



The role of the pectoral fins in body trim of sharks

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In a large aquarium the leopard shark *Triakis semifasciata*, sand tiger shark *Odontaspis taurus*, sandbar shark *Carcharhinus plumbeus*, and spiny dogfish *Squalus acanthias* cruised steadily at 0.1–0.7 body lengths s^{-1} . Relative to the trajectory of the shark, the pectoral fins were maintained at a positive angle of attack regardless of vertical direction. For level swimming the mean angle of attack for the pectoral fin was $11 \pm 1.7^\circ$, $10.1 \pm 1.3^\circ$, $9.3 \pm 1.3^\circ$, and $15.0 \pm 0.0^\circ$ for *T. semifasciata*, *C. plumbeus*, *O. taurus*, and *S. acanthias*, respectively. The long axis of the body was canted at an angle of attack for *T. semifasciata* and *S. acanthias*, but trim was maintained during level swimming for *C. plumbeus* and *O. taurus*. Hydrodynamic analysis of the body and fin design of *T. semifasciata* indicated that the pectoral fins could develop sufficient pitching moment to maintain depth and keep the body in trim. Demonstration of positive angles of attack support the hypothesis that lift is generated in the anterior body to counterbalance the lift produced by the heterocercal tail.

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Key words: angle of attack; swimming; shark; induced drag; trim.

INTRODUCTION

The primary means of sustained swimming by most fishes is by use of a modified tail with a caudal fin (Breder, 1926; Webb, 1975; Lindsey, 1978). The majority of fish within the Osteichthyes possess a homocercal tail in which the dorsal and ventral fin lobes are of equal size. The homocercal tail is assumed to generate a reaction force parallel with the longitudinal axis of the body while perpendicular forces from the tail are balanced. For sharks (Chondrichthyes: Elasmobranchi), the tail is described as heterocercal, whereby the notochordal axis extends into the upper lobe of the tail producing an asymmetry which is manifest as a larger and stiffer epichordal lobe relative to the hypochordal lobe (Thomson, 1976; Moss, 1984). The function of the heterocercal tail appears to be two-fold in the generation of an anteriorly directed thrust and vertically oriented lift (Breder, 1926; Grove & Newell, 1936; Harris, 1936; Affleck, 1950; Alexander, 1965; Simons, 1970; Webb & Smith, 1980; Ferry & Lauder, 1996).

In the classical model of shark swimming (Ferry & Lauder, 1996), the lift generated at the tail is counterbalanced by lift generated from the anterior end of the animal by the pectoral fins and underside of the head (Harris, 1936; Gray, 1968; Aleyev, 1977). The hydrodynamically generated lift is necessary to maintain trim (i.e. balance) and oppose the negative buoyancy of many sharks (Budker, 1971). The combined lift from head, pectoral fins, and heterocercal tail

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produces a resultant force equal and opposite to the effect of gravity and resists the tendency to sink (Gray, 1968). An alternative model proposed by Thomson (1976) has the thrust generated from a center of effort in the epichordal lobe acting through the center of gravity of the fish. For this model, the lift generated by the pectoral fins is slight and it is the hypochordal lobe that acts as a trimming device (Thomson, 1976, 1990; Thomson & Simanek, 1977). Thomson's model predicts that the shark should experience less induced drag by the pectoral fins and thus more efficient propulsion for the shark (Thomson, 1990).

Despite the relevance of the function of the pectoral fins with respect to the competing models, there has been little analysis of the fins and their contribution to lift generation and maintenance of trim. The morphology of the pectoral fins strongly suggests a function associated with lift production. Cross-sections of the pectoral fin show streamlined profiles reminiscent of cambered airfoils (Budker, 1971). Harris (1936) observed that the dogfish *Mustela canis* (Mitchill) swims with the pectoral fins inclined at an angle of 8–10° to the body axis. Experiments in a wind tunnel on a static model of *M. canis* indicated that the pectoral fins produced a positive lift and a fairly large positive pitching moment (Harris, 1936). This pitching moment was hypothesized to be balanced by the actions of the heterocercal tail to keep the shark in trim.

The present paper reports a study of the function of the pectoral fins in four species of sharks with differing morphologies. The angle of inclination of the body and pectoral fins were determined from video analysis of the sharks as they freely swam in large aquaria. This information was used to compute the pitching moment. It was hypothesized that the angle of attack of the pectoral fins and body would be sufficiently large to generate a positive lift. This lift would produce a positive pitching moment which could counterbalance that from the heterocercal tail and support the classical model (Breder, 1926; Harris, 1936; Affleck, 1950; Alexander, 1965; Simons, 1970; Webb & Smith, 1980; Ferry & Lauder, 1996).

