Squids: The missiles of the sea
The effect of size on the hydrodynamics and movement of squids

Written by Stephan van Dijk 2104334
Supervisor: Eize Stamhuis
University of Groningen
Bachelor Essay
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Cephalopods of the order *Teuthida* vary wildly in size, both between different species and during ontogeny. However, they all have the same body plan and use the same movement methods, the jet and the fins, while occupying a Reynolds number range ranging from 1 to more than $10^6$ and live in most ocean habitats. Thus the ecology they live in can differ enormously. Because of this diversity, a closer look will be taken in how the hydrodynamics of a squid will change with size. The usage of the fins and jet will also be looked to see whether it coincides with size, or if it depends more on function. Jet propulsion accelerates a mass of water in order to generate thrust. These jets can form different vortex structures, increasing thrust and efficiency. The usage of these structures goes down with increasing size, while the whole-cycle propulsive efficiency is approximately the same after the mantle length of the squid exceeds 1 cm. The fins can be used for movement in various ways, which include flapping, undulating and being used as a control surface. While not used by paralarvae in intermediate Reynolds number regimes, the hydrodynamics and usage of fins in juveniles and adults is highly dependent on the ecology of the squid in question. The squid’s body is very streamlined and the drag on the squid is primarily caused by friction drag and the negative forces that occur during refilling. Due to the allometric growth of length and the isometric growth of mantle diameter, bigger squids have a relatively more streamlined body.

The oceans contain an enormous diversity of life, ranging in size from the tiny zooplankton of less than two micrometer to the huge blue whale (*Balaenoptera musculus*), which can grow up to 33.5 meter and weigh as much as 190 tonnes (Fox, 2002). Among this myriad of different creatures, the squids of the order *Teuthida* cover a wide range of sizes. The brief squid (*Lolliguncula brevis*) is one of the smallest species of squid with a mantle length of 9 centimeter and a total length of 12 centimeter (Bartol *et al.*, 2001 and Bartol *et al.*, 2009a). On the other end of the spectrum are the giant squid (*Architeuthis dux*) and the colossal squid (*Mesonychoteuthis hamiltoni*). *A. dux* individuals with a mantle length of 2.25 meter and a total length of 13 meters have been observed (Vaughan, 2000). While no live or intact adult individuals of *M. hamiltoni* have been found or observed, several body parts and juvenile individuals have been found. Based on this, it is estimated that *M. hamiltoni* can reach a total length of up to 14 meters and a mantle length of 2 to 4 meters (Ravaioli & Youngster, 2012). Even within the same species, the size of an individual can change drastically during their lives. Paralarvae of the Humboldt squid (*Dosidicus gigas*) have a mantle length of only 1 millimeter, while adult *D. gigas* can grow up to a total length of 3 meter and a mantle length of 1.5 meter (Staaf *et al.*, 2014), with the paralarvae having a similar body shape as the adult. While squids do vary in size, they all share the same characteristics. Every single species in the order *Teuthida* has the same general body plan, of an arrow shaped body with two fins attached to the mantle on the posterior and ten tentacles attached on the anterior, and methods of propulsion. Compared to adults, paralarvae are relatively wider and shorter than adults, they have a relative greater funnel area than adult individuals and their fins are relatively smaller (Bartol *et al.*, 2008 and Staaf *et al*, 2014).

This is peculiar, because the environmental circumstances change drastically with size for aquatic organisms. One of the factors that changes is the Reynolds number. The Reynolds number (*Re*), named after the man who first described it, Osbourne Reynolds (Reynolds, 1883), is a number that describes the relative importance of inertia and viscosity and is calculated with the following formula:

$$ Re = \frac{\text{Inertial forces}}{\text{Viscous forces}} = \frac{F_i}{F_v} = \frac{c \cdot \rho \cdot v^2 \cdot A \cdot L}{c \cdot \mu \cdot v \cdot A} = \frac{\rho \cdot v \cdot L}{\mu} $$

