BACKBONE MECHANICS OF THE BLUE MARLIN *MAKAIRA NIGRICANS* (PISCES, ISTIOPHORIDAE)

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Summary

Over most of its length, the backbone of the blue marlin, like that of all other istiophorids, contains enlarged and flattened neural and hemal spines and zygapophyses, all of which span the intervertebral joints. These plates of bone restrict dorso-ventral bending of the backbone but their arrangement permits a high degree of lateral flexion. The spines and zygapophyses also appear to be important in stabilizing the relatively large intervertebral joints against axial compression and lateral shearing during bending. Although bone is an elastic material, these overlapping structures are not arranged so as to contribute to elastic recoil of the backbone during normal swimming movements.

Introduction

The blue marlin (*Makaira nigricans* Lacépède) is among the world's most spectacular high-performance fishes. It is commonly known as a billfish, an assemblage that also includes the black marlin (*Makaira indica* Cuvier), the white and striped marlins and the spearfishes (*Tetrapturus* spp.), and the sailfishes (*Istiophorus* spp.). The blue marlin is one of the largest marine teleosts, attaining masses of 900 kg. Although marlin have been characterized for years as sprinters and are popular among sport fishermen for their acrobatic leaps out of the water, known as 'tail-walking', it has become apparent only recently that these fish are capable of remarkable transoceanic migrations. The long-distance travel record for marlin is a 9200-km tag return from a 59-kg black marlin (Pacific Gamefish Research Foundation, personal communication). Such performance indicates that these fish are capable of prolonged periods of cruising, and contrasts with the view in the literature of these fish entirely as sprinters. The recent tag returns demonstrating long-distance migrations suggest that these fish may be using

energy-conserving strategies while cruising across the oceans. Telemetry of free-swimming blue marlin off the coast of Kona, Hawaii, indicates these fish have cruising swimming speeds ranging from 1 to 8 km h^{-1} (Yuen et al. 1974).

The large size of the blue marlin and their pelagic mode of life have made it difficult for biologists to study these fish. The billfish in general have received much less study than their close relatives and competitors, the tunas (Scombridae). Recent evidence has shown that, like the tunas, the billfish have physiological specializations for protecting the nervous system from temperature fluctuations (Carey, 1982; Block, 1986). However, unlike the tunas, the temperature of the body musculature of marlin remains close to that of the ambient water. The huge mass of axial musculature in marlin is composed primarily of white anaerobic muscle fibers, which is the main reason they have been characterized as sprinters.

All istiophorids have a backbone morphology that is unique among teleosts. The osteology of the marlin backbone was described by Cuvier and Valenciennes (1831), and then received some attention early this century (Gregory and Conrad, 1937). Rockwell et al. (1938) further speculated that the istiophorid backbone may have a 'spring-like' role in locomotion. Although several workers have noted its unusual morphology (Fierstine and Walters, 1968; Nakamura, 1983), the functional significance of the istiophorid backbone has yet to be determined, and its role as a spring has remained conjectural.

Especially notable is the large quantity of bone in the backbone (Fig. 1). In the marlin the neural spines of precaudal and caudal vertebrae and the hemal spines of caudal vertebrae are elaborated into large flat plates that lie in the plane of the median septum and extend caudad across the intervertebral joints. At the base of each neural spine are a pair of laterally compressed zygapophyses that project forward, flanking the base of the neural spine of the preceding vertebra. These zygapophyses are tightly bound to the neural spine by short collagen fibers that run between the outer surface of the spine and the inner face of the zygapophysis. In addition, in the caudal vertebrae, a much smaller but analogous pair of hemal zygapophyses flanks the base of each preceding hemal spine, again projecting forward across the intervertebral joint. The result of the zygopophyses overlapping the spines – across the intervertebral joint – is an interlocking backbone.

