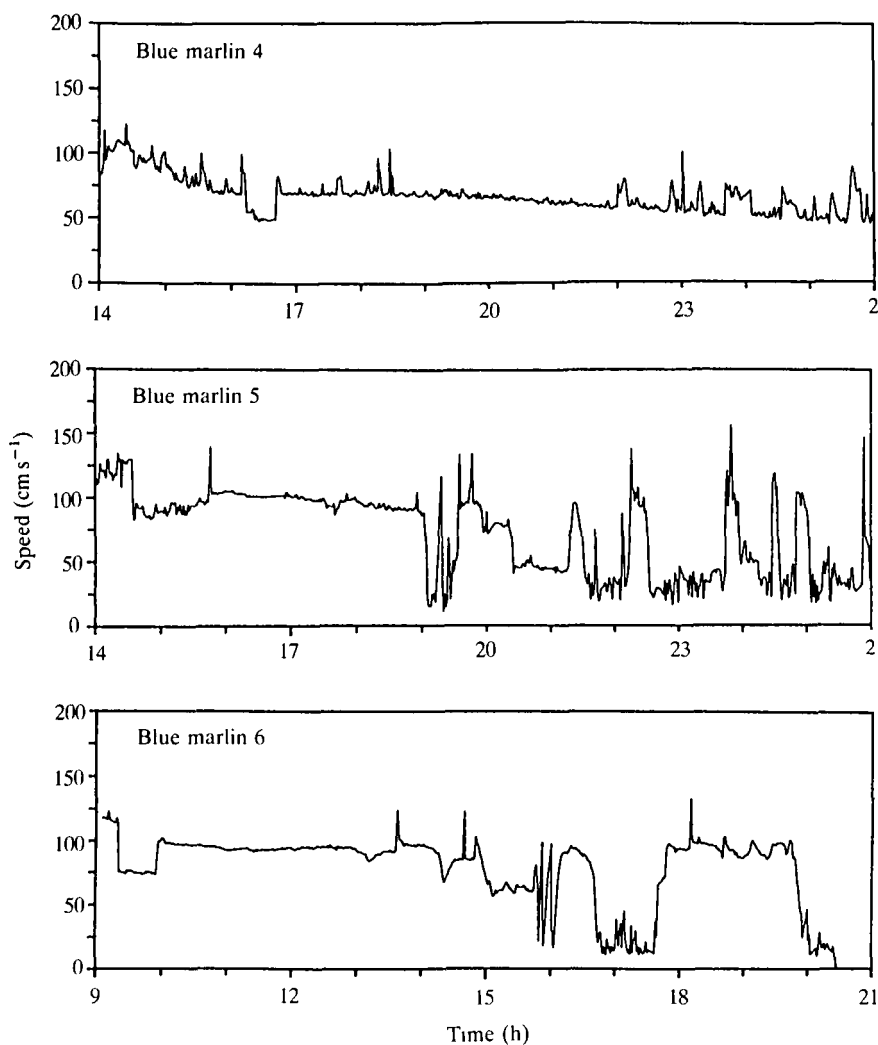


Fig. 6. Comparison of the elevated sustainable swimming speed of three marlin. This probably represents aerobic swimming powered by the red muscle mass. The elevated sustainable speeds are strikingly similar for these three fish of different body size.

line. The fish was released after being towed to irrigate the gills, which facilitated its recovery from being tagged. The marlin began a short period (<2 h) of sustained swimming ($75\text{--}100\text{ cm s}^{-1}$) but remained close to the surface (<20 m) and headed in a south-westerly direction. The behavior of this marlin was distinctly different from that of all other fish tracked. It stayed close to the surface while swimming away from the point of release and shortly after release its speed gradually slowed to a range of $55\text{--}85\text{ cm s}^{-1}$. During the early hours of the morning, the fish began changing depth erratically and rapid increases of speed ($170\text{--}215\text{ cm s}^{-1}$) were associated with the beginning of each descent. At 05:00 h,

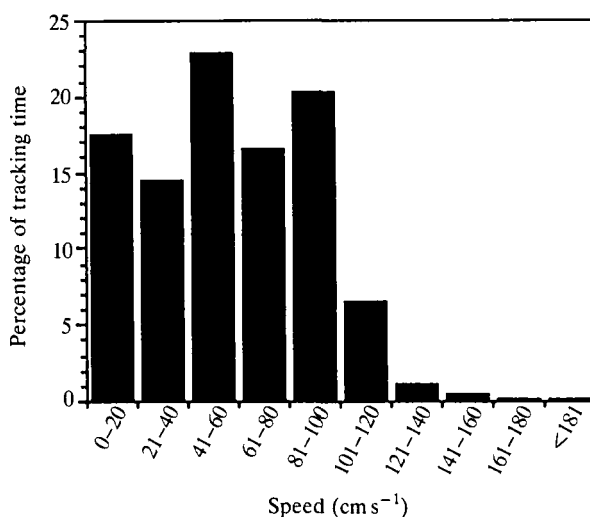


Fig. 7. Summary of the speed data for all three marlin indicating the amount of time spent at any given speed. Speed was divided into 20 cm s^{-1} bins and the percentage of time spent at each speed was calculated for the cumulative data from all tracks.

the marlin displayed a rapid acceleration (Fig. 3) while simultaneously descending to 60 m depth. This was followed by the abrupt stopping of the speedometer signal, although the depth and temperature channels continued to transmit data. As reported by Block *et al.* (1992), we associate this event with a shark attack on this fish.