MATERIALS AND METHODS

The body and pectoral fin orientation were observed for four species of free-swimming sharks in aquaria with large acrylic windows for underwater viewing. At Sea World, San Diego, California, 10 leopard sharks *Triakis semifasciata* Girard (1.1–1.4 m L_T), seven juvenile sandbar sharks *Carcharhinus plumbeus* (Nardo) (0.9–1.1 m), one adult *C. plumbeus* (c. 1.8 m) and 38 spiny dogfish *Squalus acanthias* L. (0.8–1.1 m) were observed together in a 1.6×10^6 l aquarium described by Weihs *et al.* (1981). In addition, eight adult *T. semifasciata* (1.2–1.7 m) were observed in a separate 1.3×10^5 l aquarium. At New Jersey State Aquarium, Camden, New Jersey, six sand tiger sharks *Odontaspis taurus* (Rafinesque) (1.5–2.7 m) and nine *C. plumbeus* (1.2–2.1 m) were maintained in a 2.9×10^6 l aquarium.

Sharks were video-recorded with a Panasonic Camcorder (DV-510) at 60 Hz. The camcorder was mounted on a tripod and positioned with the camera lens perpendicular to the viewing window. The bottom of the camera's viewing field was oriented parallel to the lower margin of the viewing window which was checked to be level and represented the horizontal axis. Video records were made as animals swam steadily parallel to the viewing window.

Video records of swimming sequences were analysed with a Panasonic AG-7300 video recorder and Panasonic monitor (model CTJ-2042R). No measurable distortion of the video image was detectable. Only those sequences were analysed in which the sharks

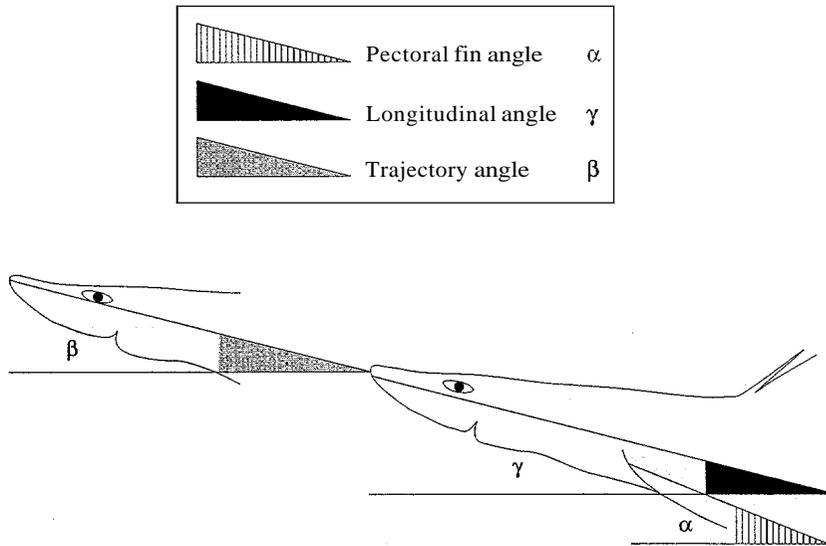


FIG. 1. The three angles measured on swimming sharks. All angles were measured with respect to the horizontal axis. Angles below the horizontal axis were negative; angles above were positive. Pectoral fin angle (PFA) was measured across maximum chord of the fin. Longitudinal angle (LA) was measured using the longitudinal axis of the body. Trajectory angle (TA) was measured using the line drawn from the tip of the snout at an initial position to tip of the snout at a second position after a 1 s interval.

swam steadily along a linear trajectory without interference from other individuals or contact with the viewing window. Data were collected when the shark's image was centered in the video monitor to reduce any error due to refraction. Three angles were measured from each sequence (Fig. 1); pectoral fin angle (PFA= α), trajectory angle (TA= β), and longitudinal angle (LA= γ). PFA was defined as the angle between the horizontal axis and the chordwise axis of the pectoral fin. The chordwise axis extended from the leading edge to the trailing edge of the fin. When the shark was swimming level with the video camera, the lateral projected image of the fin appeared as a thin line. The fin did not appear to change camber as the shark swam, although rolling motions were observed throughout a stroke cycle. TA was the angle between the horizontal axis and trajectory of the shark as the line drawn from the position of the rostrum at the start of the sequence and the position of the rostrum after a 1 s interval. LA was the angle between the horizontal axis and the longitudinal axis of the body, which remained constant for the anterior half of the shark. LA approximated an average of the ventral surface of the shark, although local curvatures of the ventral surface continuously varied along the body length. The angles of attack of the pectoral fins (PAA= x) and the body (BAA= y) were computed according to:

$$x = \alpha - \beta \quad (1)$$

$$y = \gamma - \beta \quad (2)$$

The distance travelled in 1 s intervals used to measure TA was used to compute swimming velocity of the shark. Because the precise distance travelled could not be determined, distance was normalized with respect to the total length of the individual shark giving the specific speed in body lengths s^{-1} ($L s^{-1}$). This allowed comparisons between sharks of different body size (Webb & Keyes, 1982).