The object of this study was to investigate the function of this elaborate bony structure. In particular we focused attention on the mechanical roles of the neural and hemal zygapophyses and spines. We executed a variety of bending tests on whole backbones and segments of backbones to assess the component mechanical roles, as well as to determine the backbone's ability to contribute to locomotor efficiency through elastic recoil.

Materials and methods

Experimental animals

Vertebral columns of Pacific blue marlin (*Makaira nigricans*) ranging in size from about 90 to 320 kg were obtained from fish wholesalers in Kailua-Kona.
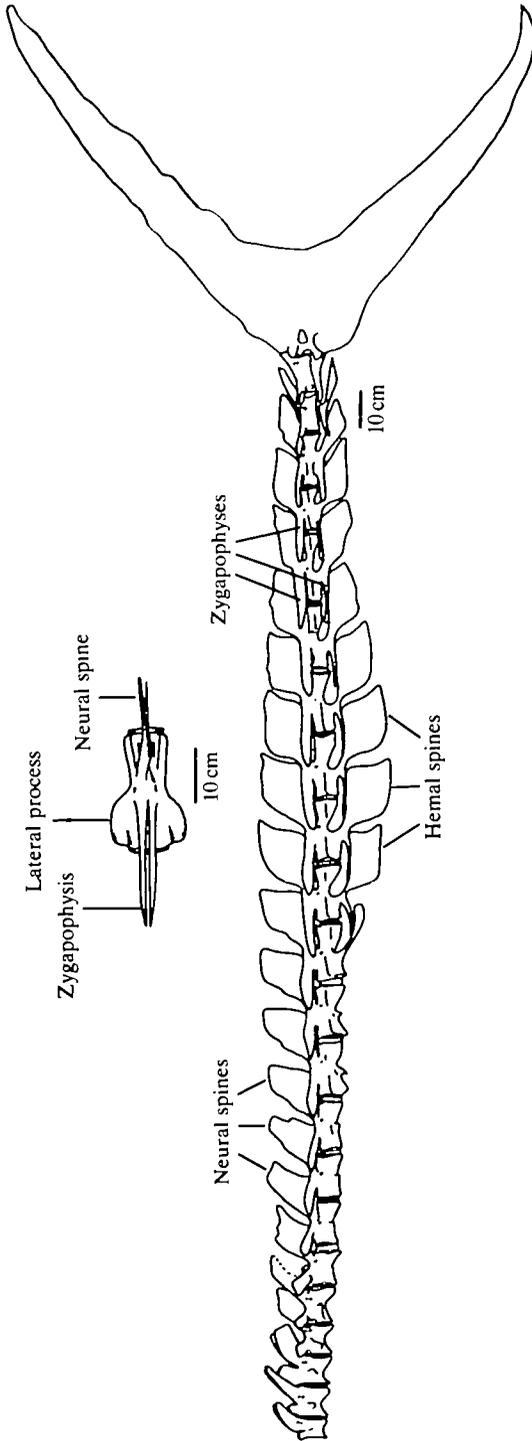
Fig. 1. Left sideview of the backbone (vertebrae 3 to 24) of a Pacific blue marlin (*Makaira nigricans*), showing how zygapophyses overlap the greatly expanded neural and hemal spines. Inset: dorsal view of vertebra 17, showing paired zygapophyses and the lateral processes.

Hawaii. The marlin were captured on hook and line by sport fishermen during the Hawaiian International Billfish Tournament. Fish were stored for variable lengths of time up to 40 h at 4.4°C before the backbone was removed. Just before mechanical testing any remaining muscle or viscera were removed from the backbone, while keeping the underlying connective tissue moist and intact. The cleaned backbone was bathed in marine teleost saline (Pantin, 1964) before and during testing.

Backbone stiffness and elastic energy storage tests

The stiffness and storage of elastic energy in whole backbones and in the caudal segments of backbones flexed laterally were measured by potting the entire backbone or a segment in polyester resin to secure the most anterior vertebra, and then loading the backbone or segment as a cantilever (Fig. 2).