Marlin 5, 60 kg, struggled at the side of the boat for several minutes during tagging but seemed in fair condition upon release. Immediately following tagging, this fish began a recovery period swimming offshore at a speed of 100 cm s^{-1} , which it sustained for 6 h. It remained below 50 m depth throughout this period then rose to near the surface and slowed to speeds between 12 and 25 cm s^{-1} . Slow swimming while at the surface was punctuated by short descents during which the fish swam at speeds as high as 155 cm s^{-1} (Fig. 4). Such increases in speed were greatest when the fish descended below 50 m. This track ended abruptly as the transmitter sank to the bottom at a constant speed. While sinking, speed from the speedometer registered 46 cm s^{-1} while change of depth with time indicated a speed of 45 cm s^{-1} , an excellent *in situ* check on speedometer calibration.

Marlin 6, 115 kg and 1.8 m in length, was brought to the boat after a 15 min struggle and was released in excellent condition. During a 6 h recovery period, this fish maintained a consistent speed of $100 \pm 18 \text{ cm s}^{-1}$ (s.d.) while swimming at depths of 50–100 m. For a short time (2.5 h), the marlin slowed down to between 20 and 50 cm s^{-1} and came to within 10 m of the surface. This was followed by another 2 h of swimming at elevated speed (100 cm s^{-1}). In contrast to the other fish observed, marlin 6 showed a clear diel variation in both depth movements and speed (Figs 5, 8). During daylight hours this marlin was usually near the surface in 27°C waters, swimming at less than 50 cm s^{-1} . It made occasional short, 20–30 s

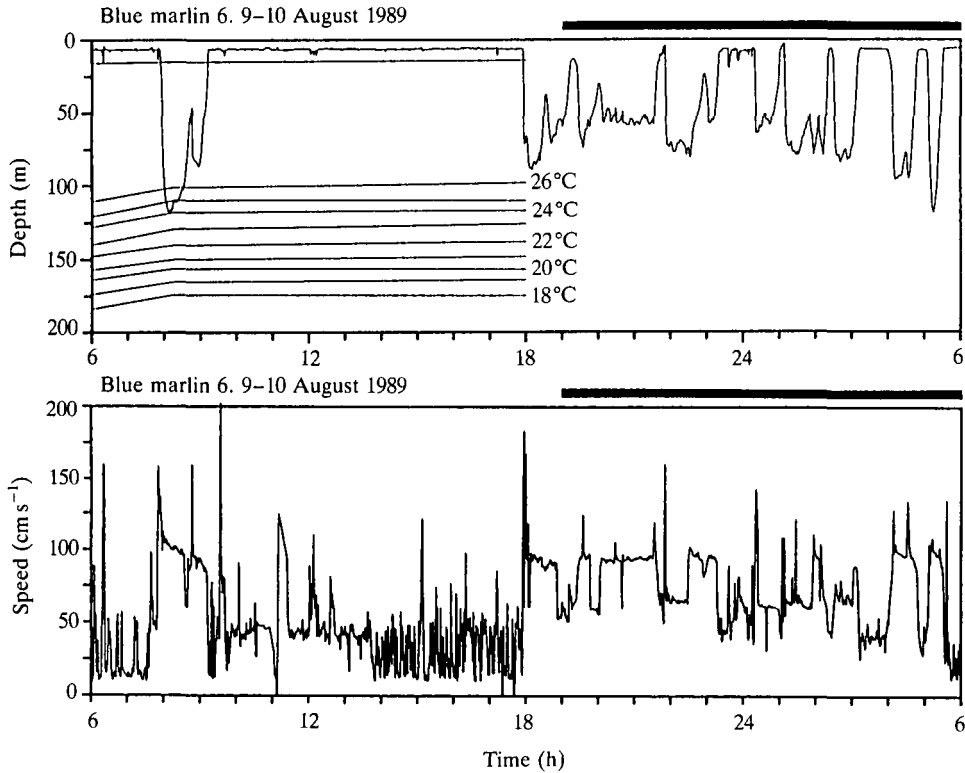


Fig. 8. Depth record of marlin 6 superimposed on 1°C isotherms from day three of the track. There is a clear correlation between depth and speed. While at the surface the marlin swims slowly, when at depth the sustained speed of the fish increases.

elevations of speed associated with dives to 70 or 100 m. In the evening, approximately at dusk, there was a period of sustained swimming, 80–100 cm s⁻¹, similar to that seen at the beginning of the track. During the night this fish made numerous dives to depths between 50 and 100 m, which were again associated with increases in speed up to 150 cm s⁻¹. There was a significant difference ($P < 0.001$; Student's *t*-test) between average speed during the day (50 cm s⁻¹) and during the night (67 cm s⁻¹). This was correlated with a significantly different ($P < 0.05$) depth distribution of the fish between day and night.

