Buoyancy regulation in sharks:

The importance of the fins and body

Written by

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Abstract

When discussing the buoyancy of sharks, it is important to understand the hydrodynamics that are of influence. In this paper I shall discuss this hydrodynamic component, paying special interest to the role of the heterocercal tail, the pectoral fins and the body as a lifting surface. I conclude that the classical model of the heterocercal tail exerting a force directed above the centre of mass is partly correct. Indeed, the force exerted by the caudal fin causes thrust and lift and a subsequent torque. However, the view of the pectoral fins as balancing this torque appears to be incorrect for certain shark species, most notably the leopard shark. It appears the body itself counters this torque by being tilted at a positive angle of attack during steady horizontal swimming. The pectoral fins are used to initiate pitching movements during rising and sinking behaviour. I support the adapted classical model of force balance Wilga and Lauder (2000) proposed, based on these findings. However, although this model is likely to prove useful when discussing leopard sharks or similar species, it should not be carelessly applied to dissimilar species, such as pelagic sharks. As these sharks have not been observed to swim with their bodies tilted at a positive angle of attack and due to the shape of the ventral body, one should not assume these sharks use their bodies in the same hydrodynamic way as do leopard sharks. The use of the pectoral fins as lifting surfaces also can not be ruled out, until proper research is conducted. However, I do argue that Wilga and Lauder's (2000) model should be used as a new standard, replacing the classical model, and should continue to evolve as data on other shark species become available. Research in this field should expand to include shark species other than leopard sharks or similar species, in order to provide the necessary data to improve this model and compose an adapted model, which can be applied to a wider variety of species.

Introduction

In effective aquatic locomotion, whether it concerns steady horizontal swimming, manoeuvring or rising and sinking in the water column, the buoyancy of the animal plays an important role (Aleyev 1977). Fish have many tissues, such as muscles, that are denser than the water, which surrounds them (Alexander and Goldspink 1977). As a result, the fish would continuously have a tendency to sink in the water column, complicating normal swimming behaviour. To prevent this several means of reducing density and thus increasing buoyancy have been described. The most well known example of this adaptation to aquatic life is the swim bladder possessed by many fish species (Harden Jones 1951; Robertson et al. 2008). This organ is filled with gas, which is less dense than water, thereby reducing the overall density of a fish. It also allows a fish some control over its buoyancy by reducing or increasing the amount of gas the swim bladder contains (Robertson et al. 2008). There are two ways the amount of gas present in the swim bladder can be regulated (Robertson et al. 2008). In physostomous fish, gas can be passed through a duct connecting the swim bladder with the oesophagus (Aleyev 1977; Robertson et al. 2008). Physoclistic fish regulate the gas level in the swim bladder by the slower method of gas exchange (Aleyev 1977).

Elasmobranchii, which includes sharks and rays, do not have this swim bladder and are thus unable to control their buoyancy in this manner (Alexander 1965; Scacco et al. 2010). These fish must utilize other methods to counter the negative buoyancy of most of their bodies. Some sharks have been observed to swallow air at the surface, increasing their buoyancy (Fish and Shannahan 2000). Many sharks have livers that contain relatively high percentages of fat, which is less dense than water (Aleyev 1977; Wetherbee and Nichols 2000). However, most sharks ultimately are negatively buoyant and thus have a tendency to sink in the water column (Lingham-Soliar 2005a).

Most fish, especially teleosts, have a homocercal caudal tail, meaning both lobes are of the same size (Ferry and Lauder 1996; Biewener 2003). However, sharks possess a heterocercal tail, which means it is asymmetrical. The dorsal lobe is longer than the ventral lobe, classifying the tail as epicercal (Videler 1993; Fish and Shannahan 2000). It has long been thought this asymmetry might result in the thrust of the tail having a vertical lift component as well (Biewener 2003). The pectoral fins of sharks have been thought to generate lift as well, possibly to counter the torque produced by the heterocercal tail (Aleyev 1977). Sharks have also been observed to swim with their bodies at a positive angle of attack, likely generating lift as well (Aleyev 1977; Wilga and Lauder 2001).

In this paper I shall review the current knowledge of the hydrodynamic component of buoyancy in sharks, focused on the role of the caudal and pectoral fins. First, I will briefly explain the buoyancy component of the liver and discuss other methods of reduction of the overall density of sharks. Then I will discuss the contribution of the caudal and pectoral fins to the buoyancy of sharks and discuss other possible hydrodynamic functions of the pectoral fins. Finally, I will discuss the role of the body and its angle of attack in generating lift during locomotion.

Density reduction

Lipids

All fish contain a certain amount of body fat (Aleyev 1977). However, some fish, including many sharks, have a larger amount of lipids in their bodies. In sharks, the majority of these lipids are often stored in the liver (Aleyev 1977; Wetherbee and Nichols 2000). The lipids in a shark's liver mainly consist of squalene, DAGE (diacyl glyceryl ether) and TAG (triacylglycerol) (Phleger et al. 1997; Lingham-Soliar 2005a).

Seawater has a density of about 1.026 g ml^{-1}, whereas squalene, DAGE and TAG are much less dense; 0.86 g ml^{-1} for squalene, 0.89 g ml^{-1} for DAGE and 0.92 g ml^{-1} for TAG (Alexander and Goldspink 1977; Wetherbee and Nichols 2000).

Since these lipids are less dense than water, this increased amount of lipids results in a lower overall density and thus aids the fish in achieving neutral or near neutral buoyancy (Aleyev 1977).

