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THE CHANGING ROLE OF FINS IN GROWING LOLIGINID SQUID
(MOLLUSCA; CEPHALOPODA)

by

Jennifer Anne Hoar

Submitted in partial fulfillment of the requirements for the degree of Doctor of
Philosophy

at

Dalhousie University

Halifax, Nova Scotia

June, 1995

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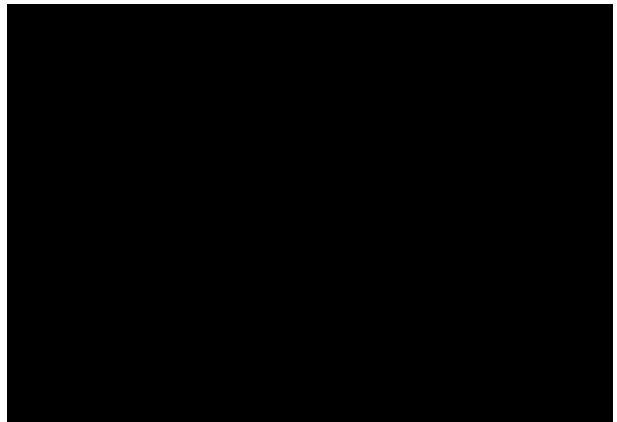
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This thesis is dedicated to my mother and my grandparents who not only gave me roots and wings, but also encouraged me to paddle in tide pools.

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ABSTRACT

From the deep sea giants to the smallest planktonic larvae, virtually all squid need and use fins for swimming, despite being archetypal jet-propelled animals. Fins vary, not only in final adult shape (i.e. small, triangular; long, marginal; or large, rhomboid) and throughout ontogenetic growth, but also with the lifestyle of the squid species. The morphometric changes occurring to both body and fins in 126 loliginid squid (*Loligo forbesi*, *L. pealei*, *L. vulgaris reynaudii*, *L. opalescens*, *Lolliguncula brevis* and *Sepioteuthis lessoniana*) were studied over a billion-fold size range in this thesis. These species all belong to the Family Loliginidae and are shallow-water, coastal species with similar lifestyles. The shape of the fins in these species is very similar and an optimal width to length ratio was indicated for these long-finned adults. Also, the final fin length appears to be determined, not by species, but by the size the squid attains during growth.

The changes in fin shape with growth and species can also be related to hydrodynamic forces such as drag and thrust and to how these forces change with scale from viscosity-dominated at hatching to inertia-dominated as adults. In consideration of these forces, not only does the squid's body undergo a marked shape change with growth, from relatively globular to slender and streamlined, but the aforementioned fin shape change also assists in this goal. From the morphometric analysis, a model for swimming was developed that can be used over the large size range and can be manipulated to reflect the changes that the squid can produce during jetting (i.e. funnel diameter changes, jet frequency changes and/or changes in mantle volume utilized). The effect of fins on drag was included in this model and the effect of fin size on swimming forces studied. Fin use in three differently sized squid, *L. forbesi*, *L. brevis*, and *S. lessoniana*, was studied to gain insight into the jet assisted finning (JAF) used by these long-finned squid. Efforts to quantify the swimming efficiency of these animals demonstrated the need for appropriate new approaches to animals using two distinct, but synergistic modes of propulsion.

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CHAPTER 1. General Introduction

For over 500 million years, since the Cambrian, cephalopod molluscs have maintained and fine-tuned the system that allowed them to rise above the benthos and dominate the water column until the advent of the fish in the Silurian. This system is the jet, which began as simple water ejection resulting from withdrawal into the shell. This mechanism has become a highly coordinated skill that allows squid to maintain their position as the most manoeuvrable animal in the seas and to compete with fish. Fish now dominate the oceans and cephalopods seem to be relegated to marginal niches, probably because the vertebrates use undulatory locomotion, a system that achieves higher efficiency by constant water acceleration using body/fin undulation, in contrast with the periodic water acceleration of squid jetting. Both squid and fish gain momentum by accelerating a mass of water backwards, but in fish there is generally a larger mass accelerated than in squid (where this volume is constrained by mantle volume; Alexander, 1977). Therefore, squid must accelerate the smaller water mass to a higher velocity to gain the same momentum as fish and much of this invested energy is lost, leading to a low Froude Efficiency for squid (Alexander, 1977). Although fish may have the upper hand (fin?) when it comes to efficiency of continuous movement, the squid's jet propulsion system does allow them to accelerate quickly, and their ability to move the funnel aperture within a 360° hemisphere also gives them superior manoeuvrability.

This manoeuvrability and unpredictability of movement is made even more striking by their ability to dive and climb vertically in the water. Unlike most fish with their complex swim bladder buoyancy systems that require time for the animal to change

depth significantly, many squid are negatively buoyant at all times, generating lift while swimming and, therefore, having no restrictions on depth. This remarkable vertical manoeuvrability of squid gives them a great advantage when chased by fish predators, especially when coupled with the ink cloud and colour change to mask their departure. It also has advantages for them as predators, since they can hunt virtually any prey (their size or smaller) and allows them to use the element of surprise in a way that fish rarely can, except by hiding or camouflage (i.e. squid can swim fin-first until ahead of a school of fish and then reverse into the school arms-first, surprising the fish and, usually, catching dinner; Foyle & O'Dor, 1988).

Although this manoeuvrability gave them advantages as predators, it was not enough for them to maintain their dominance of the oceanic hierarchy after the arrival of the fishes. Instead, squid have undergone evolutionary modifications that honed their swimming and hunting skills: a decrease in shell weight to nearly zero (in teuthoid squid), the development of their highly complex eye and the maximizing of locomotor muscle mass. This suite of modifications did not return the squid to dominance, but it did place them in direct competition with the fishes, both groups preying upon, and being preyed upon by the other.

In their competition with fishes, cephalopods have exploited a number of fairly unique niches, as well as sharing others. One of these unique niches is that occupied by the sole remaining ectocochleate cephalopod, *Nautilus*, which exploits the cephalopods vertical movement abilities in its scavenging life. Among the endocochleate cephalopods, there are animals inhabiting niches from the deep ocean benthos to the shallow reef

communities and the whole water column in between. These different cephalopods often have fin shapes that appear to be determined by the niche they inhabit and their way of life. For instance, the fast-moving, pelagic ommastrephid squid have small, triangular fins that appear to function mainly as rudders, while the slower-moving, coastal loliginid squid have large, rhomboidal fins that can be used for propulsion, manoeuvring or even "soaring" in upwelling currents (O'Dor *et al.*, 1991 & 1994). In addition, the complete marginal fins of cuttlefish are capable of highly complex wave production, providing them with efficient low speed manoeuvrability for their coastal, bottom-dwelling lifestyle. These three main fin shapes have particular advantages and disadvantages for the squid (Table 1), since no one fin is optimal for everything. Large loliginid fins, for instance, are useful at low speeds, but result in more drag at high speed than the small ommastrephid fins. The latter, however, cannot produce the efficient waves that larger fins can and, therefore, force the ommastrephid squid to rely heavily on their energetically costly jet propulsion system (Hoar *et al.*, 1994).

In addition to the different shapes found in squid with different lifestyles, the fins of squid also change shape as the animal grows. Virtually all squid hatch with small, round fins that increase in relative size with growth, until the squid forms the triangular/rhomboidal fins of the adult (Figure 1.1 for comparison of different shapes and changing shape). Boletsky (1987) noted that although squid hatchlings were fairly adept at jetting, they did not seem to have much control, possibly due to the small size of their fins. O'Dor *et al.* (1986) also noted that hatchling squid seemed primarily limited to vertical movements, again possibly a result of the small fins affecting the steering ability,

Table 1 Cephalopod fin form and function (from Hoar *et al.*, 1994).

	Ommastrephid (e.g. <i>Illex</i>)	Loliginid (e.g. <i>Loligo</i>)	Cuttlefish (e.g. <i>Sepia</i>)
Fin Form	Triangular*	Rhomboid*	Bordering/Marginal
Waving Fins	No	Yes	Yes
Flapping Fins	Yes	Yes	No
Fins Wrap in Escape	Yes	Yes	No
Balistiform Locomotion	No	No	Yes
Clap-and-Fling	Yes?	Possible	No
Flight	Yes	No?	No

*the shape of the fin varies through ontogeny, typically with fin surface area increasing faster than body length, see Figure 1.1

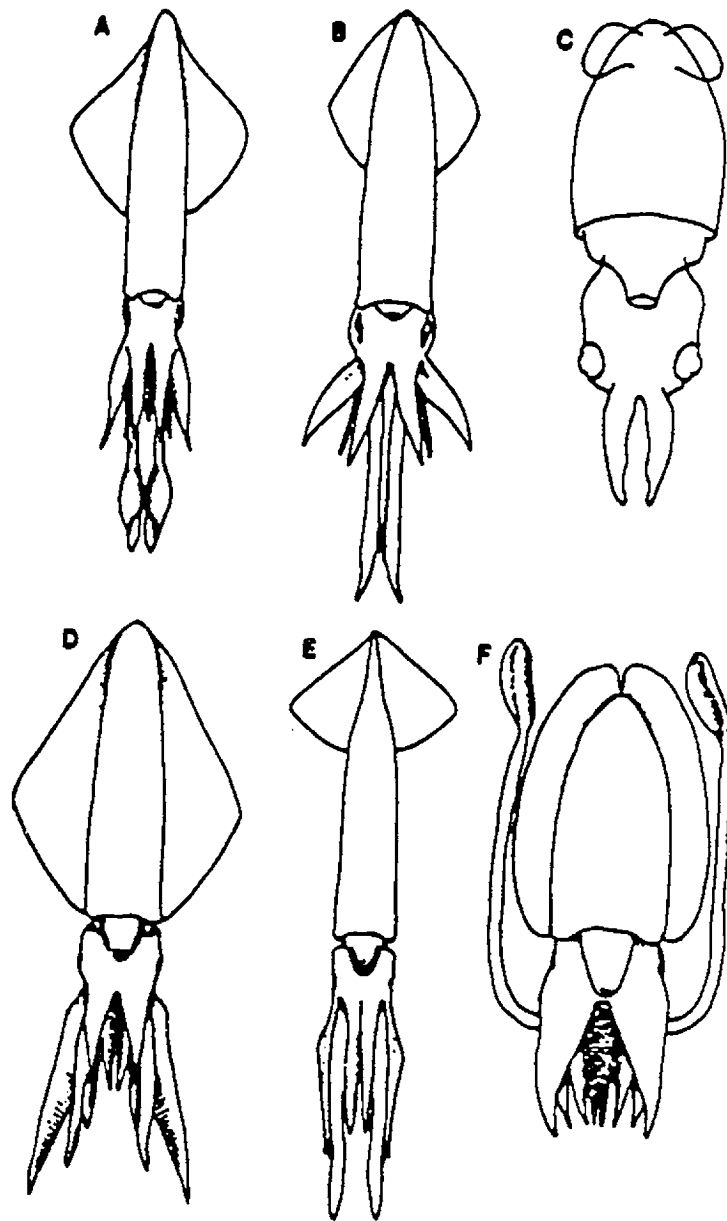


Figure 1.1. Cephalopod fin forms. A–C; Changes through ontogeny for a generalist squid, *Loligo vulgaris*: (A) adult (266mm ML); (B) juvenile (88mm ML); (C) hatchling (2.5mm ML). Other specialized fin types: (D) *Thysanoteuthis rhombus*; (E) *Illex illecebrosus*; (F) *Sepia officinalis*. (Redrawn by J.A.A. Perez from Naef, 1921/23, except for (C) from Packard, 1968; from Hoar *et al.*, 1994).