(Van der Wal, 2009)
If Re is small (<10^{-1}), then the viscous forces have the most effect on the squid. If Re is big (>10^{3}), then inertial forces have the most effect. Because viscosity (\(\mu\)) and density (\(\rho\)) are attributes of the medium (water), the only parts a squid can influence are velocity (\(v\)) and length (\(L\)). Thus, depending on the size and the speed of an individual, the importance of viscosity and inertia change (Figure 1). When an organism is small, the effects of viscosity are important, while the effects of inertia are negligible. The opposite is true when an organism is big, the effects of inertia are important now, while the effects of viscosity are negligible. There is also a range in between the two extremes, where both inertia and viscosity play a role (Bartol et al., 2009b, Purcell, 1977 and Videler et al., 2002). In order to move efficiently at a low Reynolds number, normally different methods must be used than when living at large Reynolds numbers.

Furthermore, squids have two available methods for transportation. The first method is jet propulsion. This is the movement method squids are most well known for, even though they aren’t the only animals that use jet propulsion, such as jellyfish, scallops and frogishes (Vogel, 1996). They are however, the fastest and largest species that use jet propulsion (Vogel, 1996). The squid draws in water through the openings at the underside of the mantle by expanding the mantle, filling up the mantle cavity during the refill period. By then sealing the openings and contracting the mantle using the circular muscles in the mantle, the water is pushed out through the funnel during the jet period (Figure 2) (Preuss et al., 1997). The process then repeats itself, resulting in pulsed jetting. By changing the angle of the funnel, the squid can control the direction of the jet and consequently, the direction the squid will go to (Bartol et al., 2008 and Staaf et al, 2014). The second method is through use of their fins. The fins are muscular hydrostats, unsupported by bones. This allows for a broad range of movements. By undulating or flapping their fins, squids generate lift and thrust (Anderson et al., 2001, Anderson & De Mont, 2005 and Stewart et al, 2010). The fins are also used as a wing during gliding, both underwater and in the air (O’Dor et al., 2013 and Stewart et al, 2010).

Figure 1: Typical velocities of the largest possible size range of swimming organisms as a function of the Re number (From Videler et al., 2002)

Figure 2: A schematic drawing of a squid and how their jet works. Water gets sucked in the mantle cavity through openings at the bottom of the mantle when the mantle relaxes. By contracting the mantle, water gets pushed out of the funnel, generating thrust. (Anderson & De Mont, 2000, Anderson et al., 2001 and Anderson & Grosenbaugh, 2005)
To examine the effects of the different sizes of squids, the following research questions will be asked in this report. First of all, do the hydrodynamics of squids change with size? If so, how do they change? Is there a preferred movement method depending on size, or does it depend more on function?

In order to answer these questions, the following text will be split into three parts. In the first two parts, the focus will be on the different movement methods of the squids. Both the jet propulsion and the fins will be examined separately. In the last part, the focus will be on the drag that exerted on the squid. When applicable, squids will be divided in two categories, depending on which Reynolds number range they fall in, being in a high Reynolds number range when \( Re > 10^3 \) or an intermediate Reynolds number range when \( 10^-1 < Re < 10^3 \). However, due to constraints in technology, not the whole size range of squids is equally covered in literature. It is unfortunately still impossible to test an *A. dux* in a flow tank. Therefore, the focus will primarily on the species that have been tested in the past. These include species such as the brief squid (*Lolliguncula brevis*), the long-finned squid (*Doryteuthis pealeii*), the market squid (*Doryteuthis opalescens*), the northern shortfin squid (*Illex illecebrosus*) and the Humboldt squid (*Dosidicus gigas*), including paralarvae, juveniles and adults.