The relative size of the liver and its lipid composition vary greatly between species (Aleyev 1977; Wetherbee and Nichols 2000). Some species possess livers that contribute less than 5% to its total weight, while other species contain livers that are 25% of the shark's total body weight (Aleyev 1977; Scacco et al. 2010). Size and thus age, to some extent, appear to be correlated with relative liver size as well; larger sharks have relatively larger livers or a larger percentage of lipids in these livers (Phleger et al. 1997; Scacco et al. 2010). This might be due to a different surface to volume ratio, which would have an effect on lift generated by the body. One could also hypothesize that benthic sharks would possess relatively small livers. These sharks have the possibility of resting on the sea floor and having a large liver could be less vital for these species. Pelagic sharks on the other hand do not have this option and thus might possess relatively large livers (Aleyev 1977; Withers et al. 1994).

The composition of the lipids in the liver differs between and within species (Wetherbee and Nichols 2000). It has been hypothesized some of these differences may be attributed to their role in the biosynthesis of hormones, synthesis of these lipids or the usefulness of a lipid in fine tuning of the buoyancy (Wetherbee and Nichols 2000). It is possible certain lipids, most likely DAGE and TAG, are used as a substitute for a swim bladder during vertical migration (Phleger et al. 1997). These lipids are better suited for buoyancy regulation than squalene (Wetherbee and Nichols 2000). It has also been theorized that a female shark carrying an egg, which contains a certain amount of lipids, may have an altered lipid composition in the liver or a reduction in liver lipids, due to the buoyancy provided by this egg (Wetherbee and Nichols 2000). However, evidence to support this hypothesis is scarce.

It has been reported (Wetherbee and Nichols 2000) that shallow-water sharks possess a different lipid composition compared to deep-sea sharks. Whereas the livers of deep-sea sharks contain mostly squalene and DAGE, the livers of shallow-water sharks contain relatively large amounts of TAG and very small amounts of squalene.

Urea and TMAO

Besides the positive buoyancy provided by the lipids in the liver, other compounds present in a shark's body may contribute as well. Withers et al. (1994) calculated the contribution to buoyancy of urea and TMAO (trymethylamine oxide). These substances are less dense than water and could thus play a role in achieving neutral buoyancy (Withers et al. 1994). When taking all urea and TMAO in a shark's body into account, it was calculated by Withers et al. (1994) that the total contributions of urea and TMAO to the buoyancy exceed that of the lipids in the liver. Although urea and TMAO perform other functions as balancing osmolytes and counteractive solutes (TMAO only), their positive contribution to a shark's buoyancy may be worth considering.

Role of fins

Since most sharks have an overall density higher than the surrounding water and are thus negatively buoyant (Biewener 2003; Lingham-Soliar 2005a), other methods of generating lift have to be utilized by these fish in order to prevent sinking in the water column. Such methods can make use of a shark's fins and can be of a hydrodynamic nature (Alexander and Goldspink 1977; Aleyev 1977; Videler 1993).

A shark possesses several paired and unpaired fins; most notably the caudal fin, dorsal fin, and pectoral fins (Videler 1993).

Not all of these fins play a role in the body trim of sharks. The dorsal fin of great white sharks (*Carcharodon carcharias*) for instance, functions as a stabilizer counteracting yaw and roll, but does not provide significant lift (Harris 1936; Lingham-Soliar 2005b). Anal fins may have a similar function (Harris 1938). Pelvic fins in sharks appear to be of insignificant importance in both counteracting rolling movements and producing lift, as found by Harris (1938) after amputating the pelvic fins of a dogfish (*Mustelus canis*). Although a model showed that the pelvic fins are capable of generating limited lift, the amount is very small in comparison to the lift possibly generated by the much larger, anterior pectoral fins (Harris 1936, 1937)

Of a shark's fins, the caudal fin and the paired pectoral fins are thought to be the most important fins in possibly providing lift (Alexander and Goldspink 1977; Aleyev 1977; Fish and Shannahan 2000). Therefore, these are the fins of which the hydrodynamic function and contribution to overall lift will be discussed in greater detail.

Caudal fin

As previously mentioned, sharks possess a heterocercal tail of which the dorsal lobe is larger than the ventral lobe (Fish and Shannahan 2000). The degree of asymmetry of the caudal fin varies between species. In general, pelagic species, such as the great white shark, have a near symmetrical caudal fin, whereas more asymmetrical caudal fins can be found in benthic sharks, such as the leopard shark (*Triakis semifasciata)*. However, there are exceptions, such as the thresher shark (*Alopias vulpinus*), which uses its extremely epicercal tail to feed on fish, driving them into a compact ball (Videler 1993)

Two models exist explaining the function of this asymmetrical caudal fin. The classical model states that the asymmetrical shape of the caudal fin results in a thrust comprised of horizontal and vertical component, because the stiffer dorsal lobe should lead the ventral lobe through a tail beat (Alexander 1965; Simons 1970; Ferry and Lauder 1996; Lauder 2000; Wilga and Lauder 2002; Wilga and Lauder 2004). The horizontal component results in forward motion of the fish, while the caudal fin also produced a vertical component in the form of lift (Alexander 1965; Fish and Shannahan 2000; Biewener 2003). The forces exerted by the tail are shown in fig. 1. The resultant lift force is directed above the centre of mass of the shark and will thus cause a change in pitch; the anterior part of the shark will pitch ventrally (Simons 1970; Wilga and Lauder 1999; Lauder 2000). The classical model suggests lift forces at the anterior end, presumably produced by the head and the pectoral fins, counter this rotating of the body (Aleyev 1977; Fish and Shannahan 2000; Wilga and Lauder 2002).
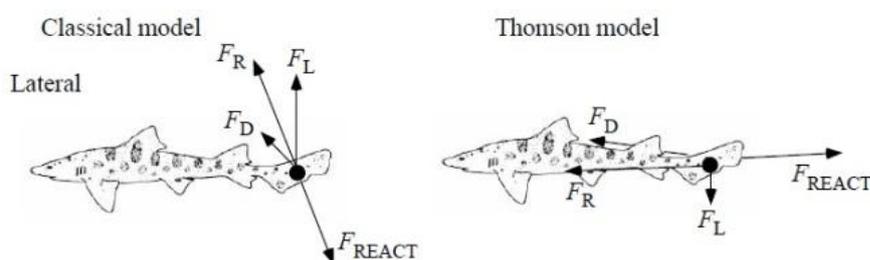