In Fig. 9 the relationship between speed and depth for marlin 6 is examined over a finer time scale. Three observations are readily made: (1) while at the surface the marlin is travelling at a relatively slow speed, less than 50 cm s⁻¹, (2) there is an increase in speed to 135 cm s⁻¹ on leaving the surface, and (3) while at depth, speed remains elevated (approximately 100 cm s⁻¹) and only returns to slower values upon ascent to the surface. This pattern of descent and ascent is typical of all marlin observed. There is a clear relationship between depth and swim speed. To examine this more critically, we made a scatterplot of speed, averaged over 32 s

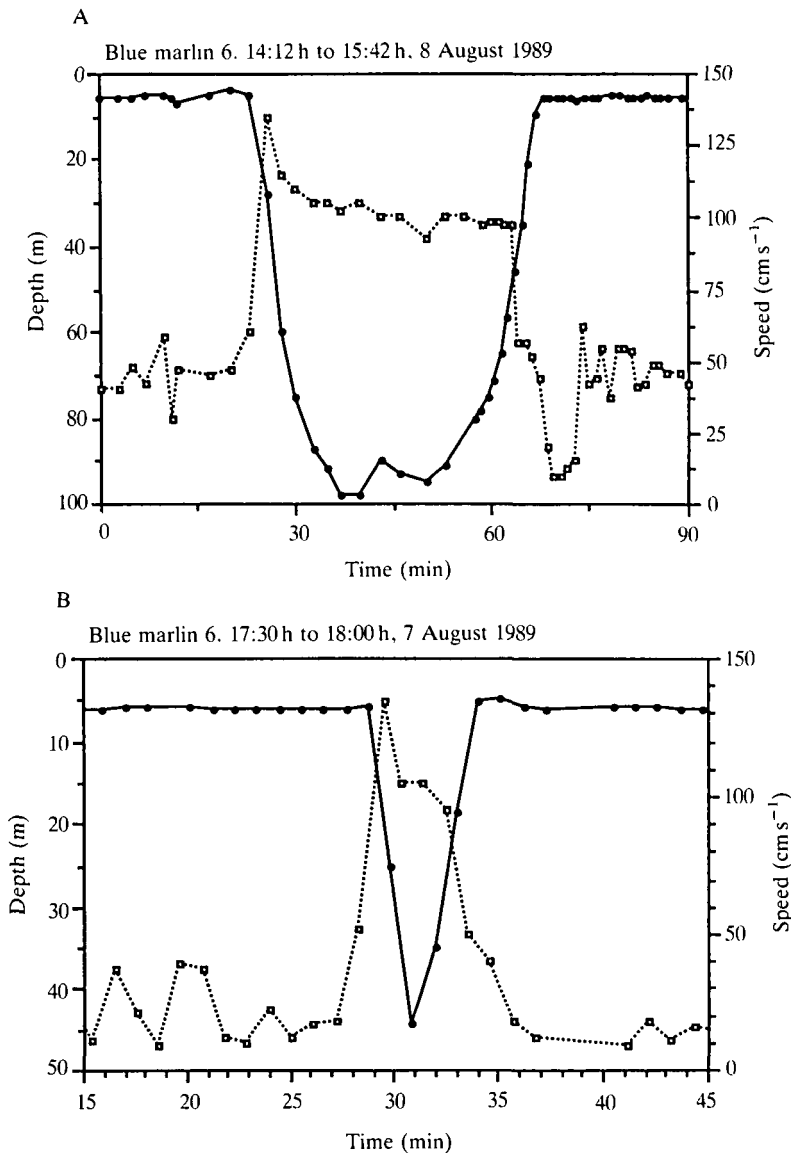


Fig. 9. (A,B) Speed during diving in marlin 6. The solid line shows depth, the dotted line speed. Marlin swim slowly while in near-surface waters. Accelerations with depth during diving suggest that the marlin is positively buoyant while at the surface. When at depth, the marlin increases speed.

intervals, against the average depth in the consecutive 24 s depth interval (Fig. 10A). While at depth the fish chose to swim at one of two distinct speeds, either 55–60 cm s⁻¹ or 80–95 cm s⁻¹. A similar profile of depth with speed was obtained for marlin 5 (Fig. 10B). Marlin 5 also increased speed at depth, but had only a single speed range at depth, 75–100 cm s⁻¹, in contrast to the dual speed range of marlin 6.