The lift and pitching moment of the pectoral fins were determined for a 45.4 cm individual specimen of *T. semifasciata* (female; ANSP 580), examined at the Philadelphia

Academy of Natural Sciences. The center of gravity was determined with <0.5% error by laying the specimen lengthwise on a $34 \times 3 \times 2$ cm Styrofoam block and moving the block lengthwise over a narrow, rounded edge until the specimen was balanced (Domning & De Buffrenil, 1991). Pectoral fin area (A_{fin}) and span, including the area of the body between the anterior insertion and posterior margin of the fin, were determined from a scaled digital photograph taken with a Sony Mavica camera (MVC-FD7). Sweep angle of the pectoral fin (angle between a perpendicular to the longitudinal axis of the body and the 1/4 chord) also was determined from the photograph. A_{fin} , fin span, and sweep were measured using NIH Image software (Version 1.57).

Lift (L_{fin}) and pitching moment (M_{fin}) of the pectoral fins were calculated according to the equations:

$$L_{\text{fin}} = 0.5\rho A_{\text{fin}} C_L U^2 \quad (3)$$

$$M_{\text{fin}} = L_{\text{fin}} l_{\text{fin}} \quad (4)$$

where ρ is the density of sea water (1024 kg m^{-3}), U is the swimming velocity and C_L is the lift coefficient. C_L was computed using Wing Design software (Version 1.0; Desktop Aeronautics, Stanford, CA). The Wing Design program computes the aerodynamic characteristics of planar lifting surfaces using extended lifting line theory. The variable inputs for the program are aspect ratio ($\text{span}^2/A_{\text{fin}}$), sweep, taper ratio (tip chord/root chord; Hurt, 1965), and PAA. l_{fin} represents the moment arm of the pectoral fin which was measured as the distance from the center of gravity to the center of lift of the fin. For a delta wing, the center of lift is at a point 0.25 chord and 0.5 wing span (Hoerner and Borst, 1975). The center of lift was geometrically calculated and provided a moment arm of 0.07 m. M_{fin} was compared with the pitching moment of the heterocercal tail (M_{tail}) using data from Ferry & Lauder (1996).

Statistical comparisons were made using Statistica (Version 4.1; StatSoft) and DataDesk (Version 3.0). Variation about means was expressed as $\pm 1 \text{ S.E.}$

RESULTS

SWIMMING VELOCITY AND ANGLE OF ATTACK

A total of 213 swimming sequences were analysed (93 *T. semifasciata*; 69 *C. plumbeus*; 34 *O. taurus*; 17 *S. acanthias*). All species examined swam routinely over a narrow range of velocities of $0.1\text{--}0.7 \text{ L s}^{-1}$, at mean speeds of $0.32 \pm 0.01 \text{ L s}^{-1}$ (*O. taurus*), $0.39 \pm 0.01 \text{ L s}^{-1}$ (*T. semifasciata*), $0.42 \pm 0.02 \text{ L s}^{-1}$ (*S. acanthias*) and $0.46 \pm 0.01 \text{ L s}^{-1}$ (*C. plumbeus*). Average swimming speeds were higher for *C. plumbeus* than previously reported (Weihs *et al.*, 1981), but lower for *T. semifasciata* (Webb & Keyes, 1982).

Sharks exhibited a range of trajectories, swimming level ($\text{TA} = 0^\circ$), ascending ($\text{TA} > 0^\circ$), or descending ($\text{TA} < 0^\circ$) (Figs 2–3). Minimum descending TA was -25° for *C. plumbeus* and maximum ascending TA was 16° for *S. acanthias*. Both PAA and BAA were affected by TA (Figs 2–3). As TA decreased (i.e. steeper descent angle), PAA and BAA increased. However when swimming level or ascending, PAA and BAA remained relatively unchanged. PAA for all sequences examined was positive. BAA was ≥ 0 in 97% of all sequences examined.