Fig. 1. A comparison of the classical model (left) and Thomson's model (right). The classical model states that the heterocercal tail produces both thrust (F_D) and lift (F_L), resulting in a combined force (F_R) directed above the centre of mass. Thomson's model states F_R acts through the centre of mass instead. Taken from Ferry and Lauder (1996).

The second model was created by Thomson (Ferry and Lauder 1996; Lauder 2000). He observed that it was in fact the ventral lobe that led the dorsal lobe through a tail beat, not vice versa (Lauder 2000; Wilga and Lauder 2002). In this model, the combined force produced by the asymmetrical caudal fin is not directed above the centre of mass, but through it (see fig. 1). According to Thomson's model, the force exerted by the tail does not cause torque about the centre of mass of a shark. Therefore, it is not necessary for lift to be produced at the anterior part of the body in order to counter torque produced at the posterior part (Ferry and Lauder 1996; Fish and Shannahan 2000).

Evidence for Thomson's model is scarce, whereas support for the classical model has been found on several occasions. Alexander (1965) and Simons (1970) performed experiments using an amputated shark's tail. Although tails and not entire, living sharks were used, both studies concluded heterocercal caudal fins generate a vertical component in the form of lift (Alexander 1965; Simons 1970). Ferry and Lauder (1996) performed three-dimensional kinematic analysis of the heterocercal tail of swimming leopard sharks and found that water was displaced posteroventrally. This means the caudal fin produced a resultant force that was directed both anterior and dorsally, providing thrust and lift. This is strong evidence in favour of the classical model. Moreover, Wilga and Lauder (2002) studied wake dynamics of leopard sharks and bamboo sharks using DPIV (Digital partical image velocimetry). They found that the heterocercal tail shed a "vortex ring surrounding a high-velocity jet of water" (Wilga and Lauder 2002; Wilga and Lauder 2004). The two models predict different angles of this vortex ring jet. According to Thomson's model, the angle should be equal and opposite to the body angle, since the force of the tail is directed through the centre of mass (Wilga and Lauder 2002), whereas the classical model predicts an angle well below the body angle. Wilga and Lauder (2002) found that the jet angles were about 30° lower than expected based on Thomson's model (see fig. 2). Since this value can be expected based on the classical model, this study provides further evidence in support of the classical view.
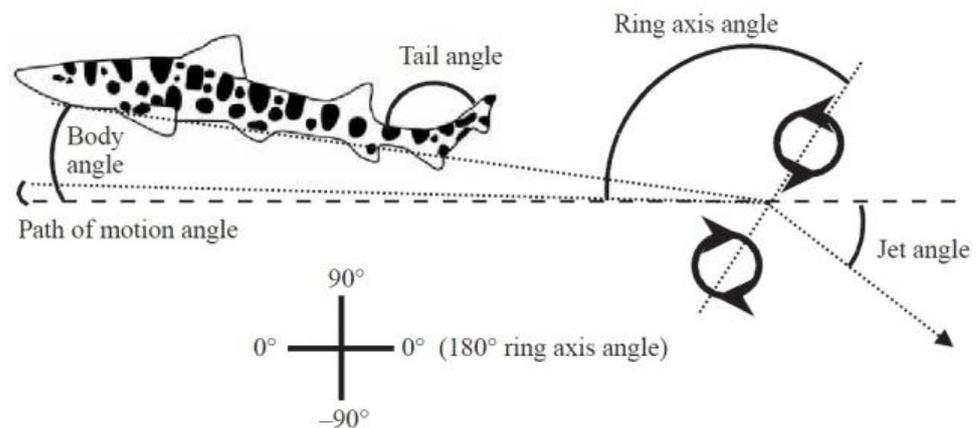

Fig. 2. A schematic depiction of wake dynamics during steady horizontal swimming. The classical model states the vortex jet angle should be below that of the body, whereas Thomson's model states it should be equal and opposite. Taken from Wilga and Lauder (2002).

It is worth noting, however, that studies of the heterocercal tail of white sturgeon (*Acipenser transmontanus*) showed that the tail of sturgeons produces a force directed near the centre of mass, which is in contrast to the classical model (Wilga and Lauder 19 99). It has been argued that this difference between sharks and sturgeons may be ascribed to the higher flexibility of a sturgeon's tail and a resulting difference in kinematics of both heterocercal tails (Wilga and Lauder 1999, 2002).

Pectoral fins

As previously stated, the classical model suggests the anterior lift necessary to balance the lift produced by the heterocercal tail, resulting in torque about the centre of mass, can be generated by the body or the pectoral fins (Simons 1970; Aleyev 1977). It has long been thought that the pectoral fins act as hydrofoils and are the dominant factor in countering this torque (Alexander and Goldspink 1977). Harris (1936) created a rigid model of a dogfish and tested it in a wind tunnel, using an air speed resulting in the same Reynolds number as a water speed likely to be similar to the cruising speed of dogfish. He found the pectoral fins to be capable of generating significant lift. In subsequent experiments Harris (1936) amputated the pectoral fins of dogfish and found that the fish tilted its head upward, suggesting it attempted to compensate for a loss of lift due to loss of the pectoral fins. However, since it is likely this procedure of amputation of the pectoral fins can cause great stress to the animal, these results should be viewed with caution.