and they may be compensating for this by maintaining a more vertical orientation when swimming. There are only limited studies of hatchling swimming (Packard, 1969; O'Dor *et al.*, 1986), due to the difficulty of quantitative study of animals that accelerate faster than can be easily determined by video analysis. These hatchlings also traverse the range of Reynolds numbers (the dimensionless ratio of inertial to viscous forces acting on an object) from 1 to 1000 where neither viscous nor inertial forces dominate.

In an attempt to quantify the importance of scaling for energetics, O'Dor & Webber (1986) studied the available data, which suggested a difference in the scaling of cost of transport between jet and undulatory propulsion; for jetting squid (0.03–3.0kg) cost of transport scales as $\text{mass}^{-0.2}$ and for undulating fish, the factor is $\text{mass}^{-0.3}$ (Brett, 1965). When projected to smaller sizes, these factors predict jetting to be more efficient than undulation below a certain size (Hoar *et al.*, 1994), which may be reflected in both the ontogeny of the squid, with relatively large funnels and mantle volume, and the relative size of the fins at maturity.

All squids have fins as adults, although none of them use them as an exclusive form of locomotion. This study was undertaken to clarify the role of fins and their relationship to the use of the jet in a squid propulsion system that can be termed jet assisted finning (JAF). Chapter 2 defines the allometric changes for squid over a wide range of sizes, and provides a model of jet swimming that can be applied over this size range and can be modified for changes in the various factors affecting the jet thrust. Chapter 3 uses a modification of this jet swimming model to study the effect of changes in fin size by including the added effect of drag on the fins. Chapter 4 examines some

examples of the use of the fins by long-finned loliginid squid applying the models and principles presented earlier.

CHAPTER 2. Scaling of Morphometric Changes in Long-Finned Squid.

2.1 Introduction

Cephalopod locomotion studies are fairly recent, dating from Trueman and Packard's (1968) study of jet performance. To maximize thrust, most jet-propelled animals have developed a separate system of large inhalant and small exhalant apertures to increase efficiency and decrease time spent refilling, thereby decreasing the fluctuation in velocity as much as possible. The notable exceptions to this include cnidarian medusae, which are restricted to slow jetting. The small exhalant aperture, the funnel, is important not only because of its directibility, but also because of the dynamic control the squid has over funnel diameter (O'Dor, 1988a). This control allows squid to regulate flow by decreasing diameter as water volume being ejected decreases at the end of the cycle, thereby maximizing the thrust generated by a single jet. This optimization is important because the volume of water a squid can accelerate in a jet is restricted by its mantle volume and will generally be less than the amount of water that a similar-sized fish can accelerate during a tail beat (O'Dor & Webber, 1986), therefore despite its ability to optimize jet propulsion, squid will always be less efficient than fish. One area in which squid can surpass fish is in oxygen extraction from the water, because every jet must pass over the gills during the cycle. Therefore, squid are rarely subjected to oxygen stress, even at very high speeds or low oxygen tensions (O'Dor & Webber, 1986) and consume oxygen at the highest rate known for aquatic poikilotherms (Webber & O'Dor, 1985). To maintain an adequate oxygen supply when stressed, the cephalopods also use cutaneous

respiration, although that of octopus is the only one measured (less than 13% in *Octopus vulgaris*; Wells & Wells, 1983). Squid probably also use cutaneous respiration to some extent.

Since momentum is produced more economically by accelerating a large mass of water than a small one, it is an advantage for cephalopods to have large bodies and therefore, large mantle cavities. This means that squid should grow as fast as possible to take advantage of larger mantle cavities and this advantage is probably why cephalopods have rapid growth rates (Packard, 1972; Forsythe & van Heukelem, 1987). Interestingly, however, Clarke's (1966) study of oegopsid squid determined that only 30% of the 176 species studied had mantle lengths larger than 15cm. As nearly all large squid are oegopsids, this indicates that the majority of squid are small and the large ones are generally those associated with large current systems which carry the young to good feeding grounds (e.g. *Todarodes pacificus* in the northwest Pacific and *Illex illecebrosus* in the northwest Atlantic; O'Dor & Webber, 1986).

In early models of cephalopod locomotion, such as Siekmann (1963), jet propulsion was considered to be a periodic fluid jet from a tube, with the body itself treated as a rigid torpedo shape of constant mass, but the expulsion of water from the mantle causes both a mass change and a body shape change. Later models have been refined to include these concepts. Johnson *et al.* (1972) produced a model that adequately described a single jet for an adult squid, but does not take into account the sustained swimming usually seen in cephalopods. Also, when considering sustained swimming, the acceleration reaction, which Batchelor (1967) defined as a force resisting changes in

animal velocity, must be considered. Daniel (1983) found the acceleration reaction to be important for unsteadily swimming medusae, since the acceleration reaction is related to unsteady motion in animals, but its importance diminishes the longer a medusa swims after starting from rest (Daniel, 1984). O'Dor (1988a) found that for sustained swimming in squid, the relative importance of the acceleration reaction was only about 5% of forces acting on the animal and not the 50% it is initially. It is, therefore, likely that although the acceleration reaction might dominate during an escape jet, it is much less important for the usual continuous swimming of cephalopods.

The advent of swim tunnels for respirometric locomotion studies of both fish and squid led to a better understanding of movement; O'Dor's (1982) study of *Loligo opalescens* is the earliest example of this for squid. O'Dor's (1988a) analysis of the forces acting on the swimming *L. opalescens* was the first to include negative buoyancy and angled swimming, as opposed to neutral buoyancy and swimming parallel to water flow, as Johnson *et al.* (1972) had modelled. O'Dor (1988a) also provided a comprehensive study of the forces that a squid encounters during a jetting sequence, taking into account the periodicity, mass change and flexibility as well as remarking on the presence of the fins and their effect on drag and thrust. O'Dor's (1988a) study is the basis for the present analysis of the forces acting on squid over a wide size range and taking into account changes in body form over that range. This chapter contains both a morphometric analysis of the growth of various long-finned squid species (Family Loliginidae) and a model for the fluid dynamic forces of jet-propelled swimming for animals over a billion-fold mass range.

2.2. Materials and Methods

The morphometric measurements used in this study included wet weight, funnel circumference, mantle diameter, mantle thickness, mantle and total lengths, fin width, length and area (see Figure 2.1 and Appendix 1 for data). These measurements were made on *Loligo forbesi* (adults in the Azores and hatchlings from the Smithsonian Institute), *Sepioteuthis lessoniana*, *Loligo opalescens* and *Lolliguncula brevis* from Texas, *Loligo pealei* from Woods Hole, MA, and *Loligo vulgaris reynaudii* from South Africa.

2.2.1 *Loligo forbesi*

Loligo forbesi were caught with Japanese style jigs on 0.5mm galvanized wire lines near the bottom at 200m depth on traditional Azorean fishing sites. Male squid in the population studied may exceed 1m in total length (TL; total length is 1.47 times the mantle length) and approach 10kg mass (Porteiro *et al.*, 1990). These large squid are very fragile out of water and their gladii tend to break when handled, unless supported along their full length in a taut net or sling. The squid measured in this study ranged from 0.9–3.1kg. Morphological measurements were made on all 10 squid used for respirometry and on 17 squid caught, but not used due to gladius damage, for the tracking experiments of O'Dor *et al.* (1994).

2.2.2 *Sepioteuthis lessoniana* and *Lolliguncula brevis*

Morphometrics for eight juvenile *Sepioteuthis lessoniana* of both sexes (0.4–2.0g wet weight) were obtained from the culture facilities at the Marine Biomedical Institute

