Intramuscular morphology and tendon geometry of the epaxial swimming muscles of dolphins

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(With 8 figures in the text)

The dolphin upstroke is powered primarily by the m. multifidus and m. longissimus—robust muscles that insert serially along the vertebral column. Intramuscular and tendon morphology coupled with kinematic data are used to hypothesize regionally specific functions of these muscles. Both muscles develop equivalent forces (approximately 2 kN) in the region of the thoraco-lumbar spine, but transmit those forces to different regions of the vertebral column. The m. multifidus transmits the majority of its force locally to the thoraco-lumbar spine, a region of the body that undergoes no measurable bending. The action of the m. multifidus appears to be to stiffen its deep tendon of insertion, forming a temporary skeletal element for the m. longissimus. The m. longissimus transmits the majority of its force to the caudal spine, by way of a novel interaction between its insertional tendons and the subdermal connective tissue sheath. This insertional pattern confers torsional stiffness on the caudal peduncle, and allows the m. longissimus to do relatively more work (118 J) than if it had a typical mammalian insertional pattern. The caudal extension of the m. multifidus does 12 J of work on the caudal spine during an upstroke. The caudal extension of the m. longissimus transmits its force to the vertebrae in the caudal flukes and is the only epaxial muscle that acts to control the angle of attack of the fluke blade.

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Introduction

Cetaceans (whales, dolphins and porpoises), unlike most mammals, are obligate axial locomotors. They swim by the alternate action of their robust epaxial and hypaxial muscles. The upstroke is powered primarily by two epaxial muscles—the m. multifidus, with its caudal extension, the m. extensor caudae medialis, and the m. longissimus, with its caudal extension, the m. extensor caudae lateralis (reviewed in Pabst, 1990).

The gross morphologies of these muscles have been described and their hypothesized functions reiterated many times over the past 100 years (e.g. by Murie, 1873; Slijper, 1936; Smith, Browne & Gaskin, 1976; Strickler, 1980; Pabst, 1990). Namely, the m. multifidus acts to elevate the caudal peduncle and the m. longissimus acts to elevate the caudal peduncle and bend the flukes.

While the gross morphology of a muscle offers one level of information about potential performance, its intramuscular morphology offers more detailed predictions about its force and excursion potentials (Gans & Bock, 1965; Gans, 1982; Sacks & Roy, 1982; Gans & de Vree, 1987). Although there exists a rich literature on the intramuscular morphology of mammalian appendicular locomotor muscles (e.g. Spector et al., 1980; Sacks & Roy, 1982; McClearn, 1986; Lieber & Blevins, 1989), only two studies to date have measured intramuscular morphological features of cetacean axial locomotor muscles (Bello et al., 1985; Bennett, Ker & Alexander, 1987). Because neither study compared the morphologies of the m. multifidus and the m. longissimus, no information exists on the relative force and excursion potentials of the major dorsal swimming muscles of cetaceans.

The epaxial muscles of cetaceans differ from appendicular muscles in the organization of their insertional tendons. Whereas appendicular muscles usually have discrete, terminal tendons of insertion, axial muscles have serially arranged tendons, i.e. individual tendon fibres insert sequentially on vertebræ along the length of the muscle (Pabst, 1990). In appendicular muscles, all force is presumably transmitted to the skeleton via a single tendon (but see Hermanson et al., 1991), and intramuscular morphological features are used to estimate a single value of potential force. In cetacean axial muscles, there is no single terminal tendon, therefore, no single estimate of the force potential is appropriate. To determine how much force the muscles develop and how that force is transmitted to the vertebral column requires a comprehensive study of intramuscular and tendon morphologies of the epaxial muscles.

The goals of the paper are three-fold: (1) to document the differences between the musculo-tendinous morphologies of the m. multifidus and the m. longissimus in bottlenose (Tursiops truncatus) and common (Delphinus delphis) dolphins; (2) to document regional variation in intramuscular and/or tendon morphologies within each muscle; and (3) to use this morphological data, coupled with kinematic data, to estimate the mechanical work done by each muscle during an upstroke.