Fish and Shannahan (2000) discussed the role of the pectoral fins in the body trim of sharks. They recorded images of several species of shark during steady swimming and determined the orientation of the body and the pectoral fins. They found the pectoral fin angle of attack to be positive for all sequences. This implies the pectoral fins produce an upward force at the anterior part of a shark (Fish and Shannahan 2000).

Using data from Ferry and Lauder (1996) on the lift produced by the heterocercal tail, Fish and Shannahan (2000) were able to compare the magnitude of the upward force and pitching moment generated by the pectoral fins to that produced by the caudal fin (see fig. 3). In assessing these magnitudes, one must include the moment arms. These are not equal for the pectoral fins and the caudal fin, since the centre of mass about which the pitching moment is centred, is not located at equal distance from the pectoral fins and the caudal fin, but is located nearer the pectoral fins, as can be learnt from fig. 3 (Fish and Shannahan 2000). The upward force and pitching moment of the pectoral fins was estimated to be 20% less than that of the heterocercal tail (Fish and Shannahan 2000). Although the force calculated was exerted by an area which included the body between the pectoral fins as well, Fish and Shannahan (2000) believed this overestimate of the force generated by the pectoral fins should be small. The remaining 20% needed to balance the force generated by the shark's tail is likely to be produced by the head of the shark (Fish and Shannahan 2000). The role of the body and its angle relative to the flow in generating lift will be discussed in greater detail further in this paper.
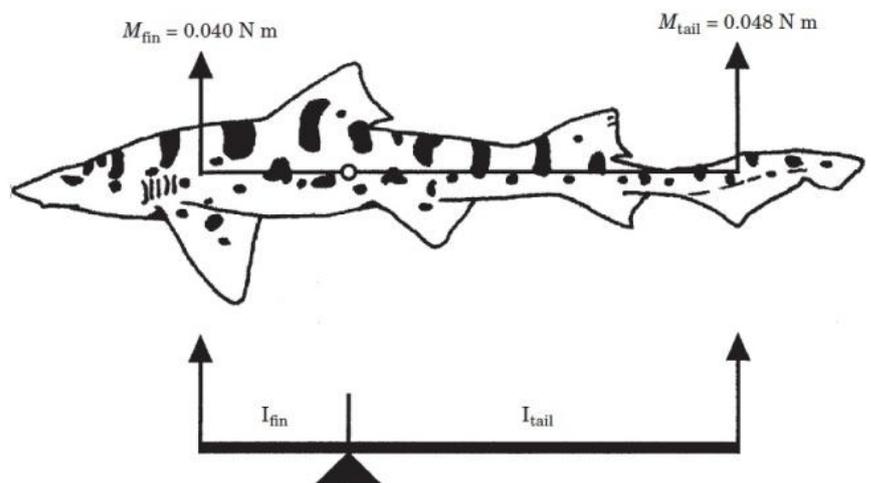

Fig. 3. Diagram showing pitching moments for the tail (M_{tail}) and pectoral fins (M_{fin}) of a leopard shark. Moment arms (l_{tail} and l_{fin}) are shown in the lower half. The circle (above) and triangle (below) represent the centre of mass. Arrows represent magnitude of the moments. Taken from Fish and Shanahan (2000).

In contrast to these studies and the prevailing view of lift production by the pectoral fins is a study performed by Wilga and Lauder (2000). Using video recordings and DPIV, they studied the three-dimensional kinematics and wake structure of the pectoral fins of leopard sharks. They found that, during steady horizontal swimming, the pectoral fins are oriented at a slightly negative (5°) angle of attack, suggesting either negligible lift by the pectoral fins or even a slight downward force (see fig. 4a). Moreover, DPIV analysis showed no signs of lift generation by the pectoral fins either (Wilga and Lauder 2000).

However, another possible hydrodynamic function of the pectoral fins has been suggested by Wilga and Lauder (2000). They observed that the angle of the pectoral fins was altered when initiating rising or sinking behaviour in the water column. They suggest the pectoral fins are tilted at such an angle as to produce either negative lift while sinking or positive lift while rising (fig. 4b and c). The pectoral fins also create a pitching moment, pitching the anterior part of the shark's body up or down while rising or sinking behaviour respectively (Wilga and Lauder 2000). The resulting change in body angle presumably assists in generating either positive or negative lift (Wilga and Lauder 2000). This subject will be discussed in the following section.

In an earlier study, Wilga and Lauder (1999) studied the role of the pectoral fins in white sturgeon. Results were similar to those found in their study of the pectoral fins of leopard sharks. The sturgeon held its pectoral fins at a negative angle of attack and changed this angle when initiating rising or sinking behaviour. Wilga and Lauder (1999) concluded that the pectoral fins of sturgeon generate negligible lift during steady horizontal swimming and produce negative or positive lift during vertical manoeuvring. In addition, no significant lift during horizontal swimming was found for bamboo sharks (Wilga and Lauder 2001).

As these findings are in conflict with the classical model, an explanation for many observations of positive angle of attack of pectoral fins was provided (Wilga and Lauder 1999, 2000). The pectoral fins of a shark do not extend horizontally from the body like the wings of an airplane. In reality, the fins extend ventrally at an angle, as can be seen in fig. 5 (Wilga and Lauder 2000). Observations of the pectoral fin angle of attack were often made while viewing the lateral side of the animal. Due to the angle, called a negative dihedral, the view is misleading in that this lateral view of the negative dihedral gives the impression that the pectoral fins are oriented at a positive angle of attack, while the angle is in fact negative.