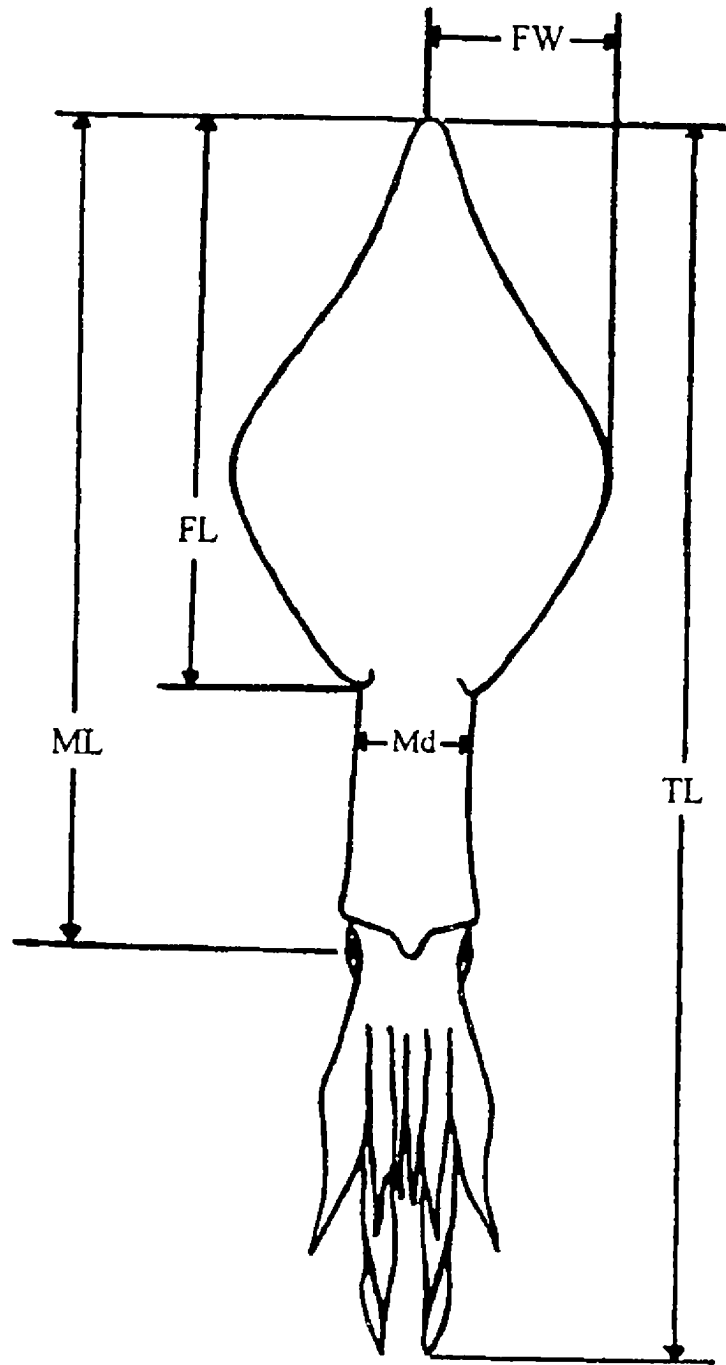


Figure 2.1. Dorsal view of adult *Loligo vulgaris* with general form and body measurements. Dimensions measured: TL, total length; ML, mantle length; FL, fin length; FW, fin width; Md, mantle diameter.

at the University of Texas, Medical Branch in Galveston for use in respirometry and swimming experiments. Eleven adult *Lolliguncula brevis* of both sexes (4.3–9.7g wet weight) were caught by bottom trawl in Galveston Bay, or the Gulf of Mexico immediately offshore from Galveston, and maintained in a 1.5m diameter by 1m deep tank until their use in swimming experiments. Morphological measurements were made on all squid following their use for experiments. Three large adult *Sepioteuthis lessoniana* (1.0–1.8kg) that were cultured in the Galveston facility and died (post-spawning mortality) during my visit were also measured and weighed.

A growth series of 11 *Loligo opalescens* from hatchling to adult (1.4mg–25g) were also obtained from the Galveston Marine Biomedical Institute and standard morphometric measurements were made.

In addition, four *Lolliguncula brevis* (1.1–2.6mg) and nine *Loligo forbesi* (5.7–7.2mg) ethanol-preserved hatchlings were obtained from the Museum of Natural History, Smithsonian Institution. Due to their small size, morphometric analysis was done under a dissection microscope using an Image Analysis System (Bioscan®–OPTIMAS). Measurements from 15 *Loligo vulgaris reynaudii* (100–810g) were provided by M.J. Smale, Port Elizabeth Museum, Port Elizabeth, South Africa and those for 30 *L. pealei* (80–110g) by M.A. Freadman at Woods Hole Oceanographic Institution at the author's request. Morphometric measurements were also obtained from the literature for three *L. vulgaris* (3.0mg–250g; Packard, 1969) and five *L. pealei* (1.0g–310g; Haeffner, 1964).

The morphometrics for a range of short-finned squid, including a larval and "standard" adult (O'Dor, 1988b) *Illex illecebrosus* and an adult *Architeuthis* are also

provided for comparison. Measurements of the former were taken from specimens in R.K. O'Dor's laboratory and the latter from dissection photographs obtained from F.A. Aldrich, Memorial University, Newfoundland. These data are not included in any regression analysis and, in all cases, are plotted on the graphs with a different symbol (\blacktriangle).

A model of the fluid dynamic forces acting on the squid was produced from the morphometric relationships as a "spreadsheet model" rather than a discrete mathematical model, using regressions from the real data and weights at power of ten intervals from 10^{-7} to 10^2 kg. These regressions produced numbers that could then be easily manipulated and graphed.

2.3. Results

2.3.1 Allometry

Standard morphometric measurements, and some extra measurements for modelling the locomotion of squid, were collected on the six species of loliginid squid. This provided a billion-fold mass range and thousand-fold mantle length range, which included both juvenile and adult squid, and allowed me to study the scaling of various body measurements and aspects of locomotion (see Appendix 1 for details). To maximize the data set measurements of preserved specimens and measurements from photographs of fresh specimens were included in samples distributed throughout the range from smallest to largest. It was not possible to make corrections for differences between fresh and preserved measurements, but it was more important to have data over the full range even though there was a contribution to the scatter on the graphs and decrease in the r^2

values for the regressions. They should provide no systematic error.

All morphometric measurements were regressed onto $\text{mass}^{1/3}$ to remove the effects of the dimensional relationship between mass (proportional to volume, a cubic measurement; density is 1023kgm^{-3}) and length (a primary measurement; measurements of area were regressed on $\text{mass}^{2/3}$), as discussed in Heusner's (1991) paper on the relationship of size and power. All relationships are expressed in the form $Y=aX^b$, where X is $\text{mass}^{1/3}$, Y the measured body dimension and the constants a and b represent the intercept and the constant of equilibrium of allometry, respectively, calculated from the linear regression of the log-transformed variables X and Y. If $b=1$, then isometry is indicated, $b>1$ indicates positive allometry and $b<1$ indicates negative allometry. These regressions were used to fill in gaps in the overall data set and as the basis of the model of jet swimming over the range 10^{-7} – 10^2 kg. Model parameters are presented relative to mass, as the work done by the squid is exerted on its mass as a whole.

Morphometric variations among the slopes of the regressions for the 6 species showed up as expected for differing species (Table 2.1), but the data were pooled to allow a more general description of the allometric growth changes for long-finned squid. The regressions for the pooled data were then used as the basis for the model of the fluid dynamic forces acting on jet swimming loliginids. In addition to the slopes of the regressions for each species, Table 2.1 contains the pooled data slopes. Whether the species slope is significantly different ($\alpha=0.05$) from the pooled slope is indicated, as well as whether the pooled slope differed significantly from 1 or isometry ($\alpha=0.05$). Morphometric variations are often used to define cephalopod species, but in the modelling

Table 2.1. The slopes of the regressions for separated species data and pooled data (* indicates either a regression is significantly different from the pooled regression or that the pooled regression is significantly different from 1 or isometry ($\alpha=0.05$)).

	<i>L. forbesi</i>	<i>L. vulgaris</i>	<i>L. pealei</i>	<i>L. opalescens</i>	<i>L. brevis</i>	<i>S. lessoniana</i>	Pooled Data
ML	1.18	1.21	1.22	1.19	1.18	1.15	1.20*
TL	1.17	1.09*	1.09	1.17	1.16	1.14	1.16*
FL	1.55	1.48	1.47	1.57	1.61*	1.31*	1.53*
FL on ML	0.69	0.67*	0.71	0.50*	0.47*	0.94*	0.71*
A _o	0.95	0.88*	0.63*	1.03	0.81*	0.89	0.98
Md	0.90	0.86*	0.81	0.85*	0.78*	1.05*	0.91*
X _m	1.28*	0.88*	NA	1.18	1.65*	1.03*	1.23*
FA	1.36*	1.34*	1.52*	1.41	1.43	1.31	1.43*
FW	1.21*	1.19*	1.56	1.25	1.35	1.35	1.34*

process the similarities are more important than the differences.

Mantle length (ML), the length from the tip of the mantle to the edge of the mantle above the head, and total length (TL), the length from the tip of the mantle to the tip of the retracted tentacle club are both positively allometric (Figures 2.2 & 2.3 respectively)

$$\text{ML } b=1.196 \quad \text{TL } b=1.165 \quad r^2>0.99$$

Fin length (FL) increases linearly with ML (Figure 2.4) and is positively allometric with $\text{mass}^{1/3}$ (Figure 2.5).

$$\text{FL} = 0.707\text{ML} - 0.0121 \quad \text{FL } b=1.527 \quad r^2>0.99$$

In all graphs, the highest and lowest mass values are those from an *Architeuthis* adult and an *Illex illecebrosus* hatchling respectively. There is also a mid-sized "standard" *I. illecebrosus* included. These three squids are represented by triangles. Since both squid species are short-finned and have a body shape unlike that of their loliginid cousins, they lie off the regression lines, which are calculated for the loliginid squid exclusively. They are included for comparison as they represent the largest and smallest squid measured, as well as the upper and lower limits for the model.

Funnel orifice area (A_o), derived from measurements of funnel diameter, dictates the thrust an animal can produce (Figure 2.6)

$$A_o \quad b=0.977 \quad r^2=0.97$$

The scatter in this graph is undoubtedly due to the state of the funnel when the diameter was measured (i.e. how stretched the animal was, how it had died and whether or not it had been preserved).

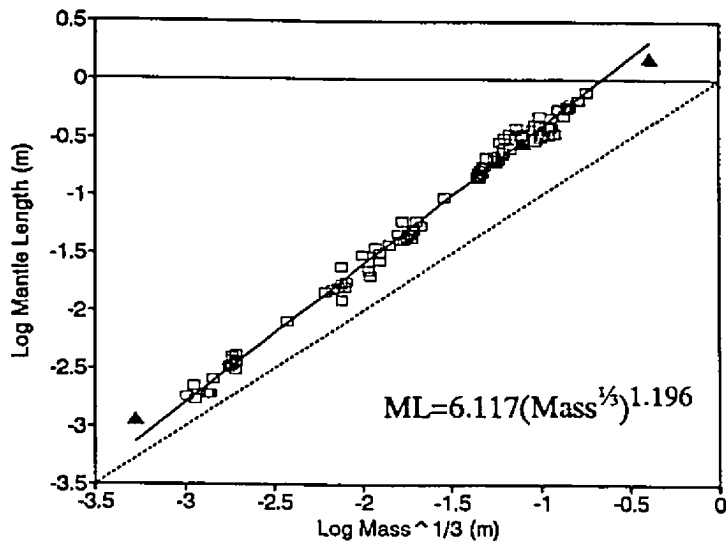


Figure 2.2. The allometric relationship between the log mass^{1/3} (m) and the log transformed mantle length data (m). The solid line indicates the linear relationship between the two log-transformed body proportions ($r^2 = 0.99$). In all morphometric graphs the three \blacktriangle s indicate the data for a larval and standard *Illex illecebrosus* and an *Architeuthis* and the dashed line represents the 1:1 relationship or isometry.