Loads applied to the backbones were measured with an Interface load cell (model SSM-50), having a full-scale force of 222 N, repeatability of 0.02 %, and hysteresis of 0.03 % of full load. The load cell was energized with 6 V, amplified by a factor of 100 or 1000 as appropriate, and sampled by a 12-bit analog-to-digital converter, resulting in a resolution of 0.18 and 0.018 N bit^{-1}, respectively. Data were sampled and recorded at a rate of 200 samples s^{-1}.

Backbone deflections were measured using a Celesco position transducer (model PT-101). This device has a thin stainless-steel cable that we attached to one end (the non-backbone end) of the load cell and that exerted a nearly constant tension of 2.22 N. Resolution of this device is rated at 0.008 % of its full-scale value of 1.83 m, and accuracy is rated at 0.10 % (1.8 mm) of full scale. The device was excited by 5 V and sampled by a 12-bit analog-to-digital converter, giving a sampling resolution of 0.5 mm.

Force was sampled approximately 100 μs before displacement; in the analysis the measured forces and deflections were therefore considered to occur simultaneously. All data were recorded on microcomputer disks for later analysis.

In practice, a string attached to the load cell was pulled by hand as smoothly as possible, so that loading and unloading were each accomplished in about 4 s. The
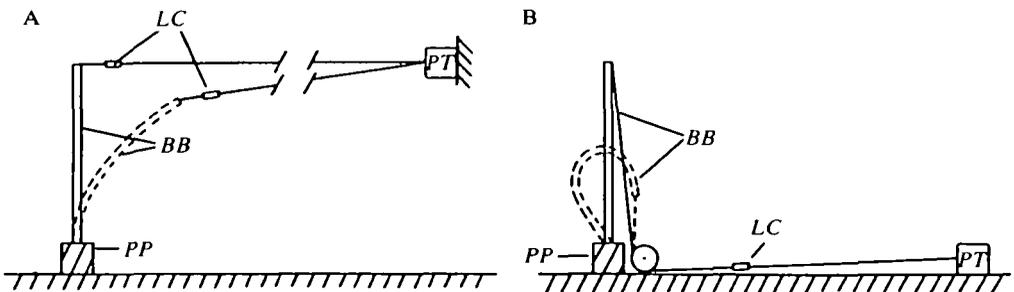

Fig. 2. Apparatus and two methods for bending backbones as cantilevers. (A) Method for small bends; (B) for extreme bends. BB, backbone; PP, polyester pot that holds the backbone; LC, load cell; PT, position transducer.

string was pulled so as to remain parallel with the cable from the displacement transducer, since work is the dot product of the force and displacement vectors.

In the data analysis, work was calculated as the area under the force–deflection curve. The efficiency of elastic energy storage, or resilience, was calculated as the work recovered from an elastic recoil expressed as a percentage of the work put in (Wainwright *et al.* 1976). Graphically, resilience is the percentage of the area under the unloading force–deflection relative to the area under the loading force–deflection curve.

Stiffness of individual joints in lateral and dorso-ventral bending

Joint stiffness was measured by clamping a segment of backbone containing either six caudal or six precaudal vertebrae, and applying a moment to the joint through a cantilever load at the free end of the segment. In caudal segments of two fish, the joint between vertebrae 14 and 15 was tested; in a third fish the joint between vertebrae 16 and 17 was tested. In precaudal segments of three fish the joint between vertebrae 4 and 5 was tested in each. Applied moment was calculated as the product of the applied force, measured by the same load cell described above, and the perpendicular distance from the point of application of the force to the joint being tested.