However, the degree to which the dihedral is negatively angled differs between species. For bamboo sharks, for instance, Wilga and Lauder (2001) found a much more horizontal dihedral, increasing stability. This less negatively oriented dihedral would limit its misleading effect. However, Wilga and Lauder (2000) rightfully suggest observations should be made using three-dimensional images rather than two-dimensional ones.
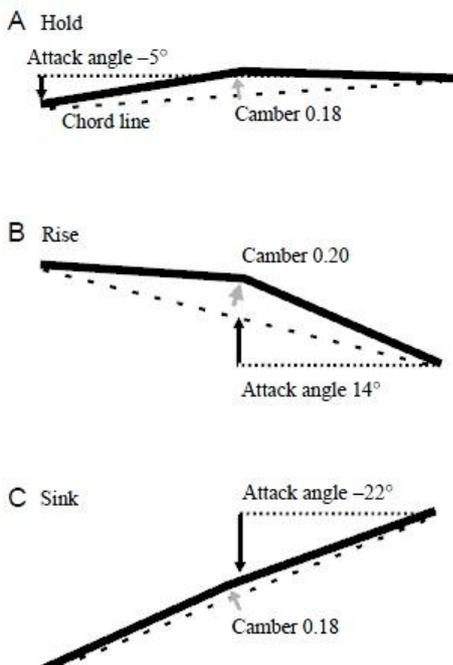

Fig. 4. Schematic representation of a shark's pectoral fins during steady horizontal swimming (A), rising (B) and sinking (C). Pectoral fin chord line, attack angle and camber are depicted. Taken from Wilga and Lauder (2000).

The aforementioned orientation of the pectoral fins as a negative dihedral changes during rising or sinking behaviour, as can be seen from fig. 5 a, b and c. Wilga and Lauder (2000) suggest this may be a way to change stability during vertical manoeuvring, since a more neutral dihedral angle provides more stability, whereas a more negative angle promotes manoeuvrability.

Another function of this negative dihedral may exist. The wings of an airplane are positioned to provide stability during a roll, which occurs when turning (Wilga and Lauder 2000). The pectoral fins of sharks, however, actually function in the opposite way, enlarging the roll forces and thereby allowing for sharper turns (see fig. 5 d and e). This suggests the pectoral fins may play a role during not only vertical, but horizontal manoeuvring as well (Wilga and Lauder 1999, 2000). However, one must take into consideration that an airplane's density is many times greater than the medium, which surrounds it whereas a shark's density is near neutral, reducing the destabilizing properties of the pectoral fins. As such, it is likely this possible function of the pectoral fins is of little importance.

A final hydrodynamic function of pectoral fins in sharks concerns station-holding in the water column. Wilga and Lauder (2001) used three-dimensional kinematics and DPIV to study the function of pectoral fins of bamboo sharks during station-holding. They found that the fish oriented its pectoral fins at such an angle as to produce negative lift in order to hold position on or above the substrate. Similar orientations of pectoral fins have been found in other fish, for example Atlantic salmon parr (*Salmo salar*) (Arnold et al. 1991) and cod and lasher (*Gadus morhua* and *Myoxocephalus scorpius*) (Webb 1989).
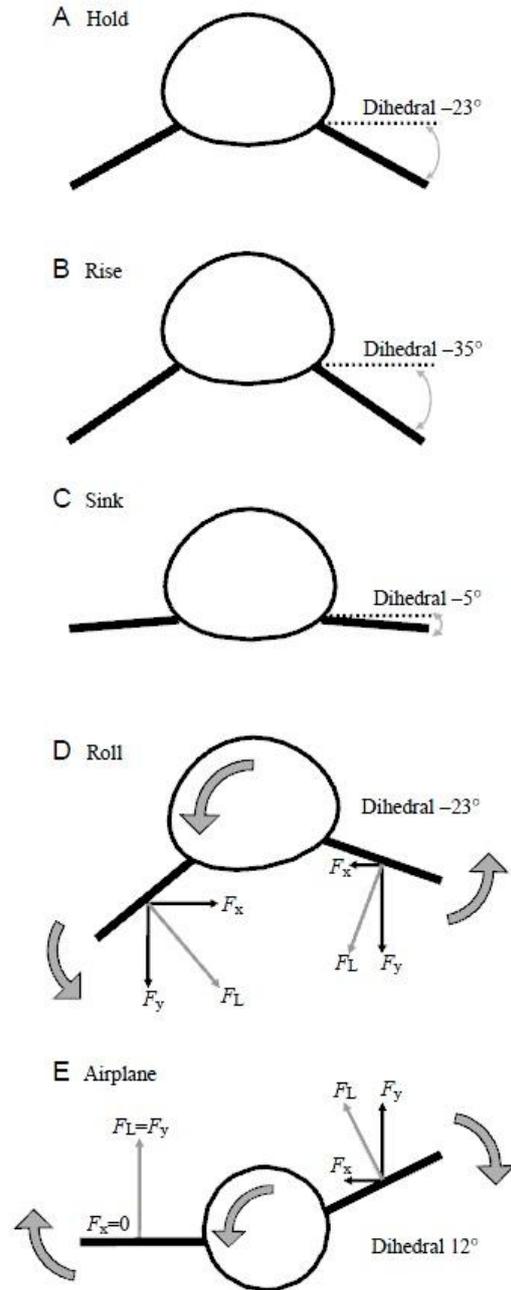

Fig. 5. Schematic representation of the dihedral orientation of a shark's pectoral fins during steady horizontal swimming (A), rising (B) and sinking (C). To illustrate the difference between the fins of a shark (D) and wings of an airplane (E), forces during a roll. Taken from Wilga and Lauder (2000).