**Jet hydrodynamics:**

As stated before, the squid’s most well known mode of movement is jet propulsion (Figure 2). By expelling water from the mantle cavity through the funnel, the squid generates thrust. It is known as a burst-and-coast type of swimming, most effective at high \( Re \) where the squid can coast during the refill-phase due to inertia (Bartol et al. 2009b). At low and intermediate \( Re \) continuous swimming is more important, due to viscosity reducing the coasting distance (Purcel, 1977). But jet propulsion isn’t the most efficient method to swim. According to Vogel (1996), the energy needed to produce a jet is proportional to the product of the mass moved per time unit and the square of the velocity of the jet, while the thrust generated by a jet is greater when the jet is only slightly faster than the surrounding water then when the jet has a greater speed. The difference in speed between the jet and the surrounding water is called slip. Thus the most efficient jet moves a lot of water per time unit while accelerating it only slightly faster than the surrounding water (Anderson & De Mont, 2000 and Vogel, 1996). Squids however tend do exactly the opposite, accelerating a small amount of water very fast (Vogel, 1996). Part of this is due to how the squid’s jet works. They can only store a limited amount of water in their mantle cavity. If they increase this amount, they increase their volume, their drag and, according to Laplace’s law, decrease the effectiveness of their circular muscles (Vogel, 1996). Furthermore, while squid can swim both tail-first or arm-first, they prefer tail-first most of the time. They prefer this, because it means that they don’t have to bend their funnel much (Anderson and De Mont 2005). This means that in order to refill the mantle cavity, water has to go against the surrounding flow, further reducing efficiency (Anderson & De Mont, 2000 and Anderson & Grosenbaugh, 2005). It was common to use the Froude
efficiency to calculate the efficiency of animals using jet propulsion (Vogel, 1996, Anderson & De Mont, 2000).

\[ \eta_f = \frac{2V}{V + V_j} \quad \text{(Anderson & De Mont, 2000)} \]

Where \( \eta_f \) is the Froude efficiency, \( V \) is the velocity of the surrounding fluid and \( V_j \) is the velocity of the accelerated fluid (Vogel, 1996, Anderson & De Mont, 2000). However, Anderson & De Mont (2000) argue that it is better to use the formula for the propulsive efficiency of a rocket motor.

\[ \eta_j = \frac{2V \cdot V_j}{V^2 + V_j^2} \quad \text{(Anderson & De Mont, 2000)} \]

Where \( \eta_j \) is the rocket propulsive efficiency during the jet, \( V \) the velocity of the surrounding fluid and \( V_j \) the velocity of the jet (Anderson & De Mont, 2000). This formula gives a better approximation to what a squid does than the Froude efficiency, which was meant for an airscrew-like propeller with a constant flow. Whole cycle efficiency also takes into account the refill phase of the squid and is given by the following formula.

\[ \eta = \frac{2V \cdot V_j}{2V_r \cdot V + 3V^2 + V_j^2} \quad \text{(Anderson & De Mont, 2000)} \]

Where \( \eta \) is the whole cycle efficiency and \( V_r \) the velocity of the fluid taken in by the squid during refilling (Anderson & De Mont, 2000).

One way to analyze the jets is by examining the vortex rings that are left in the wake of the squid. A vortex ring is a circle of rotating fluid with a jet through the center (Figure 3) (from Videler et al., 2002). Furthermore, the vortex ring accelerate ambient fluid and add extra mass to the jet, increasing the thrust and increasing the efficiency of the jet (Bartol et al., 2009a). The most optimal vortex rings are produced when the length of the jet \( L \) divided by the diameter of the jet area \( D \) is equal to 3.5. If the length of the jet is longer, not all the fluid can be processed by the ring, changing the shape and reducing the additional thrust (Linden & Turner, 2004). Additionally, the ratio swimming speed/jet speed also influences the ability to form optimal vortex ring, with a lower \( L/D \) ratio needed as the swimming and jet speed become more equal and in return, lower the propulsive benefits the vortex rings provide (Anderson and Grosenbaugh, 2005 and Bartol et al., 2009a).