Methods

The mechanical work done by a muscle is equal to the force it generates multiplied by its excursion. Mechanical work is a crude estimate of muscle work, but is a useful comparative tool to investigate the relative contributions of each muscle during an upstroke. Variations on standard intramuscular morphology techniques were used to estimate the force potential of each muscle. Also, gross morphological and kinematic data were used to develop a geometric model of the dolphin spine from which the excursions of the vertebral insertion sites of each muscle were estimated.
**Kinematics**

High-speed (200 frames/s) underwater cine films were taken of a bottlenose dolphin swimming in open water (methods described in Wainwright, Orton & Pabst, 1987). The outline of the dolphin in extreme dorso-extension was traced from individual frames of film. The radius of curvature of the animal was measured both anterior and posterior to the dorsal fin, along a mid-lateral line that approximated the position of the vertebral column (Fig. 1a). There was no measurable curvature of the dolphin anterior to the dorsal fin.

The angle described by the arc of the entire caudal peduncle was calculated as the arclength of the peduncle divided by its radius of curvature. The arclength of the peduncle was defined as the curvilinear distance between 2 points along the arc, one point at the insertion of the flukes, and the other point at the level of the dorsal fin tip (Fig. 1a). The angle described by the entire caudal peduncle was divided by the number of intervertebral joints undergoing bending (22 joints for the bottlenose; 26 joints in the common dolphin) to estimate the amount of bending occurring at each joint. Similarly, bending in a bottlenose dolphin giving birth was calculated from photographs (in Parry, 1949) and this animal was assumed to represent an upper extreme of dorsal bending.

This estimation of joint excursion assumes that each intervertebral joint undergoes the same degree of bending. Because the caudal peduncle does not describe a smooth arc when dorsally extended, this assumption probably overestimates the angle of joint bending in the anterior peduncle and underestimates the angle of joint bending in the posterior peduncle. To the best of my knowledge there are no kinematic data available for the common dolphin from which intervertebral bending angles can be estimated. The intervertebral joint bending angles of the common dolphin were assumed to be similar to those calculated for the bottlenose dolphin.

**Gross muscle and tendon morphology**

The gross morphologies of the epaxial locomotor muscles and connective tissues were investigated in bottlenose (15 specimens) and common dolphins (5 specimens). One bottlenose dolphin and 3 common dolphins were fixed in 10% buffered formalin. All other specimens were dissected fresh. Most specimens were laterally dissected; the blubber and m. cutaneous trunci were removed, and the epaxial muscles investigated in situ. Two bottlenose dolphins were frozen and cross-sectioned with a bow saw into 2-5-cm-thick sections. The anterior faces of the sections were cleaned and photographed, then computer-digitized and transformed into 3-dimensional reconstructions (*PC3D*, Jandel Scientific). The cross-sectional areas of the epaxial muscles were calculated (*Sigma Scan*, Jandel Scientific).

**Intramuscular morphology**

Dolphin axial muscles are large—the epaxial muscles of even a small (160 cm) bottlenose dolphin can weigh over 6 kg. Therefore, some of the intramuscular morphology techniques commonly used on smaller muscles (e.g. Sacks & Roy, 1982; Loeb & Gans, 1986) were not useful. I present methods for estimating intramuscular morphological features of large muscles when they cannot be reliably measured.

**Muscle fascicle angles**

Muscle fascicle angles were measured in the epaxial muscles of 1 bottlenose and 2 common dolphins. All 3 specimens were fixed by intramuscular injections of 10% buffered formalin; the specimens were then floated in a buffered formalin bath for 27-30 days, rinsed and stored in 70% EtOH.

On 1 common dolphin specimen, the muscle fascicle angles were measured directly with a protractor. On the other specimens, angles were either measured with a protractor or calculated from positional data. The $x$, $y$, and $z$ co-ordinates of 2 points along the muscle fascicle were measured with a 3-dimensional micro-
Figure 1. (a) Outline of swimming bottlenose dolphin at end of upstroke, traced from cine image. Intervertebral joint bending angles were estimated from the angle described by the arc of the entire caudal peduncle. The arc length, a, was defined by points A and B. (b) Geometric model of the spine within the caudal peduncle of a bottlenose dolphin. Lateral view of lumbar vertebra 14 and its abstracted form for model. C = vertebral centrum length. S = height of neural spine. Z = height of prezygapophysis. (c) The model spine in three positions. Top: end of upstroke; each intervertebral joint undergoing 3° bend. Middle: mid-phase of stroke. Bottom: end of downstroke; each intervertebral joint undergoing −3° bend.
manipulator mounted on a moving stage. These 2 points defined the slope of the line described by the trajectory of the muscle fascicle. The stage was positioned parallel to the long axis of the dolphin to measure the slope of the muscle fascicle relative to the long axis, and parallel to the tendon of insertion to measure the slope of the muscle fascicle at its myotendinous junction. The angles the muscle fascicles described were calculated from the slope values as \( \tan^{-1}(\text{slope}) \). Between 10 and 25 muscle fascicle angles were measured in each muscle; angles of both deep and surface fascicles were measured.