The generally low swimming speeds and small range provided regressions between swimming velocity and geometric angles (PAA, BAA) that described at most 38% of the variation in the data. For the relationship between swim speed and PAA, *S. acanthias* ($r = 0.62$; $P < 0.05$) and *C. plumbeus* ($r = 0.25$; $P < 0.05$) were

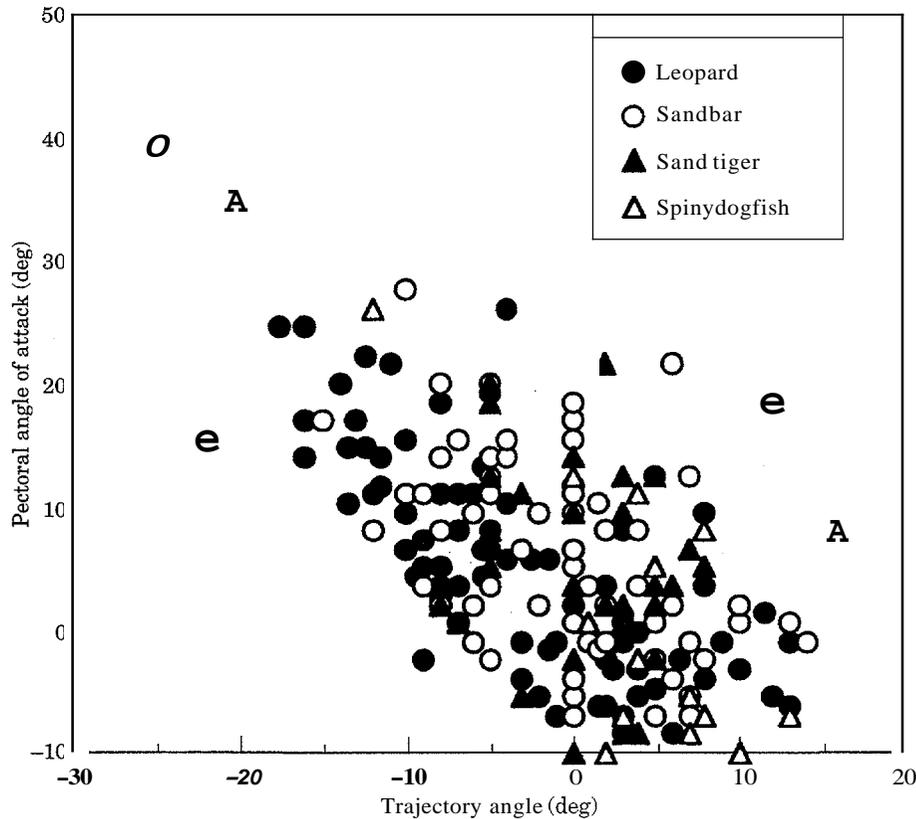


FIG. 2. Pectoral fin angle of attack (PAA) plotted as a function of trajectory angle (TA) for all sharks over the full range of swimming speeds. Individuals were swimming with a descending ($TA < 0$), level ($TA = 0$), or ascending ($TA > 0$) trajectory. Below $TA = 0$, PAA increased with decreasing TA.

significantly correlated; whereas, only *O. taurus* showed a significant correlation ($r = 0.44$; $P < 0.05$) between speed and **BAA**.

There was a significant difference (4×3 factorial ANOVA; $P < 0.001$) between trajectories and a significant interaction ($P < 0.002$) between species and trajectories for the four species during ascending, level, and descending. Mean ascending PAA (Fig. 4) for *T. semifasciata* and *S. acanthias* was lower than for *C. plumbeus* and *O. taurus*. However, *S. acanthias* had the highest mean descending PAA of $27.0 \pm 3.0^\circ$. PAA during level swimming was $11 \pm 1.7^\circ$, $10.1 \pm 1.3^\circ$, $9.3 \pm 1.3^\circ$, and $15.0 \pm 0.0^\circ$ for *T. semifasciata*, *C. plumbeus*, *O. taurus*, and *S. acanthias*, respectively.

ANOVA for **BAA** showed significant effects ($P < 0.001$) for species, trajectory, and their interaction. During descent, **BAA** ranged from $9.5 \pm 0.3^\circ$ for *O. taurus* to $16.0 \pm 0.2^\circ$ for *C. plumbeus* (Fig. 5). However during level swimming by *C. plumbeus* and level and ascending swimming by *O. taurus*, body orientation was maintained parallel to the horizontal axis with **BAA** not significantly different ($P < 0.05$; t-test) from 0° . *T. semifasciata* and *S. acanthias* were not trimmed and swam with mean **BAA** of at least 2.8° .