In the high \( Re \) range, Bartol et al. (2008 and 2009a) found that juvenile and adult \( L. \) brevis (mantle length 1 – 9.1 cm), while capable of producing multiple jet patterns, had 2 distinct jet modes. Jet mode 1, where the jet transform into an isolated vortex ring and jet mode 2, where the jet creates a leading vortex.
ring that is “pinched off” the jet (Figure 4) (Bartol et al., 2009a). Jet mode 1 was observed when L/D < 3 and had a higher propulsive efficiency, shorter jetting period and more fin activity, while jet mode 2 was observed when L/D > 3 and produced a greater amount of lift and thrust on over time and per pulse (Bartol et al., 2008 and Bartol et al., 2009a). The squids showed no preference for jet mode at certain speeds, but overall squid preferred jet mode 2. Squid with a mantle length < 5 cm used jet mode 1 more often than larger squids (Bartol et al., 2009a). Bartol et al. (2008) also observed that smaller squids used jet mode 1 more and found a preference for jet mode 1 at low speeds. Bartol et al. (2009a) also reported that the average jet rocket propulsion efficiency of 69 ± 14% for jet mode 1 and 59 ± 14% for jet mode 2. Bartol et al. (2001) also found that contraction rate was significantly higher in smaller L. brevis (Mantle length 1 – 2.9 cm), while larger squids (Mantle length > 5 cm) had a higher propulsion efficiency and slip. Furthermore, when faced with increased flow speed, small L. brevis increased their contraction rate while expelling roughly the same amount of water. Large L. brevis did exactly the opposite, increasing the amount of water expelled and keeping the contraction rate the same (Bartol et al., 2001 and Bartol et al., 2009a). Bartol et al also found that occasionally squids with a mean mantle length of 4.2 cm would produce vortex rings in their wakes, similar to jet mode 1 (Bartol et al. 2001).

Anderson and Grosenbaugh (2005) found that in D. pealeii (Mantle length 22–30 cm) only sporadically created vortex rings. They mostly created elongated jets with areas of increased vorticity with an L/D of 5.5 to 61.8. They also report a range of 42 - 49% propulsive efficiency over both the refill and jet period and an average jet propulsive efficiency of 86% at lower speeds for adult D. pealeii, with efficiency increasing with increasing speed due to reduced slip (Anderson and Grosenbaugh, 2005). However, they do mention that these values might be slightly higher than they really are. Anderson and De Mont (2000) calculated a mean Froude efficiency of 56 %, a mean rocket efficiency of 65 % and 34–48% propulsive efficiency over the entire cycle for adult D. pealeii. Bartol et al. (2001) determined the efficiencies of L. brevis (Mantle length 1.8 – 8.9 cm), which had a whole cycle efficiency of 29.0–44.4%, a Froude efficiency of 28.3–57.5 % and a rocket propulsive efficiency of 32.1–69.4%. Webber and O’Dor (1986) calculated a Froude efficiency range of 12–34 % for l. illecebrus (Total length 34 – 52 cm). They also found that peak pressure in the mantle and jet frequency increased with increased speed (Webber & O’Dor, 1986).

O’Dor (1988) found that D. opalescens (Mantle length 12 - 14 cm) reduces the time it takes to refill the mantle cavity with increasing speed. Furthermore, D. opalescens control the efficiency of their jet by adjusting jet thrust through changing the aperture of their funnels (O’Dor, 1988).

Squid paralarvae live at an intermediate Re and are relatively wider and shorter than adults, they have a relatively larger capacity to store water, a larger funnel and smaller fins. While adults move freely in all directions, paralarvae live vertically, aiming their jets almost straight down and relying mainly on currents for horizontal movement (Bartol et al., 2008, Bartol et al., 2009b, O’Dor and Hoar, 2000 and Staaf et al, 2014). Bartol et al. (2009b) found that D. pealeii paralarvae (Mantle length 1.8 mm) showed a propulsive efficiency range of 56.1 – 87.5%, but this was only over the jet period. Refill period could not be used in the calculation due to rapid sinking. Bartol et al. (2001 and 2008) found that paralarvae (87.4 ± 6.5%) had a greater jet propulsive efficiency than juveniles and adults (77.8 ± 11.6%) and that their jets had a relatively larger volume and lower velocity. Both spherical vortex rings and elongated vortex ring structures were observed (Respectively L/D 2.1 – 4.8 and L/D ~20), with the second being more prevalent at higher speeds (Bartol et al., 2009b and Bartol et al., 2009b).
The elongated structures could be either pinched off vortex ring as in jet mode 2 where the pinch-off is blurred due to the viscosity or a vortex ring where its formation is disturbed by the viscous drag (Bartol et al., 2009b) D. pealeii paralarvae always expelled water with approximately the same velocity independent of swimming speed. They did increase the volume of water expelled with increased swimming speed by increasing the amplitude of the contraction (Bartol et al., 2009b). This is in opposite to what Staaf et al. (2014) found in D. gigas paralarvae (Mantle length length 1 mm). They were found to increase contraction rate with increasing flow. They also found that D. gigas paralarvae had 3 different methods of jet propulsion, maintenance jetting to stay in approximately the same place, slow jetting used repeated jets to move vertically and fast single jets similar to the escape jets of adults (Staaf et al., 2014). During maintenance jetting, squids kept their mantle apertures open during contraction, producing a more jellyfish-like jet. As the gills are located in the mantle, Staaf et al. (2014) thought that paralarvae used this to breathe without moving. A model based on D. gigas made by Staaf et al. (2014) found that the whole cycle propulsive efficiency was highest in D. gigas with a mantle length of 1 cm (Figure 5). When they grow larger than 6 cm mantle length, they can increase efficiency and reduce mantle stress by increasing funnel aperture and decreasing jet frequency. Both these methods are supported by observations of juvenile/adult D. gigas (Staaf et al., 2014).