The joint angle resulting from the applied moment was measured by glueing or screwing thin, straight 30 cm rods (bicycle spokes) into the vertebral centra located on each side of the joint and measuring with calipers the distances between them following each increment of applied load (Fig. 3). Prior to loading, two marks spaced approximately 20 cm apart were placed on each rod. Joint angle was calculated as the arcsine of the difference in mark spacing divided by the distance between the marks on the rod. A measurement error of 1 mm corresponded to a 0.5° error in joint angle. Repeated measurements indicated actual accuracy near 0.1°. During placement of the rods, care was taken to avoid damaging the intervertebral joint capsule or the centra, and to avoid restricting motion of the joint or its parts through the addition of the measurement rods.
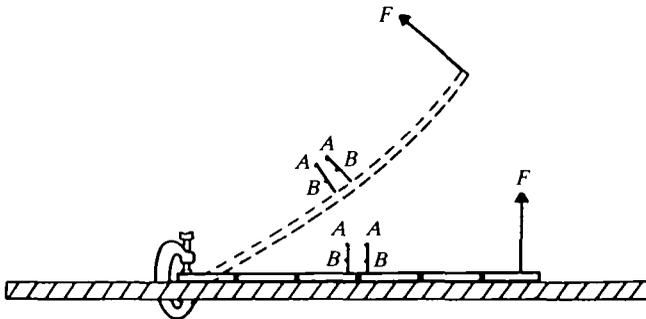

Fig. 3. Apparatus for measuring deflection of a single intervertebral joint. *A*,*A* and *B*,*B* are tabs on bicycle spokes; distances *AA* and *BB* were measured before and after bending. *F*, direction of applied force normal to backbone.

To assess the contributions of neural and hemal spines and zygapophyses to joint stiffness, we first measured the stiffness of the intact joint in the lateral and dorsal directions and then removed the neural zygapophyses (by cutting with a diamond abrasive wheel driven by a flexible shaft drill) and measured the joint stiffness in each direction again. Joint stiffness in each direction was then measured a third time after removing the neural and hemal spines, and hemal zygapophyses if present. This last pair of measurements thus reflected the behavior of a single isolated intervertebral joint, with no overlapping bone.

Results

Backbone stiffness and elastic energy storage

Force–deflection curves for a precaudal backbone segment bent in the lateral and ventral directions are shown in Fig. 4. Backbone stiffness is indicated by the slopes of these curves and, as shown here, the backbone segment was found to be about 10 times stiffer in dorso-ventral bending than in lateral bending. This observation was consistent in three lateral and three dorso-ventral bending tests of precaudal segments, and four lateral and three dorsoventral bending tests of caudal segments.

For curves such as that shown in Fig. 4, resilience was in the range 60–80 % for both dorso-ventral and lateral cantilever loading of backbone segments.

In·a bending test of an entire backbone taken from a 318-kg marlin, we measured a resilience of only 50 %. Due to its large size, this backbone was not tested in either cantilever manner described earlier, but was instead mounted vertically and bent laterally into a C-shape by tension applied to the ends of the
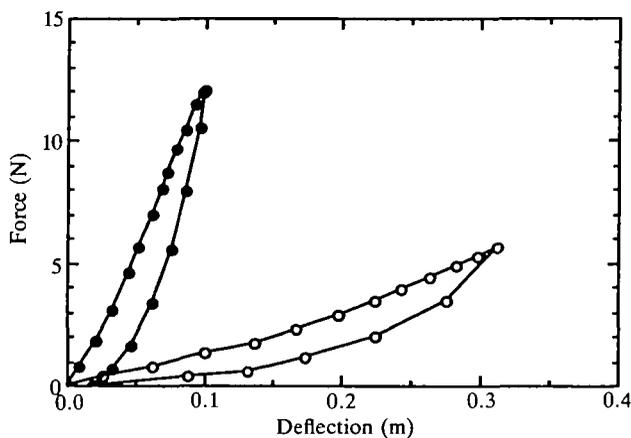