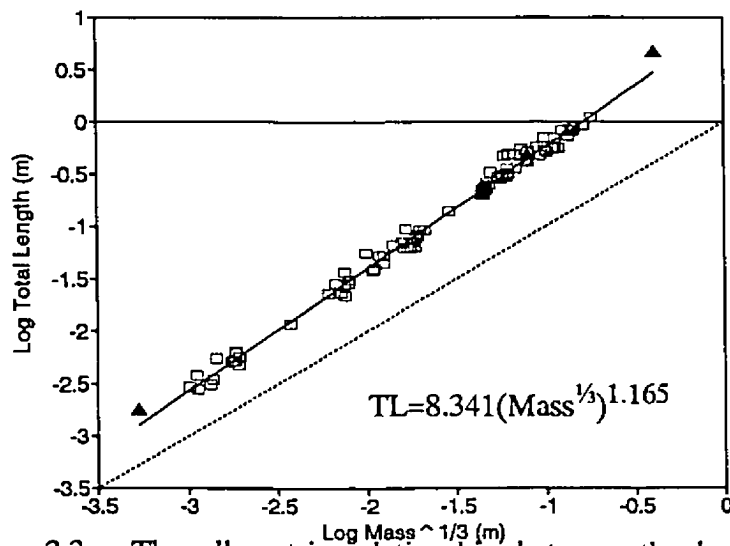


Figure 2.3. The allometric relationship between the log mass^{1/3} (m) and the log transformed total length data (m). The solid line indicates the linear relationship between the two measurements ($r^2 = 0.99$). The three \blacktriangle s indicate the data for a larval and standard *Illex illecebrosus* and an *Architeuthis* and the dashed line represents the 1:1 relationship or isometry.

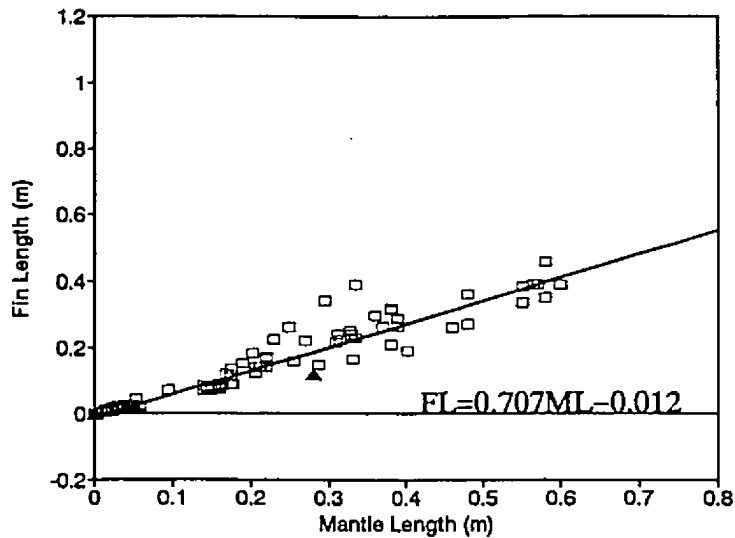


Figure 2.4. The allometric relationship between the fin length (m) and the mantle length (m). The solid line indicates the linear relationship between the two measurements ($r^2=0.98$). The graph has been truncated (does not show the *Architeuthis* specimen) to show the spread of the data more effectively.

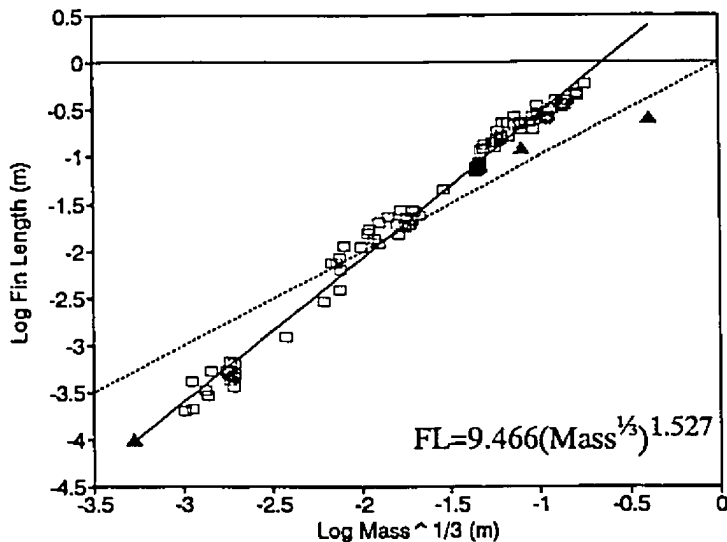


Figure 2.5. The allometric relationship between the log mass^{1/3} (m) and the log transformed fin length data (m). The solid line indicates the linear relationship between the two measurements ($r^2=0.99$).

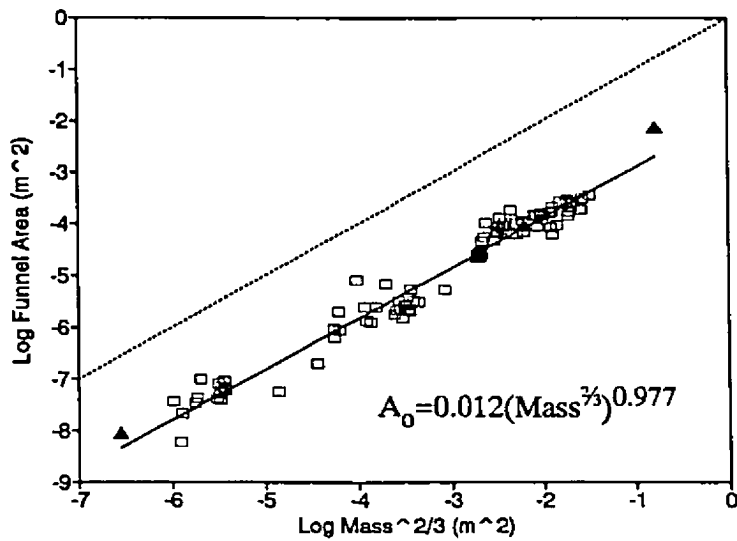


Figure 2.6. The allometric relationship between the log mass^{2/3} (m) and the log transformed funnel area data (m²). The solid line indicates the log-log relationship between the two measurements ($r^2=0.97$).

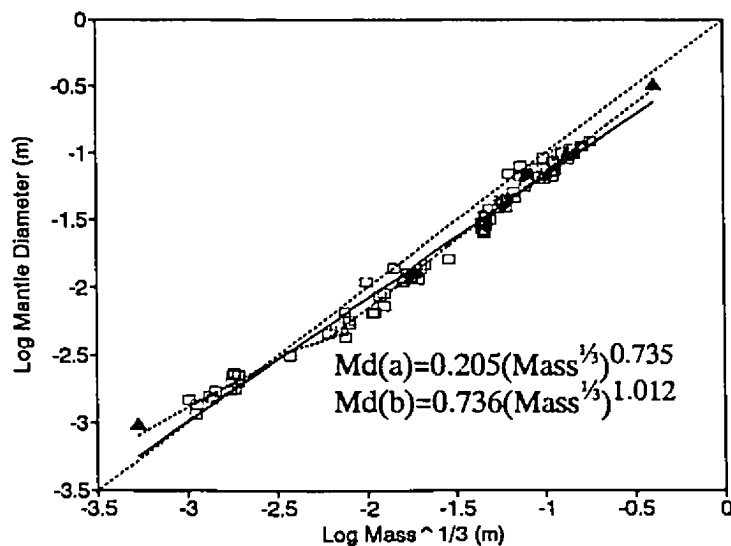


Figure 2.7. The allometric relationship between the log mass^{1/3} (m) and the log transformed mantle diameter data (m). The solid line indicates the log-log relationship between the two measurements ($r^2=0.98$) and the dashed line indicates the log-log relationships between the two measurements when the data are split at the discontinuity ((a) -3.33 to -2.33 m $r^2=0.84$ and (b) -2.0 to -0.33 m $r^2=0.99$).

Mantle diameter, which is critical because of its relation to both drag and mantle volume (and, therefore, the jet thrust) is unlike the former morphometrics in that two distinct trends in slope for the data occur, changing at about 0.1g. The regression utilizing all the data at once is

$$Md \quad b=0.910 \quad r^2=0.98$$

However, when the data are separately regressed in two sections, the r^2 for the large end of the graph improves and, therefore, two equations were used to model the change of this important body measurement with growth (Figure 2.7). The split between the sections was determined initially by eye and then by dividing the squid into those animals with Reynolds numbers below or above 1000.

$$\text{for squid } 10^{-7}-10^{-4}\text{kg} \quad b=0.735 \quad r^2=0.84$$

$$\text{for squid } 10^{-3}-10^2\text{kg} \quad b=1.012 \quad r^2=0.99$$

This shift in slopes occurs at the size of squid which perform at Reynolds numbers of about 1000, which is considered the upper limit of where viscous forces dominate and it may be a functional change which prompts the shift in growth.