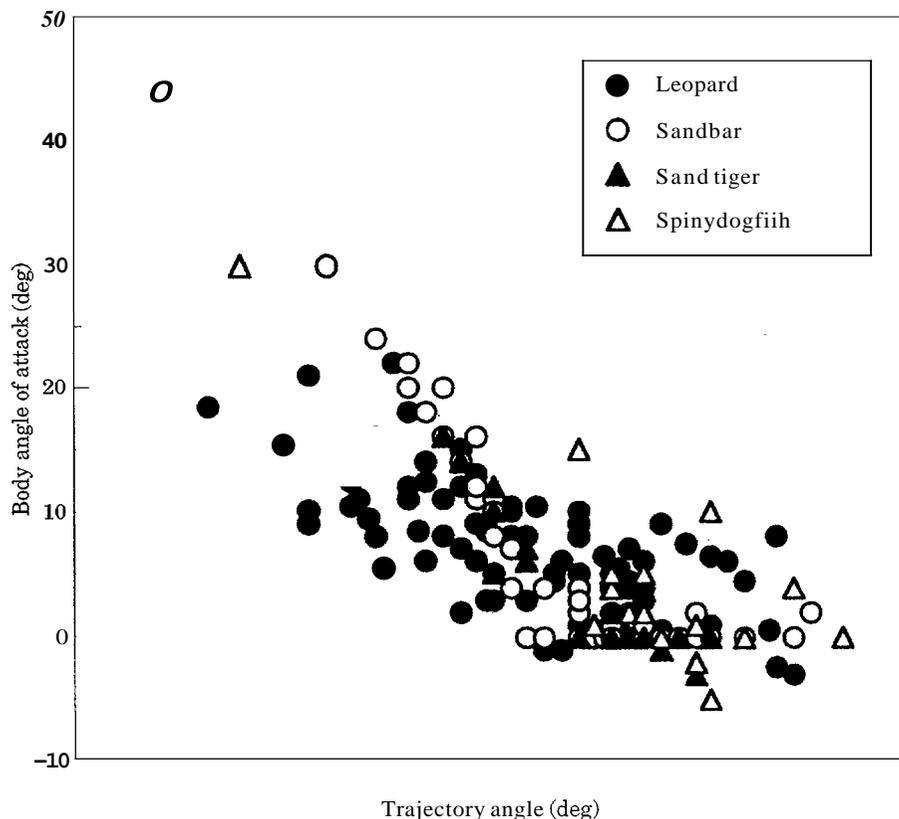


FIG. 3. Body angle of attack (BAA) plotted as a function of trajectory angle (TA) for all sharks over the full range of swimming speeds. Individuals were swimming with a descending (TA<0), level (TA=0), or ascending (TA>0) trajectory. Below TA=0, BAA increased with decreasing TA.

LIFT AND PITCHING MOMENT

The head and pectoral fin configuration of *T. semifasciata* was reminiscent of a swept delta wing design (Hurt, 1965; Hoerner and Borst, 1975). The head was pointed with a relatively flat underside. The pectoral fins had triangular planforms with pointed tips. The proximal fin margin extended from 17.6–29.5% of body length. A_p was 0.0056 m². Total fin span including the intervening body segment area was 0.16 m giving an aspect ratio of 4.55. Because of the triangular design of each fin the taper ratio was zero. Mean fin sweep was $33.7^\circ \pm 2.5^\circ$. Centre of gravity was located at 40% of body length, which was near the 36% of body length for the center of gravity of a dogfish, *S. canicula* (Magnan, 1929).

The computed C_L was 0.688 using the morphology of the pectoral fins and assuming a PAA of 11° for level swimming by *T. semifasciata*. This computed value is consistent with experimental data for C_L for swept, delta wing designs (Hurt, 1965; Hoerner and Borst, 1975). Based on a specific velocity of 1.2 body lengths s⁻¹ (Ferry & Lauder, 1996), the lift was calculated as 590.5 mN with swimming velocity of 0.55 m s⁻¹. Based on equation 4, M_{fn} was 0.041 N m (Fig. 6).