Fig. 4. Graph of cantilever bending of a precaudal backbone segment from an approximately 90-kg marlin. Length of the segment was 58 cm (length of the entire backbone was 141 cm); loading was as shown in Fig. 2A. Solid symbols, ventral bending; open symbols, lateral bending.
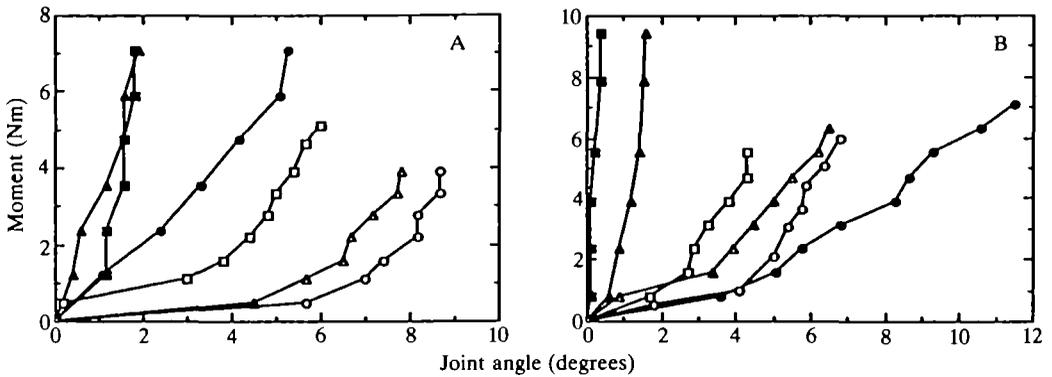
Fig. 5. Graph of bending experiments of intact backbone segments, those with zygapophyses removed, and those with neural and hemal spines removed. (A) Precaudal joint 4–5 of a 204-kg fish. (B) Caudal joint 14–15 of a 159-kg fish. Solid symbols, dorso-ventral bending; open symbols, lateral bending. Squares, joint intact; triangles, joint without zygapophyses; circles, joint only.

backbone. Subsequent testing resulted in failure, which occurred near the mid-point of the backbone, and for which 34 J of work was required.

Stiffness of individual joints in lateral and dorso-ventral bending

Measurements of joint stiffnesses with and without their surrounding bones produced the graphs shown in Fig. 5 (for one 159-kg fish). To compare the effects of removing joint parts, an average stiffness for each graph was calculated by dividing the maximum applied moment by the deflection angle occurring at that applied moment. Fig. 6 shows bar graphs comparing these stiffnesses for all backbone segments tested. (A logarithmic scale is necessary to show the range of values obtained.) The results may be summarized as follows. (1) Larger animals are proportionally stiffer in posterior backbone regions, but precaudal stiffness does not vary with size in the sizes tested here. (2) Caudal dorso-ventral stiffness for an intact backbone is about 20–30 times lateral stiffness. Precaudal dorso-ventral stiffness is about three times lateral stiffness. (3) Removal of zygapophyses and spines affects lateral stiffness only slightly. (4) Removal of zygapophyses and spines reduces dorso-ventral stiffness to a value approximately the same as lateral stiffness. (5) For caudal segments, removal of the zygapophyses approximately halves dorso-ventral stiffness, suggesting that zygapophyses and spines make similar contributions to dorso-ventral stiffness. In precaudal segments, removal of zygapophyses has only a small effect on dorso-ventral stiffness, suggesting that in these segments the spines are largely responsible for dorso-ventral stiffness.