**Adding fins to the hydrodynamics:**

The fins are the other method used by squids to generate thrust. As seen in Figure 2, the fins are attached to the dorsal side of the mantle. However, the exact shape and relative size of the fins varies among different species of squid. Overall, fast-swimming, pelagic squids such as D. gigas, I. illecebrosus, D. opalescens and D. pealeii have relative thick and short triangular fins, which do not produce a lot of drag, but are in return not very good at undulating when swimming at low speed. (O’Dor et al., 2013). At high speed, the fins are spread out and can function as rudder, wing and stabilizer (O’Dor and Webber, 1991, O’Dor et al., 2013 and Stewart et al., 2010). On the other hand, coastal squid such as Sepioteuthis lessoniana and L. brevis generally have relatively larger fins, which are better suited for generating thrust at low and intermediate speeds, while also used for maneuvering and stability. The downside is that they produce more drag, so during high speed swimming, the fins get folded against the mantle (Bartol et al., 2001 and Stewart et al., 2010). The relatively largest fins are found in certain deep-sea squids (Figure 6). It is presumed that, instead of a jet, slowly flapping or undulating

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Figure 6: A picture made with a submersible of a deep-sea squid of the family Magnapinnidae. (Vecchione et al., 2001)

Figure 5: The calculated maximum velocity of a single jet and the whole cycle efficiency of D. gigas over the ontogenic size range. The dashed line assumes maximal funnel aperture area, the dotted line assumes minimal funnel aperture area and the solid line assumes that the squid adapts the funnel aperture area depending on the situation (Staaf et al, 2014).
their fins is the main method of propulsion in these species (Stewart et al., 2010 and Vecchione et al., 2001).

In the high Re range, *L. brevis* is a coastal, slow swimming squid that relies more on its fins. The fins propulsion is a combination of drag-based and lift-based propulsion (Bartol et al., 2001). Stewart et al. (2010) found 4 different fin wake patterns in *L. brevis* (Mantle length 3.5 – 9.0 cm), each with their own vortice pattern (Figure 7). Fin mode 1 shed one isolated vortex each downstroke while flapping and was only used at low velocities. This pattern wasn’t used often (Stewart et al., 2010). Fin mode 2 creates a chain of seemingly linked vortices while undulating. This pattern also wasn’t used much during tail-first swimming, but was the most used in arm-first swimming (Stewart et al., 2010). Fin mode 3 also shed one isolated vortex on each stroke while flapping, but vortices were produced on both the downstroke and upstroke and with the downstroke vortex being being stronger than the upstroke vortex (Stewart et al., 2010). Fin mode 4 shed one linked double vortex each fin flapping cycle and was the most used pattern in tail-first swimming. This mode was also the one most used at high velocities (Stewart et al., 2010). Fin mode 3 and 4 were also found by Bartol et al. (2008), were they were called respectively fin mode 1 and 2. While all four modes were used in tail-first swimming, during arm-first swimming only fin mode 2 and 3 were used. Fin mode 1 had a lower propulsive efficiency than the other three modes and the tail-first modes were more efficient and produced more force than arm-first (Stewart et al., 2010). Bartol et al. (2001) found that *L. brevis* (Mantle length 1.8 – 8.9 cm), while swimming tail-first, fin usage decreased with increasing speed, until it reached a point where the squid wrapped the fins around the mantle. When swimming arm-first, fin-beat frequency was higher in small squids (Mantle length 1.0 – 4.9 cm) than in larger squid (Mantle length 7.0 – 8.9) (Bartol et al., 2001). Furthermore, at low speeds tail-first and at all speeds arm-first mostly used downstrokes during the contraction of the mantle and during the refilling. At higher speeds tail-first, the amount of fin activity is reduced and most of the downstrokes were during the contraction of the mantle (Bartol et al., 2001). Bartol et al. found that “the fins were used over 50–95 % of the sustained speed range and could account for potentially as much as 83.8 % of the total vertically directed force and 55.1 % of the horizontal thrust.” (Bartol et al., 2001, p 3675). This is similar to what (Bartol et al., 2008) found, with the jet contributing up to 95.5% of the total thrust and the fins up to 83.3% in *L. brevis*.