The precision of the angle measurements taken with a protractor was \( \pm 5^\circ \) (based on 10 repeated measures of each angle). The precision of the angle calculations taken from measurements with the micro-manipulator was \( \pm 0.3^\circ \) (based on 6 repeated measures of each angle).

The muscle fascicle angles measured in the m. multifidus and the m. longissimus were similar in the common and bottlenose dolphins. Muscle fascicle angles measured in the m. extensor caudae medialis and m. extensor caudae lateralis of the common dolphins are assumed to be similar to those in the bottlenose dolphin. Means and ranges from pooled data from all 3 specimens were reported.

Muscle fascicle lengths

Nitric acid dissections of fixed epaxial muscle (techniques described in Loeb & Gans, 1986) yielded only minimum muscle fascicle lengths because either excised samples did not contain the entire length of the fascicle or the fascicles tore. Nitric acid-treated muscle fibres have also been shown to shrink 10–20% longitudinally (Gans, Loeb & de Vree, 1989).

I calculated the 'effective' fascicle length (EFL) as the straight line distance between its surface of origin and its myotendinous junction, measured along the trajectory of the fascicle. The EFL can be calculated as the hypotenuse of a right-angled triangle described by the equation:

\[
EFL = \frac{T}{\sin(\alpha)}
\]

where \( T \) is equal to the perpendicular distance between the surface of origin and the myotendinous junction and \( \alpha \) is the angle the muscle fascicle describes relative to the longitudinal axis of the dolphin (Fig. 2). \( T \) was measured with Vernier callipers from projected photographs of whole-body cross-sections from 1 bottlenose dolphin.

Because muscle fascicles are often curved along their length, and are not oriented parallel to the longitudinal axis of the dolphin, the calculated EFLs are underestimates of the true fascicle lengths for both muscles. These underestimates can be as much as 7% for muscle fascicles that make angles of 20° to the long axis of the dolphin.

Each of 8 repeated measures of the vertical distance, \( T \), fell within \( \pm 0.3 \) mm of the mean, a variance that represented 0.9% of the value of \( T \). The small error associated with each angle measure is amplified as a function of the sine and has a profound effect upon fascicle length calculations. For example, if \( T \) was 5 cm and \( \alpha \) was 10° (\( \pm 5^\circ \)), the calculated EFLs would be between 22 and 41 cm. The angle measurements taken with the micro-manipulator have smaller standard errors, and yield narrower ranges of EFLs (for the above example, the EFLs would be between 28 and 30 cm). Because the fascicle angles of all the specimens were not measured with the micro-manipulator, the largest errors associated with the angle measurements are reported.

Muscle physiological cross-sectional area

A variation of the standard equation was used to calculate the physiological cross-sectional area (PCSA) of each muscle (e.g. Sacks & Roy, 1982):

\[
PCSA = \frac{MW * \cos(\beta)}{EFL * \rho}
\]
Fig. 2. Estimating the 'effective' fascicle length (EFL) for m. longissimus (L) of a bottlenose dolphin. (a) The vertical distance, T, from the surface of origin to the myotendinous junction of a muscle fascicle. T varies across the face of the cross-section. M = m. multifidus. (b) The EFL was estimated as the hypotenuse of the right-angled triangle described by T and the angle of the fascicle relative to the longitudinal axis of the dolphin. V = length of the side along the vertebral column. (c) Planar view of (b). * Indicates the parameters measured.
where $MW$ is the wet weight of the muscle, $\beta$ is the mean angle of pinnation of muscle fascicles to their tendon of insertion, and $\rho$ is muscle density (1·0564 g/cm$^3$, Mendez & Keys, 1960).

It is not possible to weigh separately the m. multifidus and m. longissimus anterior to the caudal peduncle as they share the deep tendon as a site of muscle attachment. To estimate the weight of these muscles the combined m. multifidus and m. longissimus muscle mass anterior to the caudal peduncle from a bottlenose dolphin of similar size (168·5 cm, 59·8 kg female) to the cross-sectioned animal (170·9 cm, 62·5 kg female) was weighed. From the cross-sectioned specimen, I calculated the total muscle cross-sectional area, and the mean cross-sectional area for each muscle from the region of the cervical through the lumbar spine. The individual weight of each muscle was estimated as the combined muscle weight multiplied by the fraction of the total cross-sectional area occupied by each muscle. The m. extensor caudae medialis and the m. extensor caudae lateralis were weighed directly. The PSCA of each muscle was multiplied by muscle stress (0·3 MPa, Wells, 1965) to calculate its force potential.