The occasional small *increase* in lateral stiffness observed after removal of parts is probably attributable to the difficulty of realigning an increasingly compliant backbone following removal of parts.
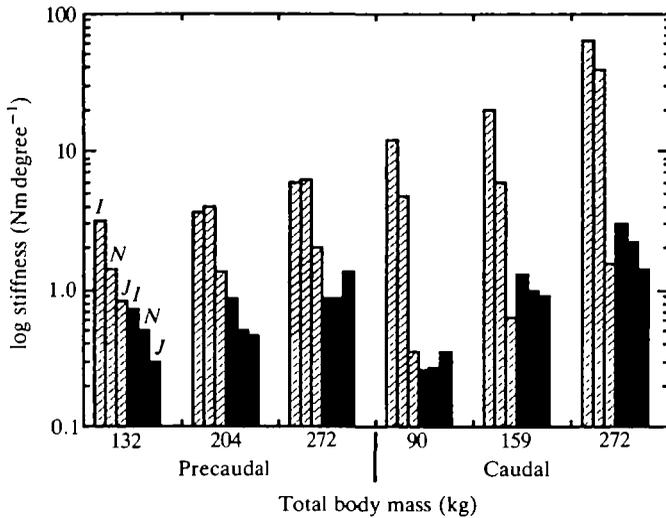
Fig. 6. Histogram showing flexural stiffnesses of either precaudal or caudal backbone segments of intact intervertebral joints (I), joints without zygapophyses (N) and joints with neither zygapophyses nor spines (J). Cross-hatch, dorso-ventral bending; black, lateral bending. Each mass signifies a single fish. (The 272-kg fish appears twice.)

Discussion

These results indicate that the enlarged and flattened neural and hemal spines, along with their overlapping zygapophyses, significantly affect the mechanical characteristics of the marlin backbone. Our observations demonstrate two important roles of these bony structures and eliminate a third possible role.

First, the zygapophyses, spines and connective tissue between them act to restrict bending in the dorso-ventral direction while allowing lateral bending. This anisotropy is largely accomplished by the placement of bone and its connections above and below the intervertebral joint. By placing these connections at a distance from the neutral plane of the joint, dorso-ventral flexural stiffness is increased. This situation is analogous to flexural stiffness in beams, where flexural stiffness is proportional to the second moment of area (Wainwright *et al.* 1976). In the marlin backbone, the connective tissue of primary importance is located between the zygapophyses and the spines, and is loaded in shear by lateral and dorso-ventral flexion, and by axial compression. The area resisting this shear is quite large, virtually the entire area of each zygapophysis.

In contrast, lateral bending is allowed by the position of the bones and their associated connective tissues near the sagittal plane of the fish, which corresponds with the neutral plane of lateral bending. Both the zygapophyses and the spines are laterally compressed: for blue marlin weighing 90 kg or more, the zygapophyses range from about 1 mm in thickness at the anterior tip to about 5 mm at the origin, compared with lengths of about 10 cm or more; spines range from about 1 to 2 mm in thickness and are also about 10 cm or more in length. In addition, the

zygapophyses are recessed into the bases of the neural spines, so that their positions close to the neutral axis do not restrict lateral bending. Phrased another way, by placing the connections between the zygapophyses and spines close to the neutral plane in lateral bending, large lateral joint angles produce only small shear strains in the connective tissue between the zygapophyses and spines.

Because of their rigid, high aspect-ratio caudal fins, marlin have been assumed to be thunniform swimmers, i.e. having a propulsive wave of low amplitude and high frequency (Nursall, 1956; Lindsey, 1978). However, in an underwater video of a blue marlin approaching a live bait (Sharkbait Productions, Kailua-Kona, HI), the marlin swam with a sinuous motion, somewhat like that of a shark, with lateral bending occurring throughout the length of the fish. To swim in this manner, clearly not thunniform, the backbone must have low lateral stiffness.

The second role of the overlapping zygapophyses and spines is in stabilizing the intervertebral joint. The marlin has only 24 vertebrae, hence the degree of angular flexure per joint is probably relatively high due to its sinuous locomotion. (Shark backbones, in contrast, have about 100 precaudal vertebrae; trout have about 60.) Large angles between adjacent vertebrae mean that axial compressive loads supported by the bent backbone [some of the loads were the result of tendon attachments directly on the centra (S. A. Wainwright and S. M. Weeks, personal communication)] will have significant components of lateral shear in the intervertebral joints (Fig. 7).