The mantle thickness (X_m) is the thickness of the mantle at the point of maximum mantle diameter (Figure 2.8) and the data showed a change in the trend of slope at about 0.1g. The regression for all the data together is

$$X_m \quad b=1.229 \quad r^2=0.96$$

The use of two equations to describe the different trends resulted in a more significant r^2 value for the larger specimens, although the smaller specimens had a poorer fit

$$\text{for squid } 10^{-7} \text{ to } 10^{-4}\text{kg} \quad b=1.927 \quad r^2=0.62$$

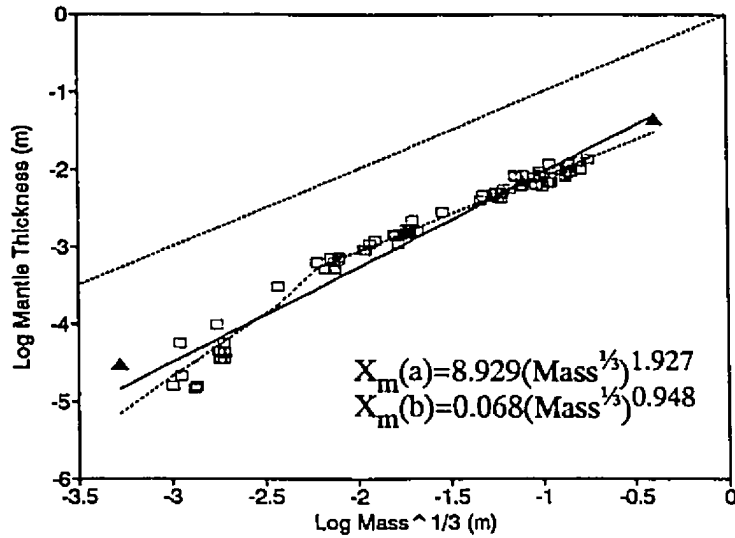


Figure 2.8. The allometric relationship between the log mass^{1/3} (m) and the log transformed mantle thickness data (m). The solid line indicates the log-log relationship between the two measurements using all data ($r^2=0.96$); the dashed line indicates the log-log relationships for the data split at the discontinuity ((a)-3.33 to -2.33m $r^2=0.62$ and for (b)-2.0 to -0.33m $r^2=0.98$).

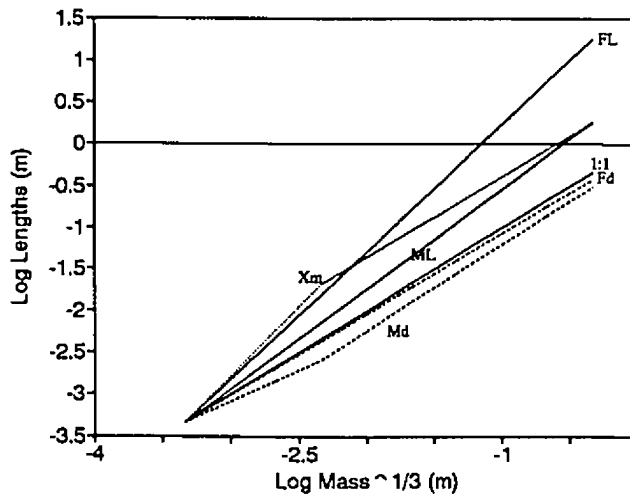


Figure 2.9. The slopes for the relationships between length changes and mass used for the swimming model, presented as the log transformed length change (m) versus the log mass^{1/3} (m). The 1:1 relationship is graphed for comparison.

for squid 10^{-3} to 10^2 kg $b=0.948$ $r^2=0.98$

The scatter at low sizes in the X_m graph can probably be attributed to the difficulty of measurements using the microscope, but may also reflect the nutritional condition of the individuals.

The regressions for the allometric length changes are compared in Figure 2.9, in which all regressions have been offset to start at the same size and then graphed against $\text{mass}^{1/3}$ to illustrate differences in slope. The most immediately apparent difference is the much higher slope of the FL regression from the increasing relative size of the fins throughout the size range. Funnel area is nearly isometric, perhaps because of its important relationship to jet thrust. X_m increases very rapidly at low sizes, compensating for the negative allometry of the mantle diameter.

2.3.2 Fluid Dynamic Modelling

Fineness ratio is the ratio of the total length over the maximum thickness (mantle diameter in this case) and increases with increasing body size from about 2 (in hatchlings) to 14 in giant squid (Figure 2.10). A fineness ratio of about 4–6 characterizes most animals swimming at Reynolds numbers above 10^5 (Blake, 1983a).

Reynolds number is the dimensionless ratio between the inertial and viscous forces acting on an object and is very important in the study of biological fluid dynamics. Using the morphometric measurements for the range of squid species and sizes, and assuming that the squid are travelling at 1 body length per second (BLs^{-1} ; see O'Dor & Webber, 1986 for critical swimming speeds), the Reynolds number (Re) was calculated as

$$Re = Lu/\text{kinematic viscosity} \quad (u=\text{velocity})$$

To calculate the Reynolds number for the body (R_b), TL was used for the standard length (L) and for the fins (R_f), FL was used.

Drag is a fluid dynamic force that acts on a body moving in a fluid, in the opposite direction to the motion of the body and is proportional to the square of the relative speed of the body with respect to the fluid and the external shape and frontal area dimensions of the body (Azuma, 1992). Drag is a product of the dynamic pressure on the object, the area of the object and the dimensionless variable that accounts for the variations in drag (which is a function of the body's Reynolds number).

$$D = 0.5dSu^2 (dLu/\mu)^a \quad (d=\text{fluid density, } \mu=\text{fluid viscosity, } S=\text{wetted surface area})$$

In practice, the exponent (a) is dealt with by calculating the drag coefficient which is a dimensionless number that is a function of the Reynolds number ($C=f(Re)$ or $(Re)^a$) and is used to describe drag (i.e. C is the drag per unit area divided by the dynamic pressure; Vogel, 1989). The drag coefficient for the body (C_b) was calculated from R_b and morphometrics using White's (1974) equation for a sphere for those squid with R_b less than 1000 (the globular-shaped hatchlings)

$$C_b = 24/R_b + 6/(1+R_b^{0.5})+0.4$$

and for squid with R_b over 1000, O'Dor's (1988a) equation corrected for a streamlined body as

$$C_b = (1.33/R_b^{0.5})[1+1.5(2r_m/TL)^{1.5}+0.7(2r_m/TL)^3] \quad (r_m \text{ is mantle radius})$$

Drag on the body was calculated using the appropriate surface area measurements (i.e. sphere frontal surface area for squid of $Re < 1000$ and wetted surface area of a prolate spheroid for squid of $Re > 1000$) and the equation from O'Dor (1988a)

$$D = 0.5CdSu^2 \quad (d \text{ is density of seawater})$$

The total drag (D_t) on the animal is merely the sum of all the drag acting on the body, in this case, the drag on the body and fins. This total drag is actually an underestimate of all the drag forces acting on the animal, since the drag for the fins is calculated as the drag acting on flat plates, as explained in Chapter 3.

Thrust is the addition of momentum to a moving object in a fluid and because drag can be viewed as the rate of removal of momentum from a flowing fluid, the thrust an animal produces to move at a steady speed must at least equal the total, or parasite, drag as well as produce some lift to counteract sinking in these negatively buoyant squid. In this model, we assume that squid climb and move parallel to their body axis. In these squid the thrust produced by the jet is calculated using O'Dor's (1988) equation

$$T_j = 0.5d(V_w/2t)^2/A_o \quad (V_w \text{ is mantle water volume calculated}$$

as $V_w = \pi 0.4(ML)[r_m^2 - (0.7r_m)^2]$, t is cycle time or the time between mantle filling cycles)

The frequency of jetting for squid over the size range 1mm–1m was counted from video of free swimming squid at 20°C and a regression calculated for the relationship of frequency to squid size (Figure 2.11). This frequency regression was then used to calculate cycle time for a jet for all animals in the data set, which in turn was used to calculate the flow rate for jet thrust through the funnel. A single funnel area, A_o (four

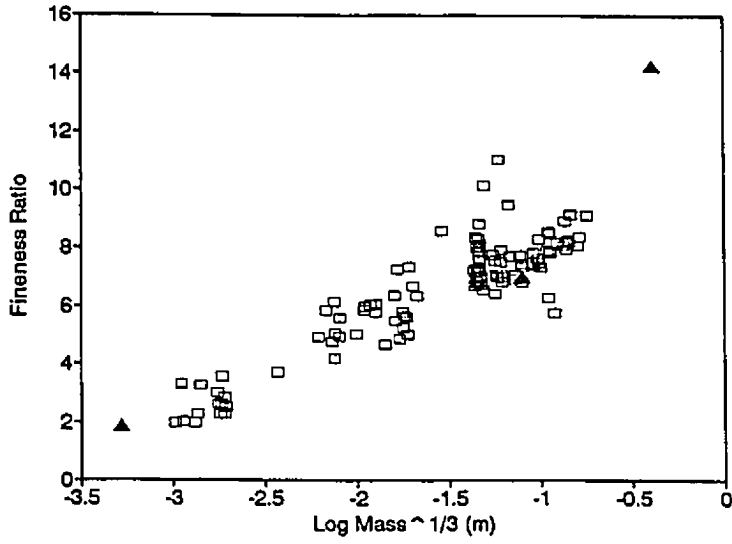


Figure 2.10. The relationship between log mass^{1/3} (m) and Fineness Ratio (TL/Md).

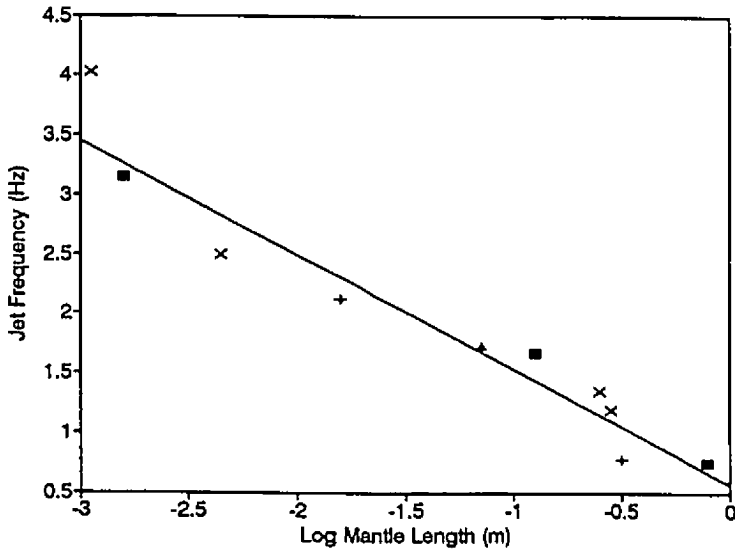


Figure 2.11. The relationship between jet frequency (Hz) and mantle length (m) for various squid species; *Illex* (x), *Loligo* (■), *Lolliguncula* (▲), *Sepioteuthis* (+).

times the measured area), was used to calculate T_j , although squid are known to vary the diameter of their funnel throughout the jet itself (to maximize the jet cycle, squid decrease the funnel area as the V_w decreases through the jet cycle; O'Dor, 1988a).