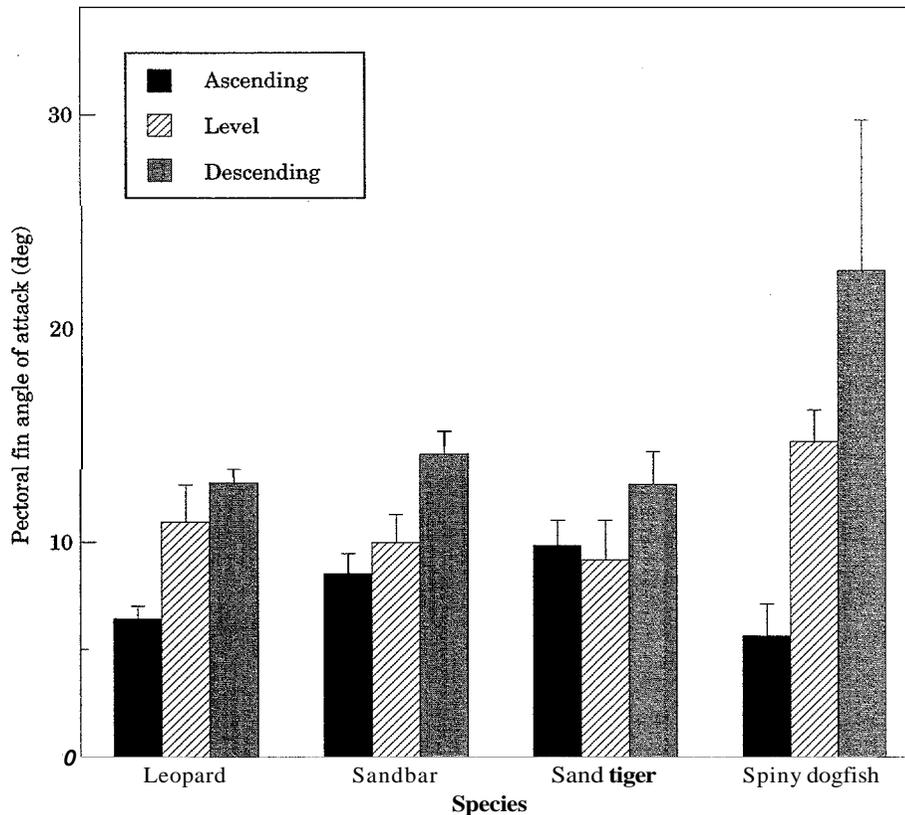


FIG. 4. Mean (+S.E.) pectoral fin angles of attack (PAA) for level, ascending, and descending swimming.

DISCUSSION

Although there has been much recent interest in the function of the heterocercal tail of sharks, the contribution of the pectoral fins to trim has been largely taken for granted. A dense animal, like a shark, can prevent itself from sinking by using its pectoral fins as hydrofoils to develop hydrodynamic lift (Aleyev, 1977; Alexander, 1990).

Breder (1926) reported that by pinning the pectorals down fish with heterocercal tails would always head downward and be unable to rise. Amputation of the pectoral fins of living *Mustela canis* produced a negative pitching moment at the head (Harris, 1936). To compensate, the shark swam with its body 45° to the horizontal. Experiments with a rigid shark model in a wind tunnel showed that it was unstable about the horizontal transverse axis unless the pectoral fins were tilted -7° to the flow (Harris, 1936). The negative angle was a consequence of the use of a rigid model which produced no lift by the tail. The normal inclination of the pectoral fins was observed as 8–10° to the horizontal to compensate for the actions of the tail (Harris, 1936, 1937).

Variation in the design of the pectoral fins and their function in lift production is associated with the ecology of sharks. Blue sharks *Prionace glauca* (L.) and oceanic whitetips *Carcharhinus longimanus* (Poey) which drift with ocean

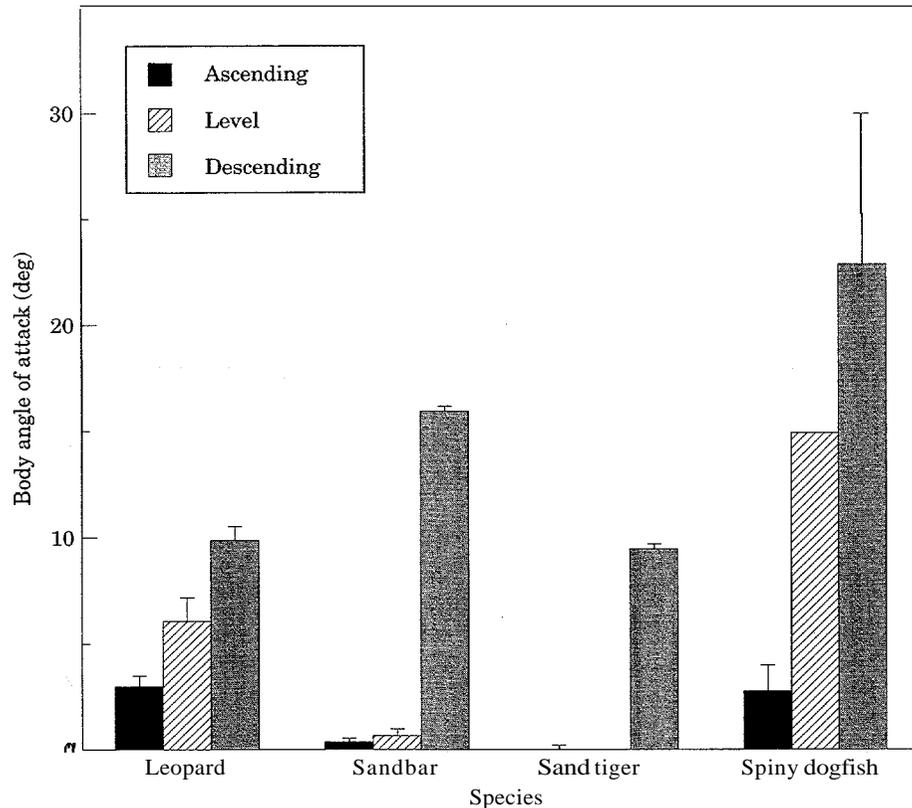


FIG. 5. Mean (+S.E.) body angles of attack (BAA) for level, ascending, and descending swimming.