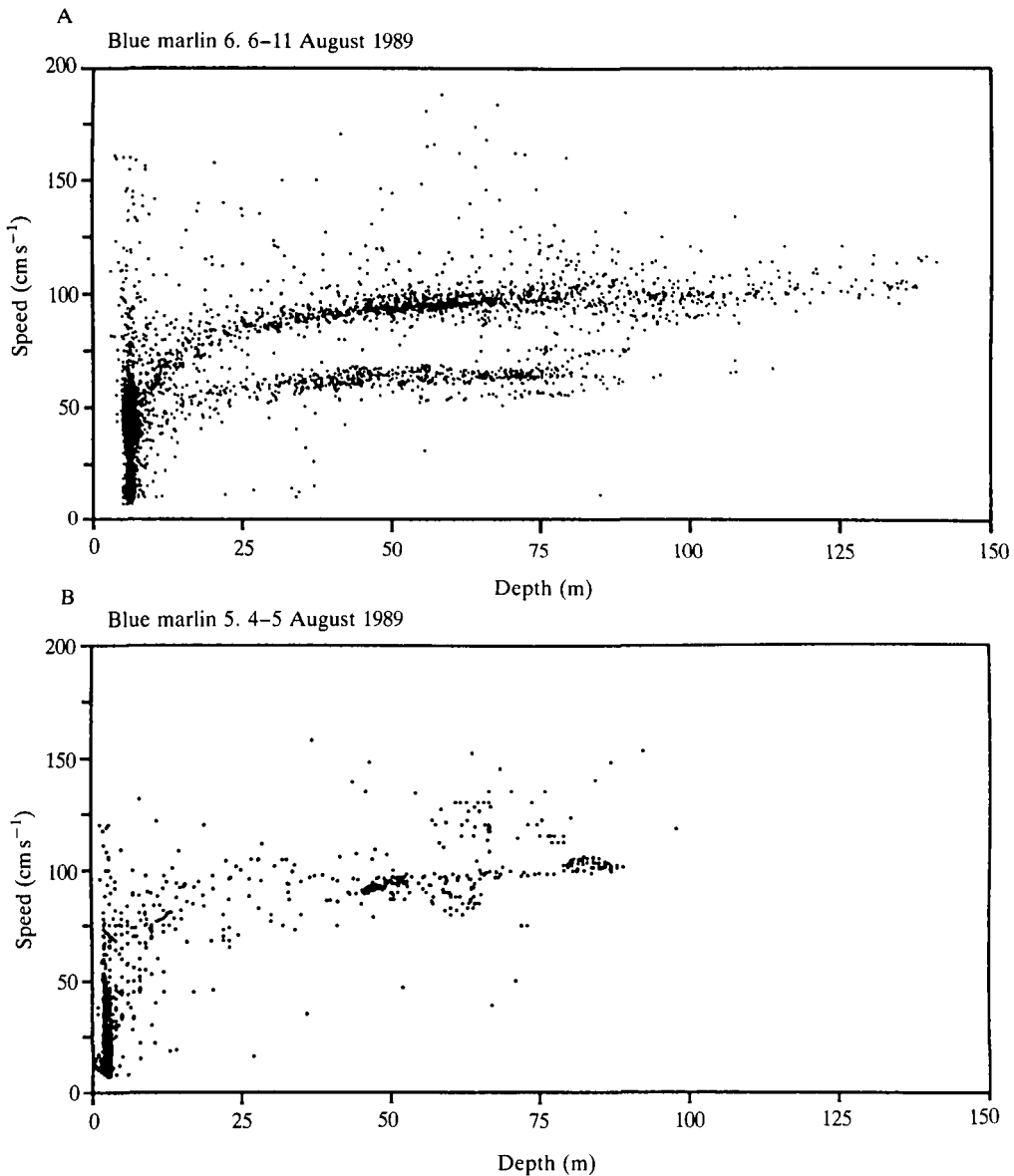


Fig. 10. (A) Recruitment of swimming speeds with depth from marlin 6, a two-‘gear’ pattern, and (B) marlin 5 with one sustained speed. It should be noted that marlin 5 was tracked for a considerably shorter period than was marlin 6 (25 h versus 120 h).

Discussion

How fast do marlin swim?

Istiophorid fish are thought to be among the fastest-swimming fishes and have been estimated to swim at speeds of up to 3610 cm s^{-1} (Table 1). In this study, swimming speed has been measured directly in three free-swimming blue marlin.

Table 1. *Maximum reported swimming speeds of pelagic fish*

Fish	Swimming speed		Method	Reference
	(cm s^{-1})	(km h^{-1})		
Black marlin	3610	130	Estimate	Walters (1962)
Blue marlin	2080	75	Estimate	Walford (1937)
Yellowfin tuna	2080	75	Rod and reel	Walters and Fierstine (1964)
Wahoo	2140	77	Rod and reel	Walters and Fierstine (1964)
Sailfish	3000	108	Estimate	Lane (1941)
Barracuda	1220	44	—	Blaxter and Dickson (1959)
Blue marlin	220	8	Tracking*	Yuen <i>et al.</i> (1974)
Blue marlin	170	6	Tracking	Holland <i>et al.</i> (1990)
Blue marlin	225	8.1	Speedometer†	This study
Striped marlin	180	6.5	Tracking	Holts and Bedford (1990)
Swordfish	225	8.1	Tracking	F. G. Carey (unpublished results)
Blue shark	200	7	Speedometer	Carey and Scharold (1990)
Bluefin tuna	150	5.4	Tracking	F. G. Carey (unpublished results)

* Tracking, speed calculated from translation of position over time.

† Speedometer, speed measured by speedometer telemetry.