Froude Efficiency (E_f) is a measure of swimming performance, relating the useful power to the power lost to the fluid and was calculated for jet swimming as

$$E_f = u/(u+0.5u_j) \quad (u \text{ is squid's swimming speed, } u_j \text{ is jet speed}$$

calculated as V_w/t_c , from O'Dor, 1988a)

Using the Froude Efficiency calculated above and the jet thrust, a measure of the squid's effective jet thrust was calculated as

$$T_{je} = E_f \cdot T_j$$

In addition to completing these calculations on the complete data set, all morphometric measurements were regressed onto the log mass of the squid and a model of the forces acting on a jet swimming squid was constructed from these regressions to cover the size range of 10^{-7} to 10^2 . This model was extended to include not only those measurements for animals moving at 1BLs^{-1} but also 0.25 , 0.5 and 2BLs^{-1} and was then manipulated to study the effect of changes in funnel area and cycle time on the thrust the squid can produce and its relation to the drag on the animal.

The stress placed on the mantle muscle during a jet was also calculated and is included in Figure 2.12 with the drag on and thrust produced by a squid moving at 1BLs^{-1} . Figure 2.13 is a graph of the drag on the body of the squid at the different speeds and the thrust generated by the squid, illustrating the masses at which crossovers occur for these two forces at different speeds ($<0.1\text{mg}$ at 0.25BLs^{-1} , 0.5mg at 0.5BLs^{-1} ,

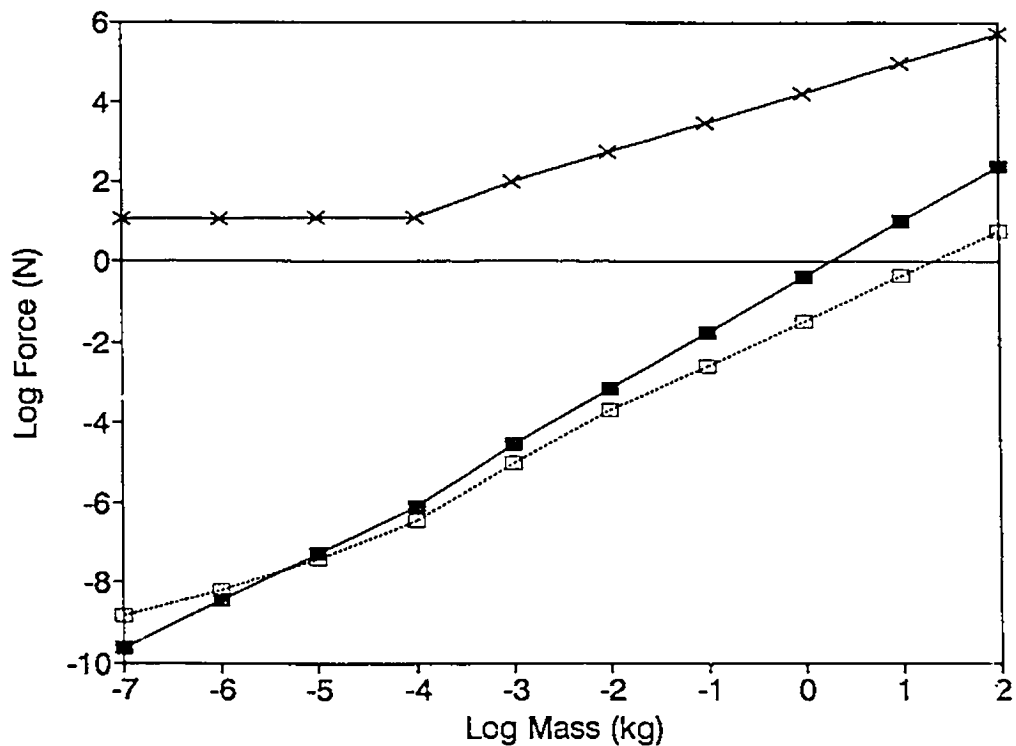


Figure 2.12. The relationship between the log mass (kg) and the log transformed model data for the stress produced on the mantle muscle by a squid moving at 1BLs^{-1} (x; N/m), the thrust produced by that squid (■; N), and the drag on the body of the squid (□;N).

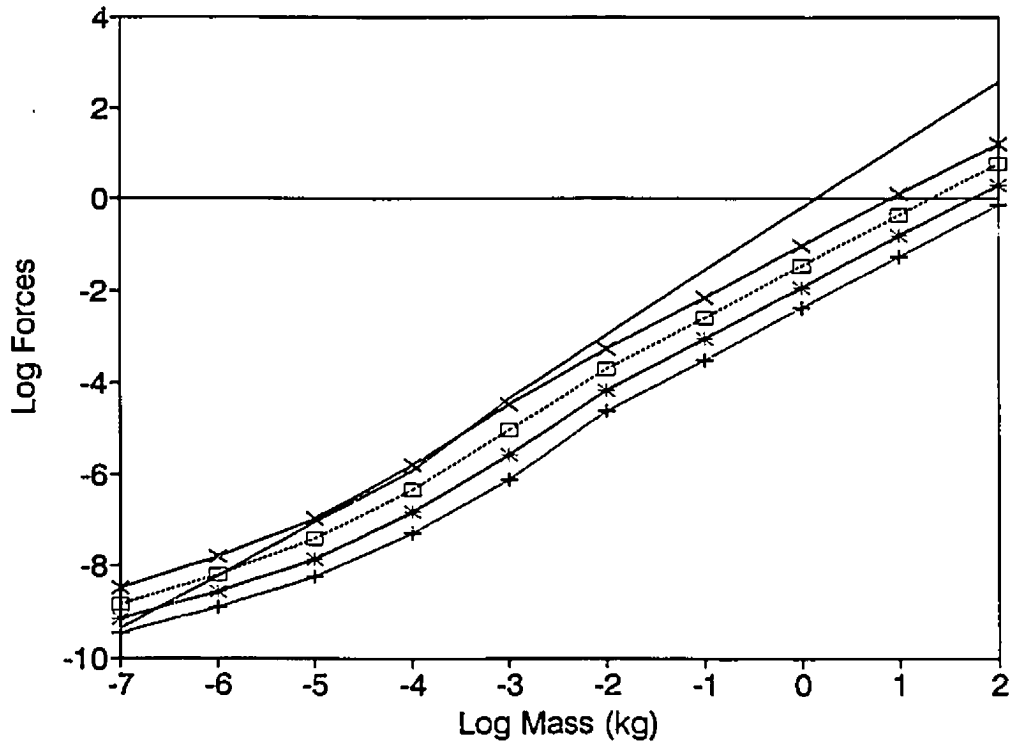


Figure 2.13. The relationship between the log mass (kg) and the log transformed model data for the effective thrust (T_{je}) the squid can produce (solid line; N) and the drag on the body at $0.25BLs^{-1}$ (+), $0.5BLs^{-1}$ (*), $1.0BLs^{-1}$ (□) and $2.0BLs^{-1}$ (x).

1mg at 1BLs^{-1} and 50mg at 2.0BLs^{-1}). To attain a certain speed, a squid must be able to produce as much thrust as the drag acting on it and therefore, animals weighing less than the critical mass on the graph should theoretically be unable to swim at the indicated speed.

The model suggests that animals below the crossover size must alter parameters such as funnel orifice or cycle time to swim at higher speeds. The model was also manipulated to study the effects of changes to the funnel area, cycle time and mantle radius since these determine the force of the jet. Figure 2.14 illustrates the changes to effective thrust that occur when A_o is quartered ($A_o/4$) and quadrupled ($A_o * 4$), cycle time is doubled ($2t$) and the mantle radius at its most contracted is 0.6 times the relaxed radius rather than 0.7 ($0.6r$). These are all compared to the standard (STD) T_{je} from the model and D_b for comparison of crossover points. Figure 2.15 illustrates the change that occurs to Froude Efficiency for the squid when the A_o is doubled, quadrupled and halved. Halving the A_o decreases the efficiency by about 50%, and both doubling and quadrupling A_o leads to a doubling or quadrupling of efficiency.

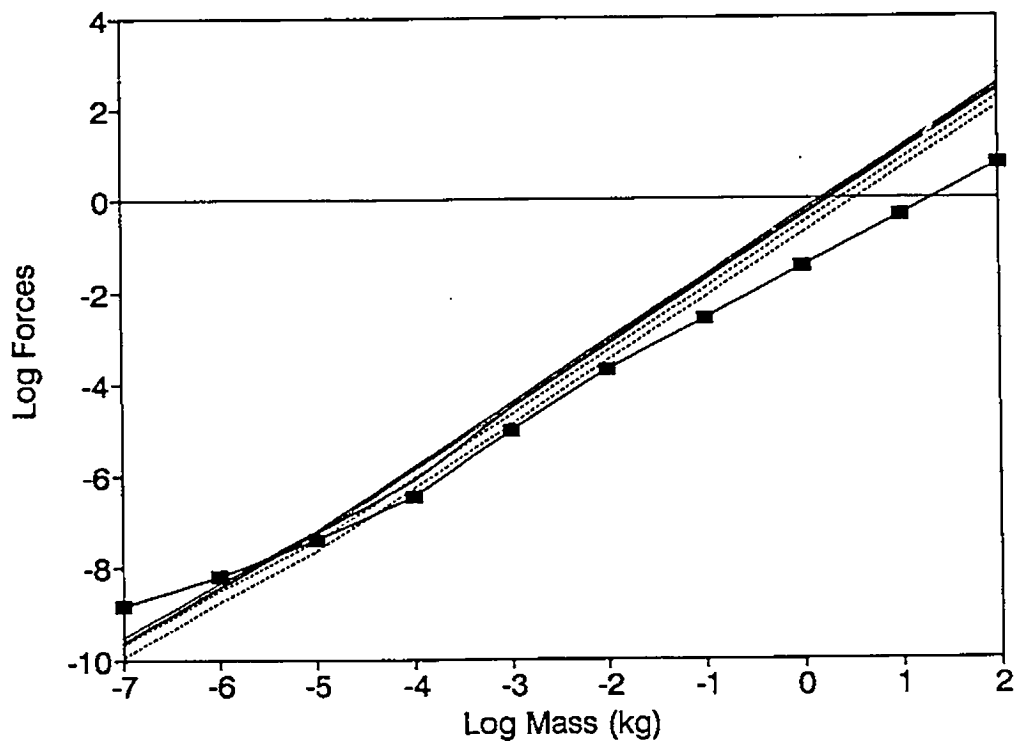


Figure 2.14. A comparison of the relationships between the log mass (kg) and the log transformed model data for the effective thrust (T_{je}) produced by a squid when changes are made to the model ($\frac{1}{4}A_0$ (dotted line), $4A_0$ (dashed line), 2 cycle time (centre-line), and 0.6 mantle radius (solid)) compared with drag on the body ($\blacksquare;N$), all at $1BLs^{-1}$.