**Tendon geometry and excursion**

I defined the excursion of a tendon as the distance through which a tendon is moved by its muscle to effect the displacement of its skeletal insertion site. Tendon excursions were estimated using a 2-dimensional ‘stick’ model of the caudal vertebral column, based on morphometric data from an articulated skeleton of a bottlenose dolphin. On each vertebra, the height of the neural spine, the length of the centrum and the perpendicular distance from the plane of bending to the sites of tendon insertions were measured (Fig. 1b). The plane of bending was assumed to lie along the vertebral column and pass through each centrum at the position of the transverse processes (i.e. approximately mid-centrum for caudal vertebrae). A computer program was written to calculate the position (as $x$, $y$ co-ordinates) of each skeletal landmark when the intervertebral joints underwent bending (see p. 161). A computer graphics program, *Acrospin* (Acrobix, 1989), was used to visualize the model spine (Fig. 1c). The tendon excursion due to positional changes of a skeletal insertion site, which was dependent upon tendon geometry, was calculated. The tendon geometry and insertion sites were determined from dissections.

To test whether the excursions predicted by the model were physiologically reasonable, I compared them to tendon excursions that would result given a uniform 10% shortening of the sarcomeres within the epaxial muscles (based on published values for other vertebrate muscle, e.g. Gordon, Huxley & Julian, 1966; Close, 1972; Muhl, 1982; Dimery, 1985).

The mean calculated tendon excursion was multiplied by the muscle’s force-generating potential to estimate the mechanical work done by each epaxial muscle.

**Results**

**Kinematics**

In the region of the dolphin anterior to the dorsal fin, bending was only obvious at the occipital-atlantal joint. There was no measurable bending in the thoraco-lumbar spine. Bending along the caudal peduncle was easily measured and varied depending on other kinematic parameters. The dolphin accelerated from a stationary position with large-amplitude, low-frequency tailbeats and it appeared that the caudal peduncle underwent maximal bending. When the animal swam past the camera, its tailbeat amplitude (and curvature) had obviously decreased. Thus, the 46° maximum bending angle of the entire caudal peduncle (approximately 2° of bending at each intervertebral joint) represents the curvature during a sustained locomotor sequence. The caudal peduncle of a captive bottlenose dolphin giving birth (Parry, 1949) was bent into an arc of 65° (approximately 3°
of bending at each intervertebral joint), and probably represents an upper limit of dorsal bending in the bottlenose dolphin.

*Gross muscle and tendon morphology*

The general features of the epaxial musculo-tendinous system of the bottlenose and common dolphin are very similar. A detailed description of the gross morphology of the axial muscles and tendons of the bottlenose dolphin appears in Pabst (1990); I will briefly describe their morphology here.

The epaxial muscles are wrapped by a helically wound, crossed-fibre array, the subdermal connective tissue sheath (SDS) (Pabst, 1990). The SDS is anchored firmly on to the vertebral column by way of medially diving septa (Fig. 3). The SDS is under biaxial tension in the dolphin body, and is mechanically stiff (Pabst, unpubl. data).

*M. multifidus, m. extensor caudae medialis and deep tendon* (Figs 4, 5)

The m. multifidus runs from the cervical through the lumbar spine. Its caudal extension, the m. extensor caudae medialis, runs from caudal vertebra 1 through caudal vertebrae 10–12. Although separately named, these muscles are structurally and functionally continuous.

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*Fig. 4.* Epaxial muscles and connective tissues of a bottlenose dolphin. (a) M. multifidus (M) and extensor caudae medialis (ECM). Cross-sectional shape of muscle is indicated at various points. Skeletal elements are shown as series of cross-sections (irregular shapes of vertebrae are artefacts of the placement of the saw cut; not all vertebrae are shown). Arrows 1 and 2 refer to cross-sections shown in Fig. 5. Arrows within muscle body approximate orientation of muscle fibres. (b) Deep tendon. The longitudinal lines indicate individual connective tissue fibres that form the deep tendon. Thick, transverse lines indicate the cross-sectional shape of tendon. (c) M. longissimus (L) and extensor caudae lateralis (ECL). Cross-sectional shape of muscle is indicated at various points. Arrows within muscle body approximate orientation of muscle fibres. (d) Superficial tendon. These tendon fibres change their orientation as they enter the subdermal connective tissue sheath (not shown) and run obliquely to the transverse processes of posterior vertebrae. The lines of medium thickness indicate the connective tissue fibres that join the sheath. (e) Tendons of the ECL. The most ventro-medial of the superficial tendon fibres coalesce to form seven cylindrically shaped tendons that insert on the caudal vertebrae in the flukes (not shown). (Figure copyrighted by the author.)
MORPHOLOGY OF DOLPHIN EPAXIAL MUSCLES