currents have elongate pectoral fins which are considered to maximize hydrodynamic lift at low cruising speeds (Moss, 1984). In sphyrnid sharks, some of the hydrodynamic role of the pectoral fins is taken over by the cephalofoil (Nakaya, 1995). Species with the broadest cephalofoils e.g. *Sphyrna lewini* (Griffith & Smith), have proportionally the smallest pectorals; whereas smaller cephalofoil species *Sphyrna tiburo* (L.) possess the largest fins (Moss, 1984). The mesopelagic shark, *Isistius brasilensis* (Quoy & Gaimard) is nearly neutrally buoyant and has little need for hydrodynamic lift, which is associated with small paddlelike pectoral fins (Marshall, 1971).

Similarly, the present study showed that the pectoral fins of sharks were oriented at a positive angle of attack to the flow and therefore could induce an upward pitching moment at the anterior of the fish. This supports the classical model of the role of the heterocercal tail in organismic stability (Harris, 1936; Affleck, 1950; Alexander, 1965; Simons, 1970; Ferry & Lauder, 1996; Wilga & Lauder, 1998) while refuting Thomson's model (Thomson, 1976; Thomson & Simanek, 1977). The anterior pitching moment would trim the shark by balancing the upward pitching moment posterior of the center of gravity that is developed by the tail.

The magnitude of the lift and pitching moment computed for the pectoral fins could be assessed by comparison with the pitching moment from the tail (M_{tail}).

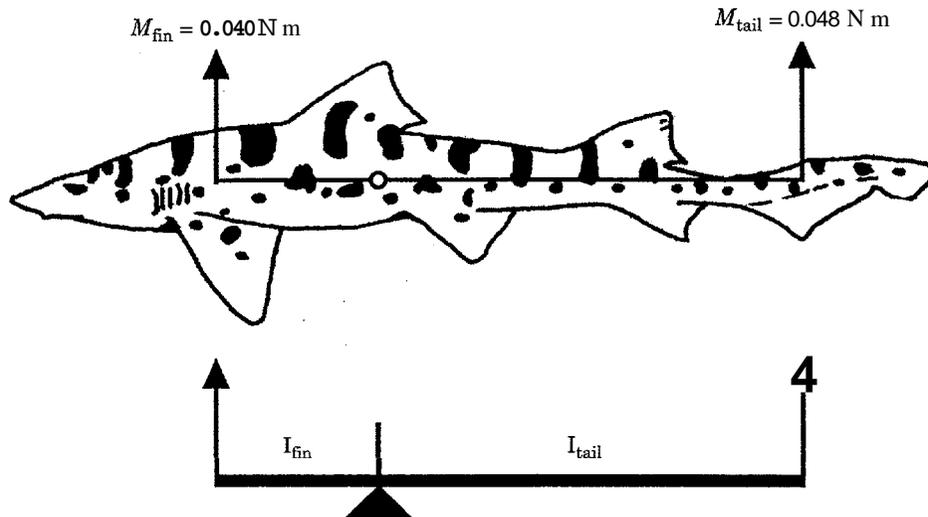


FIG. 6. Diagram of pitching moments for the pectoral fins (M_{fin}) and heterocercal tail (M_{tail}) for a 45.4 cm leopard shark *Triakis semifasciata*. The circle on the body of the shark (upper diagram) represents the position of the centre of gravity. Arrows indicate direction and magnitude of the pitching moments. M_{tail} was computed using the lift reported by Ferry & Lauder (1996) and scaled to account for the larger size of the shark in this study. The lower diagram shows the moment arms of the pectoral fins (l_{fin}) and tail (l_{tail}) with respect to the centre of gravity which is indicated by the fulcrum (triangle).

Ferry & Lauder (1996) were the only investigators to calculate the upward force from the heterocercal tail of a live, swimming shark. Using video footage of the lateral and posterior views of the tail of *T. semifasciata* in a flume, they were able to partition the tail into discrete segments and detail the tail's three-dimensional kinematics. A force vector was calculated for each segment. The total of all vectors was averaged in each dimension over a complete tailbeat. An upward vector of 144.06 mN was computed.