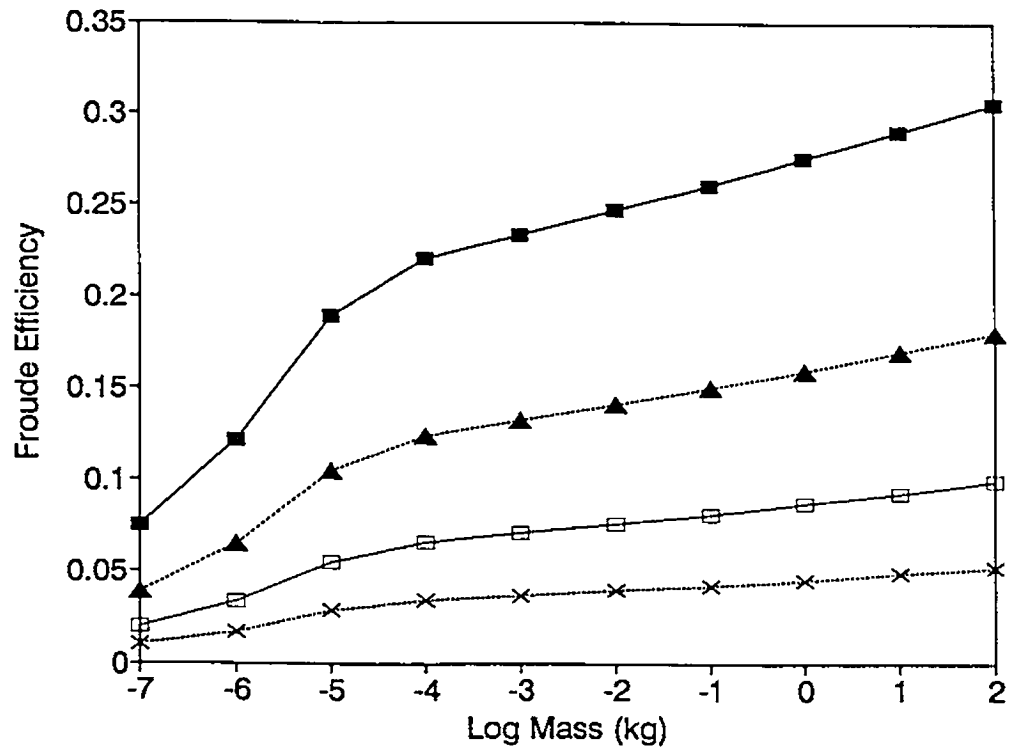


Figure 2.15. The relationship between log mass (kg) and Froude Efficiency at $1BLs^{-1}$ for model squid with changes made to the funnel area; $4A_0$ (■), $2A_0$ (▲), standard A_0 (□) and $\frac{1}{2}A_0$ (×).

2.4. Discussion

Other than Packard's (1969) comparison of the different shapes and morphometric measurements of hatchling, juvenile and adult *Loligo vulgaris*, studies of squid movement have primarily used adult squid. My study of various loliginid species from hatchling *Lolliguncula brevis* (1.1mg) to adult *Loligo forbesi* (6kg) is an attempt to extend the size range for studies of squid locomotion.

Scaling concerns the structural and functional consequences of changes in size or scale among otherwise similar organisms (Schmidt-Nielsen, 1991), so for this study, it refers to the changes that the squid undergo as they grow and also the differences between different loliginid species with different adult sizes (eg. 5g *L. brevis* to 5kg *L. forbesi*). As squid are aquatic animals that must swim or sink (due to their negative buoyancy), the changes in how they move, and the parts they move with, should be related to the change in the hydrodynamic forces acting upon them as they grow. For example, since Reynolds number (Re) is the ratio of inertial to viscous forces and changes greatly as the squid grows (i.e. from 1 to 1 000 000), there should be changes in the animals' body shape and mode of locomotion, especially since the change from a viscous- to inertial-force dominated system affects so many forces. Some of these changes are driven by scale alone, others seem to reflect the slight niche differences between species.

Most squid hatchlings have relatively round bodies with very small, circular fins that are about 15% of their mantle length (=0.15ML). *Sepia* species hatchlings are much larger (0.5g) than squid hatchlings and have fins about 0.8ML, but since they possess a cuttlebone and are, therefore, neutrally buoyant, they were not considered for this study.

Sepioteuthis lessoniana, like *Sepia* species, have complete fins (i.e. 1.0ML) as adults and, unlike the other loliginids studied, hatches with relatively long fins (0.4ML), approaching *Sepia*. Since *S. lessoniana* is also negatively buoyant, it is a good comparison to the other loliginids, whose adult fins only range from 0.4–0.7ML. As all squid grow, there is a general change in body shape from the rotund hatchling to a slender, more streamlined adult, a change that has been previously noted (Packard, 1968; Clarke, 1966). The changes in squid shape imply a need for some modification of movement and these are the changes that I studied.

As the squid grows the mantle length, mantle thickness and fin length all grow in a positively allometric fashion ($b > 1$), but fin length has the most striking relative increase with growth (Figure 2.9). This relatively fast increase with growth that produces the ontogenetic change in fin shape, seen in virtually all squid, increases drag forces and possibly fin thrust. Mantle length, although exhibiting positive allometry, has a slope much less than fin length, which leads to the relative increase in fin shape with size. To produce enough jet thrust to move a larger mantle, a squid would also require more muscle and since the mantle is virtually solid muscle (with only thin skin layers and collagen arrays; Gosline & Shadwick 1983), this would lead to increased mantle thickness. The ability to generate force is important, since there appears to be a fixed maximum tension that muscles can produce. Thus, as the tension increases linearly with increasing diameter for a given pressure according to La Place's Law the ability to produce jet pressure depends on increasing thickness.

The measurement with the greatest effect on jet thrust, funnel area, has a slope

that is virtually isometric (Figure 2.9), which may be because the squid have dynamic control of the funnel. The regression lines for mantle diameter and mantle thickness are made up of two equations (one for squid with $Re < 1000$ and one for $Re > 1000$) due to the discontinuity apparent in the slope of the raw data. M_d is an important parameter for determining the mantle water volume and it is interesting to note that at small sizes ($Re < 1000$), the M_d increases relatively slowly and therefore, it is primarily the increase in ML that affects the mantle volume increase at these sizes. This is a tradeoff related to the elongation of the squid as they grow and the transition point ($Re \approx 1000$) may indicate where the M_d begins increasing as quickly as increasing ML . To compensate for the decrease in volume due to the slow increase in mantle diameter, the rapidly increasing mantle thickness allows for a maintenance of the same jetting ability, because the thicker mantle can produce higher pressure on the mantle water volume. Funnel area, on the other hand, maintains its almost isometric growth with $mass^{2/3}$ throughout the size range, which appears anomalous since $T_j \propto 1/A_o$ and therefore, A_o dictates the thrust the squid can produce. Dynamic funnel control would also allow the squid to maintain high pressure throughout the jet if they decrease funnel diameter towards the end of the jet cycle and, therefore, maintain flow rate throughout the jet cycle as the diameter of the contracting mantle decreases. A fast flow rate is not always the most efficient system, however, as it is the larger, slower moving water masses that are more efficient than smaller, fast ones (Alexander, 1977). Therefore, when the A_o is increased, although there is a decrease in T_j (Figure 2.14), there is an increase in Froude efficiency (Figure 2.15). For squid with dynamic funnel orifice control, which can be used to maximize these

changes for better efficiency, the maximum diameter of the funnel is the major limiting factor.

There are two different types of flow regimes in fluids; laminar flow, in which all fluid parcels move parallel to each other in a smooth path, so that both large- and small-scale fluid movements are the same, and turbulent flow, in which fluid parcels move in an irregular manner, even if the fluid as a whole is moving in one direction. Therefore, in turbulent flow, there are small-scale motions occurring in directions other than the main large-scale flow (Vogel, 1989). The transition between these two flow regimes is typically at a Reynolds number of about 10^5 , and many biologically important events occur near this transition point. To remain below the transition point (and moving above it can be energetically costly), animals may either choose to move slowly or may maintain an optimal body profile, which is a streamlined body form in which the length to width (or fineness) ratio is about 5. This optimal body profile allows the animal to maintain laminar flow at a higher Re than is possible without it. Adult loliginid squid have a fineness ratio of above 4–5 (Figure 2.10) and do not have a perfectly optimal profile due to the presence of the long fins, thus at high speeds, rolling the fins along the mantle is one way to improve the body profile (Webber, 1985; O'Dor, 1982; Bradbury & Aldrich, 1969; Zuev, 1965a).

Why would a large squid deal with energetically expensive turbulent flow when moving at 1BLs^{-1} and above? The answer probably is that they generally do not. In the wild, larger adult loliginids do not venture above 1BLs^{-1} (and in fact swim significantly slower than 1BLs^{-1}), unless being chased by a predator or for short accelerations to

capture prey (O'Dor *et al.*, 1994). For large squid moving slower than 1BLs^{-1} , the Reynolds number remains below the transition (since Re is proportional to speed and body size) and the large fins become important for undulatory locomotion. This form of locomotion is energetically more efficient at low speeds than pure jet propulsion (Hoar *et al.*, 1994). Since they move slowly in nature, loliginids can usually operate within the laminar flow regime without having an optimal body profile since the presence of the large fins disrupts the animal's streamlining (Aleyev, 1977). It is interesting to note that those squid which do habitually move at high speeds, such as the oceanic, ommastrephid squid, have relatively smaller fins (ie. *Illex illecebrosus* has fins of 0.2ML , equivalent to a hatchling loliginid; Hoar *et al.*, 1994) and more closely resemble the optimally streamlined body profile that would allow them to remain within the laminar flow regime up to the higher speeds at which they operate.