The highest continuous swimming speed (speed maintained for longer than 0.5 h) was almost the same (100 cm s^{-1}) for the three marlin although the mass of the fish varied by a factor of two. The most striking result of these direct speed measurements from free-swimming fish is the slow speeds at which blue marlin swim. In the literature on scombroid fish there are frequent references to these fish as swift swimmers (Davie, 1990), and our results are in sharp contrast to the very high swim speeds that have captured the imagination of many writers. The fact that they can strike a bait trolled at 800 cm s^{-1} leaves no doubt that they are capable of short bursts of high-speed swimming, but we saw no such rapid movements in 160 h of speed observations. High-speed swimming and agility must have a place in the repertoire of activities displayed by blue marlin but, during the summer near Hawaii, such behavior is rare. There were only infrequent 10 to 30 s bursts of speeds exceeding 200 cm s^{-1} . Short periods of fast swimming are undoubtedly important for catching certain prey, and hence important in terms of survival, but the characteristic mode of swimming we observed for this species was quite slow.

Our swimming speed values for blue marlin are similar to those recorded for free-swimming blue sharks (*Prionace glauca*) using speedometer transmitters. Blue sharks ranging from 2.2 to 2.8 m in length commonly swim at speeds of $40\text{--}70 \text{ cm s}^{-1}$ for periods of many hours (Carey and Scharold, 1990). The fastest blue shark speed was about 200 cm s^{-1} in short bursts. Similarly, a 1.8 m mako shark (*Isurus oxyrinchus*) swam at an average speed of 90 cm s^{-1} over a 24 h period and had a maximum speed of 150 cm s^{-1} (F. G. Carey, unpublished data). Weihs (1981) also found carcharhinid sharks (1.5–3 m in total length) swimming in an

aquarium to have swimming speeds ranging from 60 to 80 cm s⁻¹. Although no direct measurements are available, swordfish and bluefin tuna speeds, determined from translation of position during tracking, fall within the range of swimming speed observed for marlin (Table 1). Swimming speeds measured with speedometers on marine mammals of comparable body size to these fish are similarly slow, 100–200 cm s⁻¹ (Fedak and Thompson, 1990; Ponganis *et al.* 1990). When moving over long distances in the open ocean, large animals travel slowly to minimize the cost of transport.

Estimates of sustained and maximum swimming speeds of pelagic fishes vary widely in the literature. The fastest speeds recorded were obtained by Walters and Fierstine (1964), who measured the speed at which line ran off a fishing reel during a strike. They found that wahoo (*Acanthocybium solanderi*) and yellowfin tuna (*Thunnus albacares*), species much smaller than blue marlin, accelerated to 2100 cm s⁻¹ (19 BL s⁻¹) within the first 5 s after striking a bait. Magnuson (1978) has compiled the most comprehensive speed data for comparing continuous *versus* burst swimming in various scombroid fishes. These data were obtained by a variety of techniques ranging from aerial photographs to acoustic tracking. Continuous swimming speeds ranged from 0.3 BL s⁻¹ in wahoo to 1.6 BL s⁻¹ in bluefin tuna. Reported burst swimming speeds of scombrids range widely from 8 BL s⁻¹ in the bonito to 27 BL s⁻¹ in yellowfin tuna. Speed estimates from cinematography of feeding tuna were in the range 9–14 BL s⁻¹ (Yuen, 1966). Some of Yuen's records are faster than any speeds from tracking, but even the speeds of these actively feeding fish are an order of magnitude lower than many of the estimated speeds cited in the literature.

Speeds measured from translation of position over time while tracking blue marlin range from 20 to 222 cm s⁻¹ (Yuen *et al.* 1974; Holland *et al.* 1990; Block *et al.* 1992). Comparison with other scombroid data is difficult owing to the absence of length measurements on these fish which, as explained earlier, are difficult to obtain from free-ranging fish. The speed estimates from tracking other billfishes, striped marlin (*Tetrapturus audax*) and swordfish (*Xiphias gladius*), are similar to those for telemetered data from marlin (Holts and Bedford, 1990; Carey and Robison, 1981). Such speeds are an order of magnitude lower than most of the values reported in earlier literature (Table 1). Tag and recapture programs in both the Pacific and Atlantic have shown that blue and black marlin are capable of yearly transoceanic journeys covering thousands of kilometers (Squire, 1974, 1985, 1987). A black marlin, released off southern California, was recaptured 3 months later off Peru, a journey requiring a straight-line speed of at least 55 km day⁻¹ (64 cm s⁻¹). Mather (1976) reported a speed of 76 cm s⁻¹ for bluefin tuna migrating from the Bahamas to the latitude of Bergen, Norway. These tag recapture data give minimum estimates: the fish had to move at least this fast, although they may have moved faster.

Theoretical and empirical data on fish locomotion have suggested that maximum cruising speed will increase in fish as BL^{0.43} (Weihs, 1977, 1981). Wardle *et al.* (1989) also predicted that cruising speeds in large aquatic vertebrates will

decrease with increasing size as a result of the large increases in drag that occur when the flow in the boundary layer changes from laminar to turbulent. Perhaps our surprise at the slow speed of marlin lies in the fact that the literature as well as laboratory measurements of swimming speed and performance in small scombroid fishes suggest that we should expect higher sustained swimming speeds. Most studies on fish swimming performance have been made on relatively small specimens (<3 kg) swimming in confined water tunnels. It is not clear how these measurements scale with body mass. Thus, their relevance in predicting the behavior of fishes several orders of magnitude larger is questionable. Only recently, with the construction of a large swimming tunnel (Graham *et al.* 1990), has it been possible to work on larger fishes. Although this new tunnel provides an unparalleled situation for studying several parameters of performance in oceanic fishes, natural behavior can only be studied in the field where the fish sets the limits for its activities. The speeds observed by telemetry from free-swimming fish are determined by the fish themselves. With advances in recorder and telemetry technology, the ability to study fish in the wild will increase, allowing better integration between laboratory and field data.