(a)  

(b)  

(c)  

(d)  

(e)  

Fig. 4
The muscle fascicles of the m. multifidus and m. extensor caudae medialis originate on: (1) the vertebral neural spines (dorsal to the prezygapophyses), (2) the deep surface of the superficial tendon that covers the m. multifidus and m. extensor caudae medialis and (3) the deep surface of the SDS (just lateral to the neural processes) from the mid-lumbar vertebrae posterior.

The m. multifidus and m. extensor caudae medialis insert via the deep tendon, an aponeurotic sheet composed of many long, flat tendon fibres. Each tendon fibre runs from the ventral aspect of the muscle and inserts upon each prezygapophysis from the first thoracic vertebra through caudal vertebra 18.
M. longissimus, m. extensor caudae lateralis and superficial tendon (Figs 4, 5)

The m. longissimus runs from the skull to the first caudal vertebra. Its caudal extension, the m. extensor caudae lateralis, runs from caudal vertebra 1 to caudal vertebra 15. These muscles are continuous.

The m. longissimus originates on the posterior edge of the zygomatic process and the lateral margins of the exoccipital bones, and on the lateral aspects of all the cervical vertebrae. The m. longissimus and m. extensor caudae lateralis also originate on: (1) the dorsal surfaces of the transverse processes and lateral surfaces of the neural arches of all post-cervical vertebrae, (2) the deep surface of the lateral SDS and (3) the ventral surface of the deep tendon.

The m. longissimus inserts on to the deep surface of the SDS in the anterior thoracic region. The m. longissimus also inserts via the superficial tendon, an aponeurotic sheet composed of many, long flat tendon fibres. Each tendon fibre runs from the body of the m. longissimus posteriorly towards the mid-dorsal line. Just lateral to the mid-dorsal line, the tendon fibres split into smaller fibres, and the paths of these smaller fibres diverge.

A small population of these tendon fibres inserts as do the m. longissimus tendons of terrestrial mammals—on to the neural spines of the thoracic and anterior lumbar vertebrae. Because the robust m. multifidus completely surrounds the neural spines, these tendon fibres dive through the body of the m. multifidus to insert on to the spine (see Fig. 5a and b).

The majority of the tendon fibres approach, but do not insert on to, the neural spines. Instead, just lateral to the mid-dorsal line, the tendon fibres join the SDS. The tendon fibres either: (1) cross the mid-dorsal line and run at about 45° through the SDS towards the vertebral transverse processes on the contralateral side of the dolphin, or (2) turn laterally away from the dorsal midline as they enter the SDS, and run at about 45° through the SDS towards the ipsilateral vertebral transverse processes. To the best of my knowledge, this is a novel insertional pattern for the tendons of the m. longissimus.

The m. extensor caudae lateralis inserts on to the dorsal surfaces of the caudal vertebrae contained in the flukes, by way of seven cylindrical tendons, formed by the most ventro-medial fibres of the superficial tendon.

Intramuscular morphology

See Table I for muscle weights, PCSAs, EFLs and fascicle pinnation angles for the epaxial muscles.

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Pinnation angle to tendon (deg.)</th>
<th>‘Effective’ fascicle length (cm)</th>
<th>Muscle weight (g)</th>
<th>Physiological cross-sectional area (cm²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>M. multifidus</td>
<td>32 (29-40)</td>
<td>6 (1-11)</td>
<td>535</td>
<td>77.6</td>
</tr>
<tr>
<td>M. extensor caudae medialis</td>
<td>17 (10-24)</td>
<td>10 (7-14)</td>
<td>240</td>
<td>21.9</td>
</tr>
<tr>
<td>M. longissimus</td>
<td>15 (7-24)</td>
<td>23 (14-33)</td>
<td>1968</td>
<td>77.7</td>
</tr>
<tr>
<td>M. extensor caudae lateralis</td>
<td>12 (2-22)</td>
<td>17 (14-20)</td>
<td>220</td>
<td>12.0</td>
</tr>
</tbody>
</table>
Tendon geometry and excursion

I did not estimate the excursion of the deep tendon in the region of the thoracic and anterior lumbar spine, owing to the lack of measurable bending here. The excursion of a deep tendon fibre (E_D) in the region of the caudal peduncle is equivalent to the change in the horizontal position of its prezygapophysis of insertion, calculated as:

\[ E_D = Z \cdot \sin(\gamma) \]  \hspace{1cm} (3)

where \( Z \) is the perpendicular distance from the plane of bending to the prezygapophysis and \( \gamma \) is the bending angle at the intervertebral joint (Fig. 6).