The upward force vector was geometrically scaled proportionally to 187 mN to account for the 30% larger size of the specimen of *T. semifasciata* examined in this study compared to the specimen studied by Ferry & Lauder (1996). With a level arm for the tail (center of gravity to mid-point between tips of epichordal and hypochordal lobes) equal to 0.26 m, the estimated M_{tail} was 0.049 N m (Fig. 6). M_{tail} is only c. 20% greater than M_{fin} . The M_{fin} , however, may be an overestimate, because the lift contribution of the intervening body area between the pectoral fins would be less due to its smaller angle of attack ($\text{BAA} = 6^\circ$ v. $\text{PAA} = 11^\circ$). However, interaction of the flow from the body and pectoral fins can induce an added lift. Despite any overestimate, the near congruence of M_{tail} and M_{fin} and additional lift generated by the ventral aspect of the head and camber of the fins (Alexander, 1983) should effectively balance the shark.

The most notable difference between swimming patterns of the various species examined was the orientation of the body. Whereas *C. plumbeus* and *O. taurus* maintained trim while swimming level and ascending, *T. semifasciata* and *S. acanthias* exhibited a posture with a positive tilt (elevated anterior). Similar observations were made for *T. semifasciata* and the sturgeon *Acipenser*

transmontanus Richardson swimming in a flow tank (Wilga & Lauder, 1998, 1999), although the sturgeon was not using its pectoral fins to generate lift (Wilga & Lauder, 1999). A tilted body will generate lift and counter the tendency to sink if there is insufficient lift generated by the pectoral and caudal fins. Alexander (1965) computed the critical swimming speed of a dogfish to maintain trim as $0.5 L s^{-1}$. The lower swimming speeds observed for *T. semifasciata* and *S. acanthias* may have produced less lift than required. The body would be used as a lifting surface (Aleyev, 1977) to compensate for the reduced lift by the fins. Lift on the body of *M. canis* increased directly with increasing angle of attack when subjected to a flow (Harris, 1936). *T. semifasciata* is adapted for unsteady swimming and periodic resting and foraging on the bottom (Castro, 1983; Graham *et al.*, 1990). As a benthic shark, it would have a high density and negative buoyancy (Aleyev, 1977). Similarly, *S. acanthias*, which feeds at or near the ocean bottom, can have a body composition up to 4% denser than sea water (Aleyev, 1977; Stevens, 1987).

The level swimming orientation of *C. plumbeus* and *O. taurus* indicated that no lift produced by the body was required to maintain trim. Trim could be maintained at low swimming speeds for *C. plumbeus* and *O. taurus* using the lift generated by the pectoral and caudal fins. In addition, trim could be maintained if their bodies were of a density close to that of sea water. *O. taurus* was observed to swallow air at the surface and hold it in its stomach to achieve neutral buoyancy (Castro, 1983). Adult nektonic sharks have neutral or near buoyancy due to the accumulation of low density oil in the liver (Aleyev, 1977; Moss, 1984; Alexander, 1990).

A shark in trim will experience a reduced drag by presenting a small frontal area to the flow. However, Thomson (1976, 1990) argued that a counterbalancing lift generated by the pectoral fins would incur increased drag and thus limit performance and reduce efficiency. The lift generated by the fins will increase induced drag which can be the major drag component for negatively buoyant animals (Magnuson, 1970). Induced drag is incurred from the production of lift as fluid is deflected around a finite wing (Webb, 1975; Vogel, 1994). The deflected fluid produces a pressure difference between the two surfaces of the wing. The pressure difference generates spanwise cross flows around the wing tips resulting in the formation of spiraling vortical flow. The flow is shed from the wing tip as longitudinal tip vortices. The energy dissipated by the vortices represents the induced drag.

Because sharks swim with their fins erect (Budker, 1971) at an angle of attack, induced drag will occur. However, Harris (1937) believed that the small angle of attack of the fins would produce little drag. Furthermore, the tapered, sweptback, delta wing configuration of the pectoral fins reduces tip vorticity and induced drag (Webb, 1975; Rayner, 1985; van Dam, 1987; Daniel *et al.*, 1992). Minimal induced drag is fostered by a swept wing planform with a root chord greater than the chord at the tips giving a triangular shape (Kuchermann, 1953; Ashenberg & Weihs, 1984).

Other advantages may be realized from the swept, delta wing design of the pectoral fins which would be beneficial and offset any penalty from increased drag. A delta wing with low aspect ratio is resistant to stall (i.e. loss of lift) at high angles of attack (Hurt, 1965; Stevenson, 1975). This would be particularly

important in instances where angle of attack is high such as when descending and maneuvering. Indeed, *Squalus* is highly maneuverable and capable of climbing rapidly with a sharply inclined body (Simons, 1970). Swept, tapered wings also enhance stability by resisting yaw and roll (Hurt, 1965; Webb, 1975). Such a capability is necessary because yawing occurs due to propulsive undulations of the body (Webb & Keyes, 1982) and roll results from twisting of the tail (Ferry & Lauder, 1996).

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