On the other hand, the fins of the pelagic *D. pealeii* (Mantle length 15 – 30 cm) were examined by Anderson and De Mont (2005). They found that the *D. pealeii* had 2 distinct gaits involving fins and the jet. The ABCD gait involved constant flapping of the fins, with a downstroke at the start of the jet, an upstroke during the expulsion of the water and a downstroke at the end of the jet. Occasionally, the squid added two upstrokes and a downstroke during the refill period. This gait was mostly used at low speed. The AB-wrap gait was used at higher speed. The squid makes a downstroke during the

![Figure 7: Schematic representation of the four different fin wake patterns found in *L. brevis* (Stewart et al, 2010).](image)
onset of the jet and wraps them against the mantle while coasting, reducing drag (Anderson & De Mont, 2005).

O’Dor (1988) found that the pelagic D. opalescens that the fin activity decreased with speed, until the fins are folded against the mantle. When used at low speed, the fins contribute up to 25% of the total horizontal thrust (O’Dor, 1988). Hunt et al. (2000) observed that D opalescens had 4 different gaits (jetting, slow swimming, gliding and hovering in place), both in a tail-first position and an arms-first position. Each of these different gaits used jet propulsion and the fins in a different amount, with jetting used the jet for propulsion and the fins either folded against the mantle at higher speeds or used as steers at lower speeds, slow swimming combined fin flapping with jetting, gliding combined slow jetting with using rigid fins as control surface and hovering primarily used the fins to stay in the same spot (Hunt et al., 2000).

Certain squids of the family Ommastrephidae are also able to fly and glide in the air, similar to flying fish. By using their jets, they are able to launch and propel themselves into and through the air, while using their fins and arms as wings and ailerons (O’Dor, 2013). O’Dor (2013) analyzed the flight of two different species of squid: S. pteropus (Mantle length 6.0 cm) and D. gigas (Mantle length 1.219 m). S. pteropus was indirectly observed to fly for 11.5 bodylengths at a speed of 25.6 bodylengths per second powered by its jet (O’Dor, 2013). D. gigas flight was filmed by Gilbert and analyzed by Cole & Gilbert (1970). D. gigas flew 0.9 bodylengths with a speed of 3.84 bodylengths per second powered by its jet (O’Dor, 2013). Both glided in the air for an indeterminate length after powered flight ended (O’Dor, 2013). O’Dor (2013) also found that the acceleration S. pteropus in the air is triple that of the acceleration in the water, while the maximum velocity of D. gigas in the air was about doubled compared to the maximum velocity in water. These increases are likely caused by the lower resistance of air compared to water (O’Dor, 2013).

In the intermediate Re range, both Bartol et al. (2008 and 2009b) and Staaf et al. (2014) found that, for respectively paralarvae of D. pealeii and D. gigas, while paralarvae did flap their fins during their jets, the force this produces is negligible compared to the jet propulsion. The fins were also extended fully during the refilling period, most likely to increase surface area and reduce sinking rate (Bartol et al., 2008, Bartol et al., 2009b and Staaf et al., 2014).