For the few superficial tendon fibres that insert on to the dorsal tips of the neural spines, their excursion (E_S) would similarly be:

\[ E_S = S \cdot \sin(\gamma) \]  \hspace{1cm} (4)

where \( S \) is the perpendicular distance from the plane of bending to the tip of the neural spine. The mean neural spine height of the vertebrae in the caudal peduncle is 1.6 times that of the prezygapophyseal height, i.e. the superficial tendons that insert on to the neural spines undergo, on average, one and one-half times the excursion of the deep tendon for a given bending angle. The difference in the excursion of the two tendons is, in fact, larger. The majority of the superficial tendon fibres do not insert on to neural spines, but travel through the SDS at oblique angles and insert on to the transverse processes of more posterior vertebrae (Fig. 7). During an upstroke, the distance between the neural spine tip and the more posterior transverse process decreases. The

![Fig. 6. 'Stick' models of a caudal vertebra of a bottlenose dolphin. (a) Neural spine height (S) indicated. (b) Prezygapophyseal height (Z) indicated. The solid lines indicate the position of the vertebra before, and the dashed lines indicate the position of the vertebra after the intervertebral joint bends through an angle, \( \gamma \). E_D, the excursion of the deep tendon, is less than E_S, the excursion of the superficial tendon, for an equivalent intervertebral joint bending angle.](image-url)
change in this diagonal distance represents the excursion of the oblique tendon \((E_{OT})\). Thus, the total excursion \((E_T)\) of the superficial tendon is:

\[ E_T = E_S + E_{OT}. \]  

The \(E_S\)s and \(E_{OTS}\) were calculated for the ten anteriormost superficial tendon fibres in the caudal peduncle given a 3° bending angle at each intervertebral joint (Table II). The \(E_{OTS}\), calculated using oblique tendon angles between 38–50°, accounted for between 30 and 60% of the total excursion of the superficial tendon fibres. By joining the SDS, the superficial tendon fibres increase their potential excursion, relative to inserting on the neural spines. The geometric model estimates total superficial tendon excursions well within the range (1–3 cm, given a uniform 10% sarcomere shortening) predicted by the intramuscular morphology of the m. longissimus.

*Estimated mechanical work of epaxial muscles*

The lack of measurable bending in the region of the thoracic and anterior lumbar spine and, thus, the potentially small excursions of the deep tendon suggests that the m. multifidus does little work on these vertebrae. The m. multifidus lacks direct tendinous connections to the caudal vertebrae and thus does no direct work in bending the caudal peduncle during an upstroke. The m. extensor caudae medialis does 12 J of work on the vertebrae in the caudal peduncle (combined estimate for both left and right muscles for a full upstroke).
Table II

Estimated excursions of the superficial tendon fibres. The values were calculated at the first ten vertebrae in the caudal peduncle, from lumbar (L) 11 through caudal (Ca) 6, given a 3° bend at each intervertebral joint. E_S = excursion of tendon due to the change in position of the neural spine during an upstroke; E_OT = excursion of tendon due to the change in the distance traversed by the obliquely oriented tendon during an upstroke; E_T = E_S + E_OT = total excursion of a superficial tendon fibre.