Body angle

During the aforementioned station-holding in bamboo sharks, Wilga and Lauder (2001) concluded that body angle may play a role as well. As flow speed increased, body angle relative to the substrate decreased as the bamboo shark pressed its body against the substrate in an attempt to lower possible positive lift due to the ventral body surface and maintain its position (Wilga and Lauder 2001). Similar behaviour has been observed for several species of fish, for example the Atlantic salmon parr (Arnold et al. 1991).

It has long been suspected this exposure of the ventral surface of the body may play a role in generating lift necessary to maintain depth (Aleyev 1977; Carrier et al. 2004). For instance, Harris (1936) observed dogfish to tilt its anterior body upwards after amputation of its pectoral fins, presumably to compensate for the loss of lift. It then often overcompensated to high angles of up to 45° and was unable to return to its normal posture until it stopped swimming (Harris 1936).

Wilga and Lauder (2001) observed that bamboo sharks swam at a positive angle to the flow during steady horizontal swimming. Similar observations were made for sturgeons and leopard sharks (see fig. 6), with reported body angles of up to 20° for sturgeons and up to about 11° for leopard and bamboo sharks (Wilga and Lauder 1999, 2000, 2002; Fish and Shannahan 2000; Carrier et al. 2004). These body angles were found to decrease with increasing flow speed (see fig. 7), presumably because with increasing flow speed, the contribution of the body and pectoral fins to positive lift would increase as well (Aleyev 1977; Biewener 2003; Carrier et al. 2004).

Interestingly, Fish and Shannahan (2000) found that sandbar sharks (*Carcharinus plumbeus*) and sand tiger sharks (*Odontaspis Taurus*) did not elevate the anterior part of their bodies during steady horizontal swimming.

This difference can be explained by several factors. First, these two species of shark are not benthic species. As such, their buoyancy is likely to be closer to neutral than that of the more benthic leopard and bamboo sharks (Aleyev 1977). Thus, less lift has to be generated in order to maintain steady horizontal swimming. It is possible the lift of the caudal fin and the non-elevated anterior body is sufficient in doing so (Fish and Shannahan 2000).

Second, it is possible the shape of the body may be a contributing factor. This is easiest explained using the great white shark as an example. This species of shark has a conically shaped anterior body. As such, the relative lifting surface is greatly reduced as opposed to that of the bamboo shark. It seems unlikely a tilted body would be of significant importance in generating positive lift for this kind of shark (Lingham-Soliar 2005a). In order to generate the same relative amount of lift, it may even be possible the body angle of attack should be so great that stalling might occur (Alexander 1983).

Besides the positive body angle during horizontal swimming, Wilga and Lauder (2000) observed the body angle to be altered during vertical manoeuvring. For leopard sharks as well as bamboo sharks and sturgeons, body angle has been reported to increase during rising behaviour and decrease to a negative body angle during sinking behaviour (Wilga and Lauder 1999, 2000, 2001; Carrier et al. 2004). This tilting of the body can be seen in fig. 6. This change in body angle is thought to aid in rising and sinking in the water column as the lift produced by the anterior body increases or decreases during rising and sinking respectively (Wilga and Lauder 2000). This will result in an increase in total lift causing rising and likely a pitching moment rotating the anterior body ventrally, or a decrease in total lift causing sinking and a dorsal rotation of the anterior body (Wilga and Lauder 2000). This appears to be a mechanism to facilitate rising and sinking behaviour.
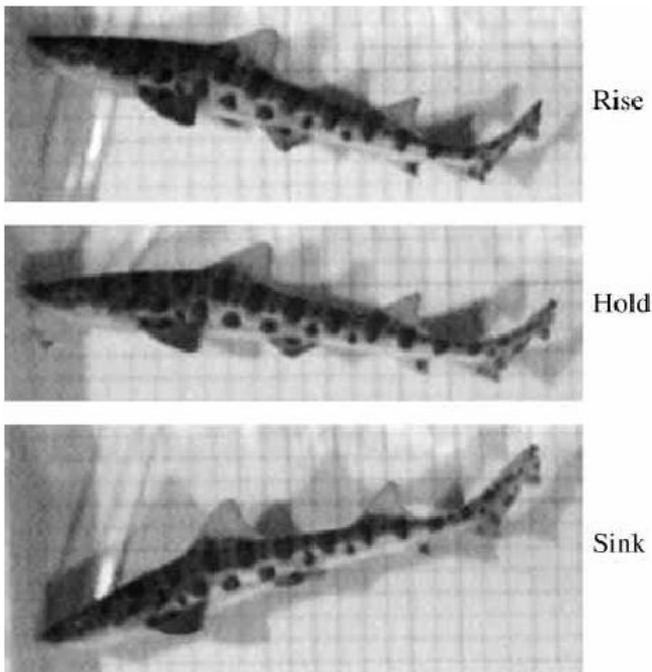
Fig. 6. Images (top) and plot (bottom) of the body angle of a leopard shark during rising, sinking and steady horizontal swimming. Taken from Wilga and Lauder (2000).
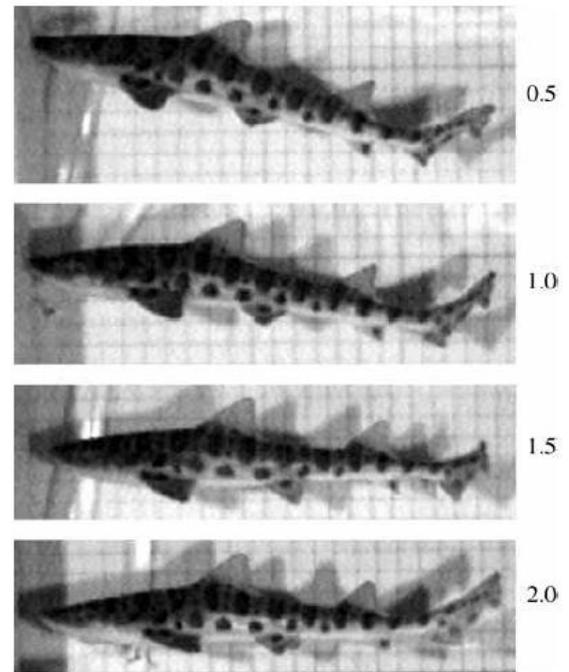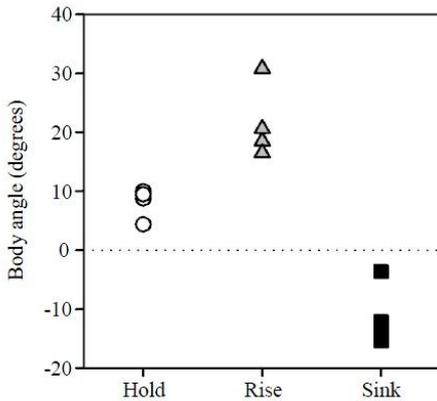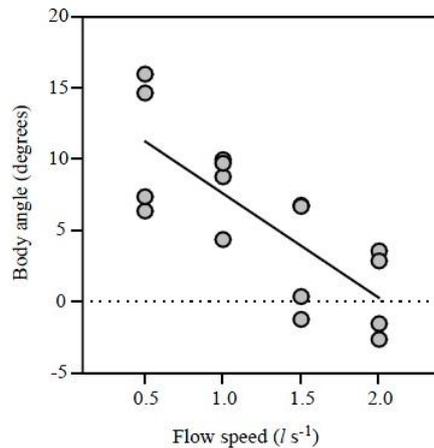