**Drag and allometry:**

The drag forces on a moving object are given by the formula:

\[ F_d = \frac{1}{2} \rho v^2 C_d A \]  

(Vogel, 1996)

Where \( \rho \) is the density of the fluid, \( v \) is the velocity of the moving object, \( A \) is the area exposed to the flow and \( C_d \) is the drag coefficient. \( C_d \) is the sum of the drag coefficient of friction drag, drag caused by the water “sticking” to the surface of the object due to viscosity and thus increases with additional surface area, and the drag coefficient of pressure drag, drag caused due to accelerating water out of the objects path and increases with and increased frontal area and a less streamlined object (Vogel, 1996 and O’Dor and Hoar, 2000). The relative importance of friction drag and pressure drag is thus dependent on the \( Re \) and on the form of the object. For a streamlined object at low \( Re \) the major source of drag is friction drag, while for a bluff body at a high \( Re \) the major source of drag is pressure...
drag (Vogel, 1996). For highly streamlined bodies like squid, O’Dor (1988) used this formula to calculate the drag coefficient for the entire body at high \( Re \):

\[
Cb = C \left[ 1 + 1.5 \times \left( \frac{2Re}{length} \right)^{1.5} + 7 \times \left( \frac{Re}{length} \right)^{3} \right] \quad (O’Dor, 1988)
\]

Where \( C \) is the drag coefficient of the flow against the front of the squid \( (C = (1.33/Re)^{0.5}) \) (O’Dor, 1988).

Anderson et al. (2001) determined that that the primary sources of the drag on \( D. pealeii \) (Mantle length > 20 cm, \( Re > 10^4 \)) were friction drag and the negative forces caused by refilling the mantle, while the pressure drag and added mass contributions were small due to the streamlined shape of the squid body. Bartol et al. (2009b) says that for a specific weight, drag increases with increasing \( Re \) for high \( Re \). However, at intermediate \( Re \), drag decreases with increasing \( Re \). Staaf et al. (2014) calculated the drag for three different size classes of \( D. gigas \) paralarvae for the intermediate range of \( Re \) (Figure 8).

One of the most important factors in the difference in hydrodynamics is whether the squid is in the intermediate or high \( Re \) regime. The turning point where the squids enter the high \( Re \) range is around 1 to 3 cm mantle length (O’Dor and Hoar, 2000, Staaf et al., 2014 and Yang et al., 1986). Around this point, the squids transition from a paralarval state to a juvenile or adult state, complete with a set of morphological changes to be more adapted to a high \( Re \) regime. The ratio of fin to mantle length increases rapidly at this size in \( D. opalescens \) and \( D. gigas \) (Staaf et al., 2014 and Yang et al., 1986). At this point, the squids change from exponential to logarithmic growth. (O’Dor & Hoar, 2000, Staaf et al., 2014) An allometric analysis was done by O’Dor and Hoar (2000). It showed that there was a positive allometric relationship of mantle length, total length, fin length, fin width and fin area, but the fin data is in this case mainly based on loligonid squid and does not describe other families well (O’Dor and Hoar, 2000). Funnel aperture is isometric with weight. Mantle diameter increases slower than weight in small squids, but is isometric in individuals weighing more than 1 g (O’Dor and Hoar, 2000). Mantle thickness is the opposite, increasing faster than weight before becoming isometric in individuals weighing more than 0.1g (O’Dor and Hoar, 2000).

**Conclusion:**

To reiterate, the questions asked were: 1) Do the hydrodynamics of squids change with size? And 2) is there a preferred movement method depending on size or is the function of the movement method more important? The short answer to the first question is yes. When looking at the efficiency of the jets, two things get noticed. The efficiency of a single jet is high in paralarvae and decreases until it reaches a mantle length of 5 cm. After that, the efficiency seems to increase again. When looking at the whole cycle efficiency, the squids in the range of 1.8 – 30 cm mantle all have similar whole cycle efficiencies. They also fit nicely on the graph 5b. While this graph was made for \( D. gigas \),

![Figure 8: Drag versus the Reynolds number for three differently sized squid over 10 jet cycles, showing a slight hollow curve (Staaf et al, 2014).](image-url)
this indicates that there might be a similar graph for multiple species. This could be partly tested by calculating the whole cycle efficiencies of some other, differently sized squid species. At least some squids with a mantle length of around 1 cm should be tested, as the model predicts that squids with a mantle length of 1 cm have the highest whole cycle propulsive efficiency. Contraction rate is also higher in smaller squids and paralarvae. This is also reflected in the muscles. Adults have longer thick muscle filaments than paralarvae. This results in a higher maximum tension strength and lower contraction rate (Thompson and Kier, 2006).