<table>
<thead>
<tr>
<th>Neural spine</th>
<th>No. of joints crossed</th>
<th>Oblique tendon angle (deg.)</th>
<th>E_S (cm)</th>
<th>E_OT (cm)</th>
<th>E_T (cm)</th>
<th>E_OT/E_T</th>
</tr>
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<tbody>
<tr>
<td>L11</td>
<td>3</td>
<td>46</td>
<td>0.62</td>
<td>0.52</td>
<td>1.14</td>
<td>0.46</td>
</tr>
<tr>
<td>L12</td>
<td>3</td>
<td>45</td>
<td>0.59</td>
<td>0.66</td>
<td>1.25</td>
<td>0.53</td>
</tr>
<tr>
<td>L13</td>
<td>3</td>
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<td>0.49</td>
<td>0.64</td>
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<td>L14</td>
<td>3</td>
<td>41</td>
<td>1.25</td>
<td>0.65</td>
<td>1.90</td>
<td>0.34</td>
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<tr>
<td>Ca1</td>
<td>3</td>
<td>40</td>
<td>0.64</td>
<td>0.66</td>
<td>1.30</td>
<td>0.51</td>
</tr>
<tr>
<td>Ca2</td>
<td>3</td>
<td>39</td>
<td>0.60</td>
<td>0.90</td>
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<td>Ca4</td>
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The m. longissimus does 118 J of mechanical work on the vertebrae in the caudal peduncle (combined estimate for both left and right muscles for a full upstroke). I could not estimate the mechanical work done by the m. extensor caudae lateralis because I could not accurately measure the change in position of the flukes from the cine films.

Discussion

The dolphin m. multifidus and m. longissimus, although highly derived mammalian axial muscles, exemplify fundamental intramuscular designs found in other mammalian locomotor systems. For example, dolphin epaxial muscles have very different intramuscular designs yet complementary actions, a pattern analogous to two mammalian hind limb dorsi-extensors, the m. tibialis anterior and the m. extensor digitorum longus (Goslow, Cameron, & Stuart, 1977; Sacks & Roy, 1982; McClearn, 1986; Lieber & Blevins, 1989). The short muscle fascicles, steep pinnation angles and large PCSA of the m. multifidus suggests that it, like the m. extensor digitorum longus, is designed to produce large forces, but not large excursions of its insertional tendons. The extremely long muscle fascicles, small pinnation angles, and large PCSA of the m. longissimus suggest that it, like the m. tibialis anterior, is designed to produce both large forces and large excursions of its insertional tendons.

The intramuscular morphologies of the two epaxial muscles imply great potential differences in their performance. The pattern of their tendinous insertions, coupled with kinematic data, suggest more precisely their individual contributions to the dolphin upstroke.

M. multifidus and m. extensor caudae medialis

The function generally ascribed to the m. multifidus is bending of the caudal peduncle during an upstroke (reviewed in Strickler, 1980). The majority of the force generated by this muscle, though, is not directly transmitted to the caudal peduncle. Instead, the large forces developed by the
m. multifidus are transmitted to the thoracic and anterior lumbar spine. Why does the m. multifidus transmit large forces, via the deep tendon, to a region of the spine that undergoes no obvious bending during an upstroke? I hypothesize that the action of the m. multifidus is to stiffen the deep tendon, to form a temporary skeletal element for the m. longissimus.

The deep tendon is both the site of insertion of the m. multifidus and the site of origin for the dorsally-placed fascicles of the m. longissimus (Fig. 8). To be an effective skeletal element for the m. longissimus, the deep tendon must: (1) not undergo large excursions that could potentially stretch the fascicles of the m. longissimus and (2) not deform when loaded by the contracting m. longissimus—i.e. the deep tendon must be stiff. When the m. multifidus contracts, the whole muscle stiffens, and the deep tendon is tensed, apparently forming a functional skeletal element for the dorsally-placed m. longissimus muscle fascicles.

Muscles whose action is to create temporary skeletal elements from flexible connective tissues are found in a variety of muscle systems. In fishes and most urodeles, muscle fibres of anterior myomeres contract and stiffen their myosepta, which in turn act as sites of origin for the next posterior myomeres (Nursall, 1956; Wainwright, 1983). In humans, the m. tensor fasciae latae contracts and stiffens the fascia lata, which acts as the site of insertion for the m. gluteus maximus (Gray, 1973). When the m. genioglossus of certain Rana spp. contracts, it forms a stiff rod surrounded by a (presumably) tensed fascia. This muscle forms a ‘temporary skeletal element’ for other muscles acting on the frog tongue (Gans & Bock, 1965; Gans, 1982).

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**Fig. 8.** Schematic representation of a sagittal section through the epaxial muscles, illustrating the relative angles of the muscle fascicles of the m. multifidus and m. longissimus to the deep tendon. Muscle fascicles of the m. multifidus use the deep tendon as a site of insertion. Dorsally placed muscle fascicles of the m. longissimus use the deep tendon as a site of origin. SDS = subdermal connective tissue sheath. Thick solid lines represent skeletal elements. Thick obliquely dashed lines represent tendons.
Interestingly, in the caudal peduncle, where the deep tendon undergoes estimable excursion, it is not used as a site of origin by the m. extensor caudae lateralis. A connective tissue septum separates the m. extensor caudae lateralis from the deep tendon (see Fig. 5).