Fig. 7. Images (top) and plot (bottom) of the body angle of a leopard shark during steady horizontal swimming at differing flow speeds. Taken from Wilga and Lauder (2000).

A special mention should be made of the hammerhead sharks (*Sphyrnidae*). It has been argued that the cephalofoil of these sharks performs a hydrodynamic lift function (Fish and Shannahan 2000; Kajiura et al. 2003). In these sharks, the cephalofoil might provide additional lift, allowing for a more horizontal body angle compared to for instance leopard sharks (Kajiura et al. 2003). Evidence for this can be found in the observation that species with broader cephalofoils generally have smaller pectoral fins, suggesting functions may be similar (Fish and Shannahan 2000). However, other factors of the relatively large pectoral fins may exist. As mentioned before, the positioning of a shark's pectoral fins might promote rolling during turns (Wilga and Lauder 2000). In hammerhead sharks, this may be detrimental as their cephalofoil may be more likely to contact the sea floor. Indeed, Kajiura et al. (2003) have found that while hammerhead sharks are able to perform sharp turns, the cephalofoil rolls to a much smaller extent than the body of other sharks. If a hammerhead shark would possess large pectoral fins, the facilitation of the roll due to the pectoral fins could provide a problem and would require additional countermeasures in order to prevent the cephalofoil from touching the sea floor.

Discussion & Conclusions

Most sharks are negatively buoyant, which means they have a tendency to sink in the water column (Aleyev 1977; Lingham-Soliar 2005a). In this paper, I have discussed the importance of several methods in preventing or counteracting this tendency to sink.

The livers of sharks contain an increased amount of lipids, which reduce a shark's overall density (Aleyev 1977). The size of the liver and the relative amount of lipids it contains vary between species. Benthic sharks often swim with their bodies at a positive angle of attack, generating lift. For these sharks, the tilting of the body seems to be a preferred and likely relatively important method of lift generation, rather than an increased liver size or lipid content. A possible reason for this could be increased control over buoyancy when utilizing easily altered body tilt, rather than relatively static liver size and lipid content. Uncovering the reasons for these differences in liver size and composition between and within species, as well as the possible use of other substances, such as urea, requires more research.