This lateral shear could potentially cause dislocation, especially since the intervertebral disk appears to be relatively long. We obtained joint length to centrum length ratios of about 0.28 for precaudal vertebrae and 0.13 for caudal vertebrae in blue marlin over 90 kg. For comparison, in the American eel (*Anguilla rostrata*), which has over 100 vertebrae, this ratio is 0.17; in the Norfolk spot (*Leisostomus xanthurus*), having 24 vertebrae, it is 0.13; and in the skipjack
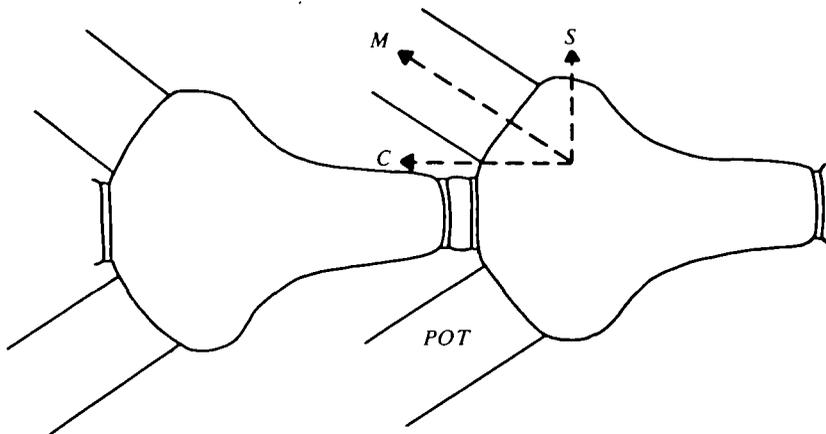

Fig. 7. Diagram of forces applied in the horizontal plane to a vertebra through a posterior oblique tendon (*POT*) seen in dorsal view. Anterior is to the left. *M*, direction of muscle pull; *C*, compression component; *S*, shearing component.

tuna (*Katsuwonus pelamis*), having about 40 body vertebrae, it is 0.07 (M. R. Hebrank, unpublished data). Since the intervertebral disks probably allow relatively large joint angles, the connections between the zygapophyses and the spines appear to act as brackets, allowing bending but not displacement.

The axial compressive forces and their corresponding components of lateral shear acting on the marlin backbone must be quite large. These fish capture their prey by 'sprinting', and cross-sections through the blue marlin indicate the body musculature is primarily composed of white, fast-twitch glycolytic fibers. Scombrid fish such as the skipjack tuna are often the preferred prey (Brock, 1984). The skipjack is another high-performance fish capable of swimming speeds over $10 \, m \, s^{-1}$ (Dizon *et al.* 1978). Furthermore, the acceleration required to hurl several hundred kilograms of marlin out of the water requires very high muscular forces, which will compress, shear and bend an intervertebral joint. Stabilizing the joint should be an important role of the bony processes surrounding the marlin backbone.

Finally, although bone is an elastic material, these bony structures do not appear to be arranged to contribute to elastic recoil by the backbone. Based on measurements of muscle power output of individual fibers and small bundles of fibers, Johnston and Salamonski (1984) estimate a marlin mean muscle power output of $37 \, W \, kg^{-1}$ body mass during high-speed swimming. For us to bend the backbone of a 318-kg marlin to breaking, 34 J was required. Assuming a 50 % efficiency of elastic energy storage by the backbone and a tail beat frequency of 2 Hz (based on unpublished data of B. A. Block and F. G. Carey) for fast swimming, this backbone would be capable of contributing 68 W of power. This represents only 0.6 % of the 11 772 W of muscle power required, as determined from the $37 \, W \, kg^{-1}$ figure of Johnston and Salamonski (1984). Similar power relationships can be estimated from the data shown in Fig. 4. It is therefore unlikely that elastic energy storage by the backbone can make any significant contribution to marlin swimming energetics. Instead, the roles of the elaborated marlin backbone appear to be mechanical – restricting dorso-ventral bending while permitting lateral bending, and stabilizing the intervertebral joints against axial compression and lateral shearing dislocation during locomotion.

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