Unlike the m. multifidus, the m. extensor caudae medialis is designed to do work (12 J) on the caudal spine during an upstroke.

**M. longissimus and m. extensor caudae lateralis**

The large forces developed by the m. longissimus in the region of the thoracic and anterior-lumbar spine are transmitted to the posterior lumbar and caudal spine. The m. longissimus ‘postpones’ its insertion on to the vertebral column, relative to other mammals, owing to its unusual morphological interaction with the SDS. What are the functional consequences of this tendon morphology?

1. By joining the SDS, the m. longissimus distributes its muscular contractile force evenly along the entire length of the caudal peduncle, rather than point-loading individual vertebrae. This pattern of insertion seems advantageous since the action of the muscle is to bend a flexible beam smoothly. Because the tendon fibres run at oblique angles through the peripheral SDS, they also add torsional stiffness to the caudal peduncle (Wainwright, Vosburgh & Hebrank, 1978; Hebrank, 1980), which might be particularly important to counter asymmetric loading of the broad caudal flukes.

2. The oblique tendon geometry increases the distance through which these tendons can be pulled by the very long-fascicled m. longissimus. At their approximate 45° orientation to the long axis of the dolphin, the excursion potential and thus the mechanical work potential of the m. longissimus is 30–60% larger than it would be if the tendons inserted on to the neural spines.

3. The trajectory of a superficial tendon fibre suggests that of a jib wire on a mechanical crane (see Fig. 7). By running across the tall neural spine (the jib analogue), the tendon fibre creates a large moment arm relative to the plane of bending, thus increasing the bending moment of the muscular contractile force of the m. longissimus. The trajectories of the superficial tendon fibres suggest that the m. longissimus acts to elevate and bend the jointed, ventrally flexed vertebral column to the dorsally extended position.

These functional hypotheses are based, in part, upon a geometric model that assumes that the tendons do not change length. Bennett *et al.* (1987) estimated that the epaxial tendons in two cetacean species, the harbour porpoise (*Phocoena phocoena*) and the Atlantic white-sided dolphin (*Lagenorhynchus acutus*) probably experience strains of up to 2% during locomotion. Thus, the tendon excursions calculated in this study might be reduced by as much as 2%. This reduction in overall tendon excursion does not affect the result that superficial tendons that join the SDS undergo relatively larger excursions than the superficial tendons that insert on to the neural spines.

The m. extensor caudae lateralis is apparently the only epaxial muscle that controls the angle of attack of the flukes. Although I could not estimate the mechanical work done by this region of muscle, it is clear that the fluke does undergo large changes in position during an upstroke. Given that the force-generating capacity of the m. extensor caudae lateralis is the smallest estimated for any cetacean epaxial muscle, it suggests either: (1) the position of the fluke is primarily a passive result of hydrodynamic forces across the fluke blade, and/or (2) the forces required to move the fluke are substantially less than those required to bend the caudal peduncle.
Summary

This study is the first to use kinematic data, coupled with detailed information on musculoskeletal morphology, to hypothesize regionally specific functions of the two principal dorsal swimming muscles of the dolphin, the m. multifidus and the m. longissimus.

In the thoracic and anterior lumbar spine, the m. multifidus produces large forces, but small excursions of its deep tendons of insertion. In this region of the body the m. multifidus appears to act to stiffen the deep tendon, forming a temporary skeletal element for the m. longissimus. This function is analogous to that found in the axial locomotor systems of fishes, where muscle fibres of anterior myomesos contract and stiffen their myosepta, which in turn act as the sites of origin for the next posterior myomesos. The caudal extension of the m. multifidus is designed to do work on the caudal spine during an upstroke.

Regional differences in the intramuscular design of the m. longissimus are not as profound as those between the anterior and posterior regions of the m. multifidus, but their tendon insertional patterns vary greatly. In the thoracic and anterior lumbar spine, the m. longissimus produces large forces but transmits the majority of those forces to the caudal peduncle, owing to an apparently novel connection between the superficial tendons and the subdermal connective tissue sheath. The geometry of this unique tendon pattern allows the m. longissimus to do relatively more work on the caudal spine than if it inserted in the standard mammalian pattern, and adds torsional stability to the peduncle. The caudal extension of the m. longissimus inserts directly on to the vertebrae in the caudal flukes via seven tendons and appears to act to control the angle of attack of the flukes.

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REFERENCES