It is surprising these sharks did not use their pectoral fins to alter lift generation. The opposite has been suspected for some time and is part of the classical model of a shark's buoyancy. The model states that the anteriordorsally directed force produced by the heterocercal tail is countered by the anterior body and the pectoral fins. Ferry and Lauder (1996) confirmed the existence of the anteriordorsally directed force produced by the tail. However, Wilga and Lauder (1999, 2000, 2002) have shown the pectoral fins do not counter this force.
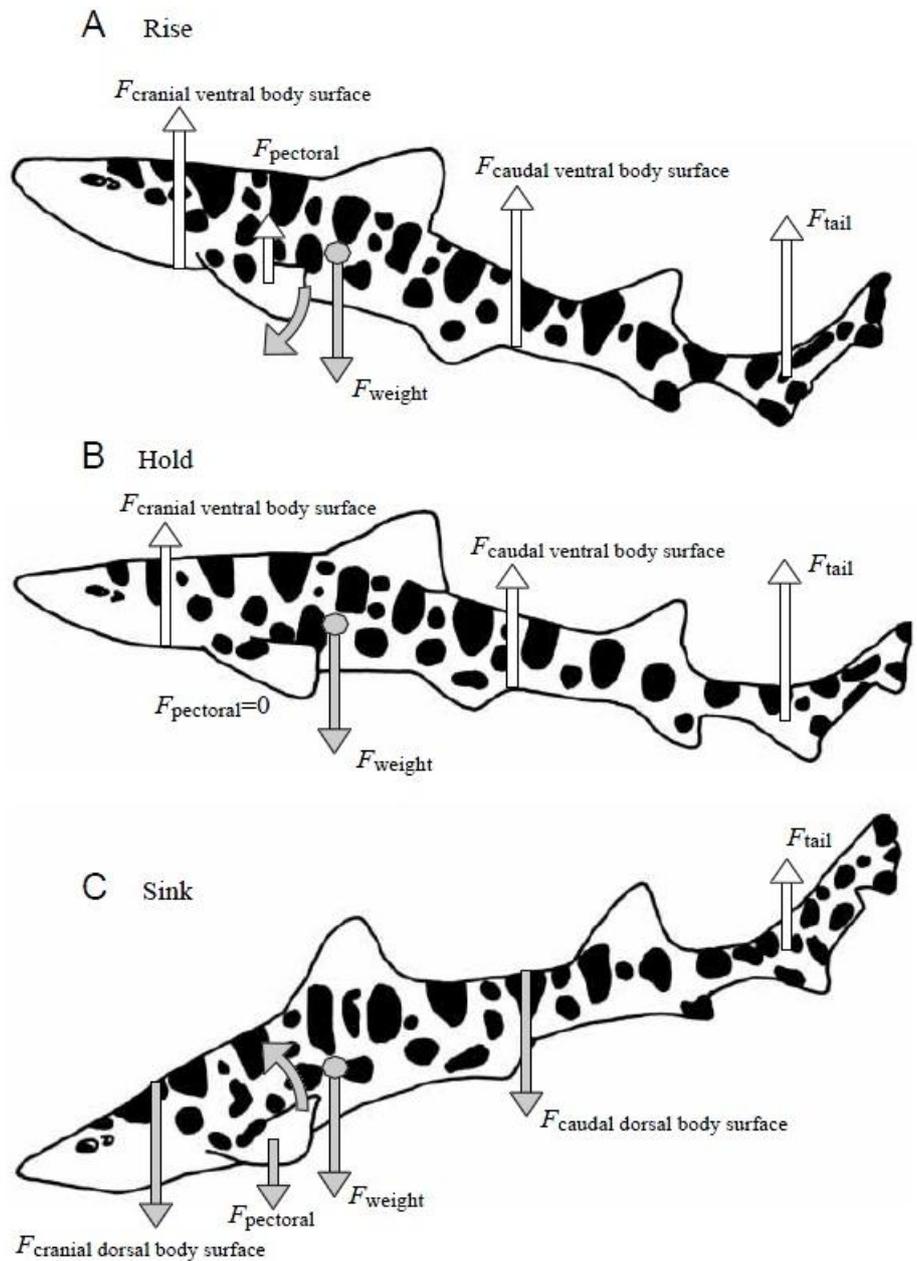
It appears the pectoral fins of leopard sharks are more important during vertical manoeuvring. The pectoral fins initiate a pitching moment, positioning the anterior body in such a way that the body angle can play a role.

Based on their findings in leopard sharks and bamboo sharks as well as sturgeon, Wilga and Lauder (2000, 2002) suggested an adaptation of the classical model, specifically in the role of the pectoral fins. Their proposed model is shown in fig. 8. During steady horizontal swimming, the pectoral fins generate negligible lift. The anterior head balances the forces exerted by the tail. During rising behaviour, the pectoral fins generate a significant amount of positive lift resulting in a pitching moment, which rotates the head dorsally and thus increases the body angle. The body then generates the lift necessary to rise in the water column. During sinking, the opposite occurs.

This adapted classical model by Wilga and Lauder (2000, 2002) is an improvement over the original classical model. However, it does not hold for all species of shark. Many studies made use of leopard sharks or sharks that have similar ecological habitats. Most species studied were benthic or semi-benthic sharks. The observations made by Fish and Shannahan (2000) of more pelagic sharks showed that these species do not utilize body angle as a method of lift generation. It is likely their conical body shape simply does not allow for lift generation as effectively as the relatively flattened ventral surface of benthic sharks does. It is possible that pelagic sharks, for instance great white sharks, do utilize their pectoral fins as lifting surfaces, even during steady horizontal swimming. Therefore, the model presented by Wilga and Lauder (2000) should not be applied to these kind of sharks without substantial adaptations. However, this new model does appear to be of considerable value when discussing the force balance of certain species of shark, such as leopard sharks or bamboo sharks. When dealing with benthic or semi-benthic sharks, the adapted classical model presented by Wilga and Lauder (2000) should be used rather than the original model. It would be interesting to attempt to adapt this model to pelagic shark species using similar research methods, such as DPIV. The magnitude of the lift component of the relatively symmetrical caudal fin of most pelagic sharks, compared to benthic

Fig. 8. Proposed adaptation of the classical model of a shark's force balance during rising (A), steady horizontal swimming (B) and sinking (C). The circle from which F_{weight} emanates depicts the centre of mass. Arrows indicate magnitude of the forces. Taken from Wilga and Lauder (2000).

sharks, would be important in the force balance of these sharks. The function of the pectoral fins also merits more research, since Wilga and Lauder (1999, 2000, 2002) have shown the classical view to be incorrect for leopard sharks and bamboo sharks, but the classical view of the pectoral fins as mechanisms balancing the torque produced by the heterocercal tail still stands for pelagic shark species. The next step in this kind of research is to expand studies to include shark species other than the limited number of species currently being utilized, in order to provide a better view of the force balance of sharks and to adapt Wilga and Lauder's (2000, 2002) model into a more general model, which can be applied to a larger number of shark species.

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