Recruitment of swimming speeds

There is a striking relationship between depth and speed for marlin 6 (Fig. 10A). These high and low 'gears' may be analogous to gait changes in terrestrial tetrapods, and thus represent fixed neural patterns of fiber recruitment; red fibers being recruited during slow sustained swimming ($<50 \text{ cm s}^{-1}$) and red plus fast-twitch oxidative fibers being recruited during faster sustained swimming ($>80 \text{ cm s}^{-1}$). The red slow-twitch oxidative fibers constitute only 5–6% of the total muscle mass (Davie, 1990) and are located in numerous small bundles spread throughout the peripheral region of the epaxial musculature. Most of the epaxial muscle consists of white muscle, which is a mosaic of at least two fiber types, large fast-twitch glycolytic fibers and smaller fast-twitch oxidative fibers (B. A. Block, unpublished observation). Only one preferred sustained swimming speed (100 cm s^{-1}) is apparent for marlin 5 (Fig. 10B). A preferred speed may represent the most efficient speed for irrigating the gills and extracting oxygen at minimal cost, during periods when the fish is covering large distances.

Economy of transport

In the warm seas inhabited by blue marlin, food resources are often unevenly distributed. Hence, minimizing energy expenditure while swimming long distances between food patches would be advantageous. Energy required for transport includes the energy for moving a given distance plus the energy required for routine metabolic functions. The most energy-efficient speed (i.e. minimal energy expended per unit distance travelled) will be near the low end of the speed range (Weihs, 1984). Many billfishes and other scombroids travel thousands of kilometers during extensive seasonal migrations (Squire, 1974). Several blue marlin tagged in the Western Atlantic off North Carolina have been caught along the

Ivory Coast of Africa. Large bluefin tuna feed in rich temperate waters during the summer and migrate long distances to spawn in tropical areas in winter. The time scale for these migrations is one of seasons. Travelling at 114 cm s^{-1} (2 knots) is sufficient to take a fish 6400 km (4000 miles) in the course of one season. The fact that the cruising speeds of all these fish are exceedingly low suggests that slow swimming is a way to minimize the cost of locomotion over long distances. This hypothesis may extend beyond scombroid fishes. Salmon, eels, cod and numerous other species make extensive migrations. When tracked by telemetry, such fish also travel at low speeds, ranging between 25 and 100 cm s^{-1} (Madison *et al.* 1972; Tesch, 1979). Although the swimming speeds of salmon recorded by telemetry were generally comparable to values from other salmonid studies, Madison *et al.* (1972) noted that the average speed for sockeye salmon was well below the maximum values recorded in an experimental flume.

Because of the high-aspect-ratio tail and the convergence in external design with tunas, marlin were, until recently, thought to be thunniform swimmers (Lindsey, 1978). Video analysis of free-swimming marlin and studies of the biomechanics of the backbone indicate that, unlike tunas, these fish are quite flexible and swim with a sinuous shark-like motion (Hebrank *et al.* 1990). Marlin are subcarangiform swimmers, the propulsive force being delivered by the caudal fin and the displacement of water during the side-to-side undulatory movements associated with swimming. This form of swimming may limit the maximum sustained swimming speeds of istiophorids and the stiffening of the body axis as seen in thunniform swimming may allow higher sustained swimming speeds. Direct speedometer telemetry on tunas of similar body size to the marlins should be used to compare speeds directly between these large fish that use different kinematic forms of swimming. While speeds of tunas obtained from translation of position over time during telemetry experiments are comparable to those of marlin, it would be interesting to know whether there is a significant increase in sustainable cruising speed afforded by the thunniform mode of locomotion.

Buoyancy

Blue marlin have an unusual swim bladder in the form of a thin-walled, multi-chambered sac extending from the level of the first pectoral fin to behind the first anal fin. Observations of marlin 'finning' near the surface with the dorsal and caudal fins high above the water show that the bladder is large enough for the fish to be positively buoyant near the surface. Problems associated with buoyancy are related to swimming speed in two ways. First, the observation that marlin swim at higher speeds when at depths of 50–100 m may be related to the collapse of the swim bladder at these depths. As the fish becomes negatively buoyant when swimming deeper, it may be generating the required additional lift with its pectoral fins by swimming faster. Second, the frequently observed increase in speed at the beginning of a descent may result from the difficulties in getting a positively buoyant fish away from the surface. Elevation of swim speed while descending and at depth is not observed in sharks (F. G. Carey, personal observation), which are

negatively buoyant at all depths (Bone and Roberts, 1969). The buoyancy provided by the large swim bladder allows blue marlin, swordfish and perhaps other istiophorids to swim slowly when near the surface and thus conserve energy.