Jet structure does change in with an increase in size. The jets of paralarvae and small/intermediate squid (Mantle length < 9cm) form vortex rings and elongated vortex structures, while the jets of larger squids (Mantle length > 22 cm) do not form these structures, instead having areas of increased vorticity in their jet emissions. This was also noted by Bartol and Videler (Bartol et al., 2009a and Videler et al., 2002). This seems to indicate that with an increase in size, there is a reduced dependency on the thrust benefits given by vortex rings. While vortex rings increase the efficiency of the jet, the narrow L/D ratio does limit the maximum amount of thrust a jet can generate while still producing a vortex ring, compared to a jet where the amount of water expelled isn’t limited. Perhaps due to the ability to store relatively more water than smaller squids, the larger squids forgo the increased efficiency of vortex rings and instead increase the power of their jets by increasing the volume of the expelled water, while compensating for the reduced efficiency of their jets in other ways. Possibilities include an increase in funnel area and climbing-and-gliding as part of their swimming behavior (Staaf et al., 2014).

As for the fins, fin hydrodynamics and usage does change with size. During the paralarval stage, the fins are too small and weak to provide any significant thrust, serving only to increase surface area and possibly as stabilizers (Bartol et al., 2008, Bartol et al., 2009b and Staaf et al., 2014). When the squids grow up into juveniles and enter the high Re range, the ratio fin to mantle area increases rapidly (Staaf et al., 2014 and Yang et al., 1986). In this part of the squid life cycle, the differences in hydrodynamics and use depend mainly on species and ecologies. One general trend that does show in all described species is a decrease in fin usage with increasing speed. Even L. brevis, which uses 4 different fin gaits over a wide range of velocities, follows this trend.

Based on the analysis done by O’Dor and Hoar (2000), bigger squids are relatively more streamlined. This is because total length and mantle length increase positively allometrically, while mantle diameter and thickness increase isometrically. This supports Anderson et al. (2001) results that the major source of drag on squids is friction drag. By becoming more streamlined with increased size and consequently increased Re, the squid reduces the increased pressure drag, while at the same time increasing the reduced friction drag due to the relative increase in surface area. Thus keeping roughly the same ratio of pressure drag versus friction drag.

As for the second question, only when the squid in question is of paralarval length (Mantle length < 1 cm) does it depend solely on a single movement method, the jet. Even then, the paralarvae had three different gaits for different situations (Staaf et al., 2014). For squids with a mantle length greater than 1 cm, the movement method and gaits used is dependent on the velocity the squid wants to swim at.
Discussion:

Of the more than 300 different species of squid, only 6 are described in this text. Part of the problem is that it isn’t easy or possible to keep most squids in captivity. In addition to the above mentioned size limitation, squids are skittish and delicate lab animals. Unacclimatized squid tend to use their escape jets when they see some large and unexpected movement, such as a person walking by (Yang et al., 1986). Sudden changes in light also elicit the same response (anecdotal?). Even when acclimatized, slow movement is a must during cleaning and feeding. The danger in escape jetting is that the squid will likely crash against the wall or even jet out of the tank. This, in turn, leads to injuries and can possibly be fatal (Yang et al., 1986). Squids also have cannibalistic tendencies, especially against smaller and weakened individuals. While they tend to not eat other squids when well fed, there is always a chance that they will still do it (O’Dor et al., 2013 and Yang et al., 1986).

Furthermore, the majority of the data used was from loligonid squids. In turn, the results found are skewed towards the family Loliginidae. This has mostly to do with that the most hydrodynamic data available is from loligonid squid. Even more, the data is derived from about 2% of all the squid species. Therefore the patterns seen here could not universally apply to all squid species. Especially the literature about deep-sea squids is lacking.

References


Van der Wal, S.M. (2009) Ontogeny of the Swimming Behaviour of *Sepia officinalis*