Warm muscles and sustained cruising speeds

The ability of scombroid fishes such as tunas and lamnid sharks such as the mako to conserve metabolic heat and raise their muscle temperature has often been linked to higher sustained swimming speeds (Beamish, 1978; Magnuson, 1978; Webb, 1990). However, warmer does not necessarily mean faster. Ectothermic marlin operating at temperatures ranging from 17 to 27°C were observed to have faster sustained swimming speeds than those of warm-bodied mako sharks of similar body size (B. A. Block and F. G. Carey, personal observation). Ectothermic wahoo and endothermic yellowfin tuna of similar body size both achieved the same high sprint speeds (Walters and Fierstine, 1964). The assumption that higher body temperature in warm fish is associated with higher sustained swimming speeds and sprint speeds needs to be tested. Endothermic bluefin tuna may travel for days at 100–200 cm s⁻¹, speeds that are within the range reported here for ectothermic marlin. Perhaps the most obvious advantage of a warm body temperature is unimpeded performance at all ambient water temperatures, giving warm fish the ability to forage in the cold waters beneath the thermocline, a foraging area that ectothermic fish are reluctant to enter (Block, 1991).

It remains possible that there is a direct link between the thunniform mode of locomotion and endothermy. Marlins, utilizing subcarangiform locomotion, have the generalized primitive percomorph condition of laterally placed red muscle. Concomitant with the stiffer locomotory pattern of 'thunniform' swimming is the internal localization of the red muscle that powers sustained swimming. In future studies, it would be useful to explore the relationships between swimming performance, red muscle positioning, speed and body temperature.

This work was supported by a grant from the Billfish Foundation and by grants DCB-8958225 to B.A.B. and OCE-8811421 to F.G.C. from the National Science Foundation. We wish to thank the Pacific Ocean Research Foundation, Hawaiian Big Game Fishing Club, for their support. This work would not have been possible without the skill and patience of Captains Mike Hind and Stu Miyamoto of the F/V *Heola*, and Captains Freddy and McGrew Rice who provided the opportunity to tag blue marlin 6 aboard the F/V *Ihu Nui*. Tagging of marlin was also made possible by the anglers and captains of the 1989 Kona Hawaiian and Hawaiian International Billfish Tournaments. Data processing was expedited by the careful work of Karen Mazurkiewicz and Sue Conova. Many others helped to bring this project to fruition and we are indebted to the following for their effort and encouragement: Oliver Brazier, Otis and Janet Butler, Peter Fithian, John Long and Winthrop Rockefeller.

References

- BEAMISH, F. W. H. (1978). Swimming capacity. In *Fish Physiology*, vol. 7 (ed. W. S. Hoar and D. J. Randall), pp. 101–187. New York: Academic Press.
- BLAXTER, J. H. S. AND DICKSON, W. (1959). Observations on swimming speeds of fish. *J. Cons. Perm. int. Explor. Mer.* **24**, 272–479.
- BLOCK, B. A. (1991). Endothermy in fish: Thermogenesis, ecology and evolution. In *Biochemistry and Molecular Biology of Fish*, vol. I (ed. P. W. Hochachka and T. Mommsen), pp. 267–311. Amsterdam: Elsevier Scientific Press.
- BLOCK, B. A., BOOTH, D. T. AND CAREY, F. G. (1992). Depth and temperature of the blue marlin, *Makaira nigricans*, observed by acoustic telemetry. *Mar. Biol.* (in press).
- BONE, Q. AND ROBERTS, B. L. (1969). The density of elasmobranchs. *J. mar. biol. Ass. U.K.* **47**, 754–756.
- BROCK, R. E. (1984). A contribution to the trophic biology of the blue marlin (*Makaira nigricans*, Lacépède, 1802) in Hawaii. *Pac. Sci.* **38**, 141–148.
- CAREY, F. G. AND ROBISON, B. H. (1981). Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry. *Fish. Bull.* **79**, 277–291.
- CAREY, F. G. AND SCHAROLD, J. V. (1990). Movements of blue sharks (*Prionace glauca*) in depth and course. *Mar. Biol.* **106**, 329–342.
- DAVIE, P. S. (1990). *Pacific Marlins Anatomy and Physiology*. Massey, New Zealand: Massey University Printery.
- FEDAK, M. A. AND THOMPSON, D. (1990). Circulatory responses in grey seals diving at sea: Profound bradycardia during continuous diving. *The Physiologist* **33**, A89.
- GRAHAM, J. B., DEWAR, H., LAI, N. C., LOWELL, W. R. AND ARCE, S. M. (1990). Aspects of shark swimming performance determined using a large water tunnel. *J. exp. Biol.* **151**, 175–192.
- HEBRANK, J. H., HEBRANK, M. R., LONG, J. H. J., BLOCK, B. A. AND WAINWRIGHT, S. A. (1990). Backbone mechanics of the blue marlin *Makaira nigricans* (Pisces, Istiophoridae). *J. exp. Biol.* **148**, 449–459.
- HOLLAND, K., BRILL, R. AND CHANG, R. K. C. (1990). Horizontal and vertical movements of Pacific blue marlin captured and released using sportfishing gear. *Fish. Bull.* **88**, 449–459.
- HOLTS, D. AND BEDFORD, D. (1990). Activity patterns of striped marlin in the southern California bight. In *Planning the Future of Billfishes* (ed. R. H. Stroud), pp. 81–93. Savannah, Georgia: National Coalition for Marine Conservation.
- HOPPER, C. N. (1990). Patterns of Pacific blue marlin reproduction in Hawaiian waters. In *Planning the Future of Billfishes* (ed. R. H. Stroud), pp. 123–136. Savannah, Georgia: National Coalition for Marine Conservation.
- JOHNSTON, I. A. AND SALAMONSKI, J. (1984). Power output and force–velocity relationship of red and white muscle fibres from the Pacific blue marlin (*Makaira nigricans*). *J. exp. Biol.* **111**, 171–177.
- LANE, F. W. (1941). How fast do fish swim? *Country Life*, 534–535.
- LINDSEY, C. C. (1978). Form, function, and locomotory habits in fish. In *Fish Physiology*, vol. 7 (ed. W. S. Hoar and D. J. Randall), pp. 1–88. New York: Academic Press.
- MADISON, D. M., HORALL, R. M., STASKO, A. B. AND HALLER, A. D. (1972). Migrating movements of adult sockeye salmon (*Oncorhynchus nerka*) in coastal British Columbia as revealed by ultrasonic tracking. *J. Fish Res. Bd Can.* **29**, 1025–1033.
- MAGNUSON, J. J. (1978). Locomotion by scombrid fishes: Hydromechanics, morphology, and behavior. In *Fish Physiology*, vol. 7 (ed. W. S. Hoar and D. J. Randall), pp. 240–308. New York: Academic Press.
- MATHER, C. O. (1976). *Billfish*. Sydney, Canada: Salaire Publishing.
- PONGANIS, P. J., PONGALIS, E. P., PONGALIS, K. V., KOOYMAN, G. L., GENTRY, R. L. AND TRILLMICH, F. (1990). Swimming velocities in otariids. *Can. J. Zool.* **68**, 2105–2112.
- SQUIRE, J. L. (1974). Migration patterns of Istiophoridae in the Pacific Oceans determined by cooperative tagging programs. In *Proceedings of the International Billfish Symposium*, part 2 (ed. R. Shomura and F. Williams), pp. 226–237. Kailua-Kona, Hawaii: U.S. Dept. Commerce, NOAA TR NMFS SSRF-675.

- SQUIRE, J. L. (1985). *Cooperative Marine Game Fish Tagging Program 1985 Billfish Newsletter*. NOAA, NMFS.
- SQUIRE, J. L. (1987). *Cooperative Marine Game Fish Tagging Program 1987 Billfish Newsletter*. NOAA, NMFS.
- STROUD, R. H. (1990). *Planning the Future of Billfishes. Research and Management in the 90s and Beyond* (ed. R. H. Stroud). Savannah, Georgia: National Coalition for Marine Conservation.
- TESCH, F. W. (1979). Tracking of silver eels (*Anguilla anguilla*) in different shelf areas of the Northeast Atlantic. *Rapp. P. V. Reun. Cons. int. Explor. Mer.* **174**, 104–114.
- WALFORD, V. (1937). *Marine Game Fishes of the Pacific Coast, Alaska to the Equator*. Berkeley, California: University of California Press.
- WALTERS, V. (1937). Body form and swimming performance in the scombrid fishes. *Am. Zool.* **2**, 143–149.
- WALTERS, V. AND FIERSTINE, H. (1964). Measurements of swimming speeds of yellowfin tuna and wahoo. *Nature* **202**, 208–209.
- WARDLE, C. S., VIDELER, J. J., ARIMOTO, T., FRANCO, J. M. AND HE, P. (1989). The muscle twitch and maximum swimming speed of giant bluefin tuna, *Thunnus thynnus*. *J. Fish Biol.* **35**, 129–137.
- WEBB, P. W. (1990). Locomotion in the biology of large aquatic vertebrates. *Trans. Am. Fish. Soc.* **119**, 629–641.
- WEIHS, D. (1977). Effects of size on sustained swimming speeds of aquatic organisms. In *Scale Effects in Animal Locomotion*. (ed. T. J. Pedley), pp. 333–338. New York: Academic Press.
- WEIHS, D. (1981). Voluntary swimming speeds of two species of large carcharhinid sharks. *Copeia* **1**, 219–222.
- WEIHS, D. (1984). Bioenergetic considerations in fish migration. In *Mechanisms of Migration in Fishes* (ed. J. D. McCleave, G. P. Arnold, J. J. Dodson and W. H. Neill), pp. 487–508. New York: Plenum Press.
- YUEN, H. S. H. (1966). Swimming speeds of yellowfin and skipjack tuna. *Trans. Am. Fish. Soc.* **95**, 203–209.
- YUEN, H. S., DIZON, A. E. AND UCHIYAMA, J. H. (1974). Notes on the tracking of the Pacific blue marlin, *Makaira nigricans*. In *Proceedings of the International Billfish Symposium*, part 2 (ed. R. Shomura and F. Williams), pp. 265–268. Kailua-Kona, Hawaii: U.S. Dept. Commerce, NOAA TR NMFS SSRF-675.