To understand how the forces acting on the squid change in relation to one another with increasing size in squid, I combined my morphological data with previously published data (Hoar & Freadman, in prep.; Packard, 1968; Haefner, 1964). Thrust production of the squid throughout the size range is plotted along with the body drag on the squid (equivalent to a finless squid and also to the optimal body profile that encourages the maintenance of laminar flow at higher speeds; Aleyev, 1977) for squid moving at 1BLs^{-1} (Figure 2.12). As the crossover of D_b and T_{je} occurs at 1mg , only squid below this size will have trouble moving at 1BLs^{-1} , and, since most squid (especially long-finned ones) hatch at a larger size, this problem is usually avoided.

Figure 2.13 illustrates the changes of body drag for squid moving at different

speeds and speed definitely has a significant effect on drag, so that in general these squid should move slowly. If the drag is greater than the effective thrust, a squid would be decelerating, so small animals must move slowly and avoid the higher drag.

Squid have dynamic control of their funnel diameter and so the T_{je} in the graphs may not be the thrust actually produced at those speeds. They can also change the cycle length to a degree, especially if they incorporate the radial muscle to expand the mantle in the jet refilling stage, and it is probable that they can change the maximum contraction of the mantle (thereby decreasing the mantle radius at final contraction). The effect of these changes on T_{je} were studied by manipulation of the model (Figure 2.14), but they caused very little change to T_{je} . Only quadrupling A_0 and doubling cycle time had any appreciable effect on T_{je} , decreasing it slightly, and this is due to the fact that the Froude Efficiency for these models is very low. When T_{je} is calculated, the decreased efficiencies absorb most of the increase in actual thrusts. Figure 2.15 illustrates the changes to the Froude Efficiency when just the funnel area is changed; either quadrupled, doubled or halved. The increase in efficiency seen with the doubling and quadrupling of A_0 for squid moving at $1BLs^{-1}$ occurs since by accelerating the water through a large aperture, they are more efficient at attaining speed than if the aperture were smaller (Alexander, 1977). What the squid probably do is change the funnel diameter over the course of the jet cycle, from large at the start when the mantle is full, to smaller towards the end, to increase the thrust generated from the decreased volume flow rate.

The model exaggerates the problem because it uses average animal speed. In fact, during the jet phase the squid increase speed rapidly and efficiency increases, but during

refilling the animals decelerate. There is, of course, no real loss of efficiency during this phase as there is no thrust. However, this efficiency effect makes maintaining jet velocity to the end of contraction by constricting the funnel especially important. On the other hand, this model also neglects the losses due to the acceleration reaction, which is highest at low speed (Daniel, 1984) and those due to accelerating water for refilling, which increase with increasing speed. These three sources of error probably balance each other and have been ignored to reduce model complexity and facilitate scaling.

CHAPTER 3. Fin Morphometry and Its Effect on the Forces Acting on Swimming Squid

3.1. Introduction

Models of squid swimming have generally focused on understanding the jet system (Siekmann, 1963; Trueman & Packard, 1969; Johnson *et al.*, 1972; Wells, 1990). O'Dor's (1988a) study was the first to incorporate the fins, and the forces acting upon them, into a model of squid locomotion, in an attempt to resolve the differences between the measured costs of locomotion and those predicted by earlier analyses.

Since fins are not only an integral part of any squid, but also vary in relative size and shape both among species and over ontogeny, they are a vital component of any model of squid locomotion. The paired lateral fins not only stabilize motion, but also can have other advantages and disadvantages for the squid (see Table 1: Hoar *et al.*, 1994) depending on their shapes, which seem to be correlated with the animal's lifestyle. For example, the ommastrephid squid, which are fast moving, open-ocean, pelagic animals, generally have very small, triangular fins that act as rudders to steer the animal, but are incapable of producing waves. Loliginid squid, on the other hand, are slower moving, coastal animals that are often associated with complex environments. In these environments, manoeuvrability is key and the loliginids' large rhomboid fins are capable of the finely controlled undulatory locomotion necessary to accomplish this. The ultimate example of manoeuvrability at low speed is the cuttlefish, whose bordering fins are so efficient at undulatory locomotion that its jet seems to be little more than a byproduct of

respiration, especially since the cuttlebone has solved the negative buoyancy problem.

The shape changes with growth within species are even more dramatic than the variations among species. Virtually all squid hatch with small round fins which elongate through growth to become the large and long structures of the adults. This fin shape change could have as much effect on the drag on the animal as growth alone played in the jet model. An animal with large fins will find moving fast (above $1BLs^{-1}$) to be prohibitive due to the increase in drag and therefore, when escaping from predators, most large-finned squid revert to a more optimal body profile by rolling the fins tightly against the mantle. Aleyev (1977) noted that at low speeds the squid used their fins and jet to simultaneously produce thrust, while at high speed using jets alone and folding the fins.

Aleyev's (1977) analysis of cephalopods also revealed that squid use the jet alone immediately post-hatching, when the mantle fins are incapable of undulatory movements. This chapter, therefore, focuses on the changes in fin shape with growth. To study the effects of possessing large fins versus small fins, the basic squid swimming model from Chapter 1 was modified and compared to differences between real squid.

3.2. Materials and Methods

The morphometric data collected on the 15 *Loligo vulgaris reynaudii*, 27 adult and 9 hatchling *Loligo forbesi*, 11 adult and 4 hatchling *Lolliguncula brevis*, 3 adult and 8 juvenile *Sepioteuthis lessoniana* described in Chapter 1, as well as the published data for 30 (Hoar & Freadman, in prep.) and 5 (Haefner, 1964) *L. pealei* and 3 *L. vulgaris* (Packard, 1969) were used in this analysis.

3.3. Results

Some of the morphometric measurements of the fins used here are not among the common taxonomic measurements for squid, but for a study of fin propulsion, had to be included. Fin area (FA), the surface area of a single fin and fin width (FW) (the width of a single fin, as opposed to the total fin width) also increase rapidly with increasing body mass (Figures 3.1 & 3.2 respectively). The slopes of these regressions are significantly different from that for fin length.

$$FA \quad b=1.428 \quad FW \quad b=1.335 \quad r^2>0.97$$

In loliginid squid, whose fins are located on the side of the mantle, the total fin width is significantly different from twice the fin width, since it includes a portion of the mantle. Ommastrephid squid on the other hand have fins that are located on top of the mantle, so that the total fin width is equal to twice the fin width.

When the ratio of FW:FL, an indication of the general shape of the fin, is plotted, there is a decrease in the ratio with increasing mass of the squid (Figure 3.3). The graphed relationship shows a decrease towards a ratio of 0.37, with increasing squid size over a three order of magnitude mass range (0.03–6kg) of three different species all having the same general fin shape and similar growth trajectories. The ratio of FL:ML, which is a measure of the relative size of the fins, increases with increasing mass (Figure 3.4). The clusters of points on the graph are species groupings where I have a number of measurements for animals of similar size. Those animals for which I have a size range show a general increase in FL:ML ratio and, except for *S. lessoniana's* special case due to its large fins throughout ontogeny and its full length adult fins, all adult measurements

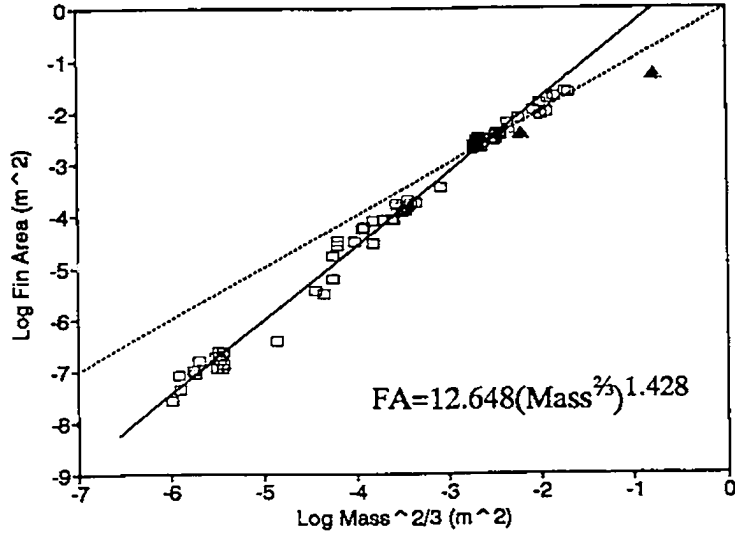


Figure 3.1. The allometric relationship between $\log \text{mass}^{2/3}$ (m) and the log transformed data for fin area (m²). The solid line represents the linear relationship between the two measurements ($r^2=0.99$).

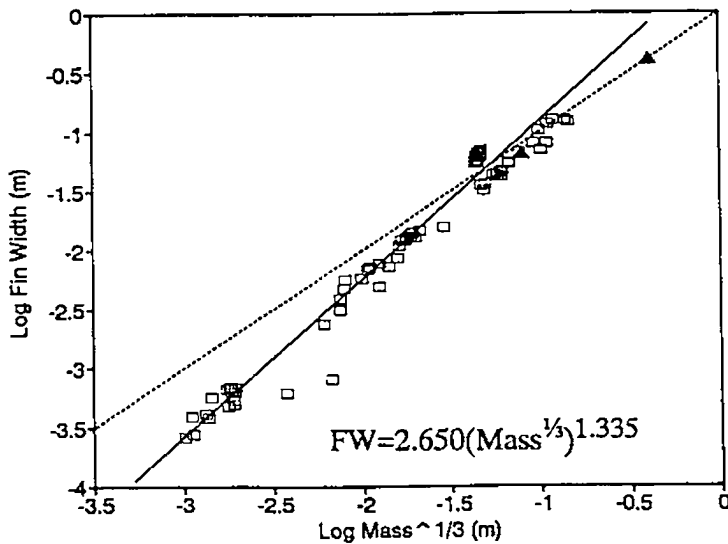


Figure 3.2. The allometric relationship between $\log \text{mass}^{1/3}$ (m) and the log transformed data for fin width (m). The solid line represents the linear relationship between the two measurements ($r^2=0.97$).

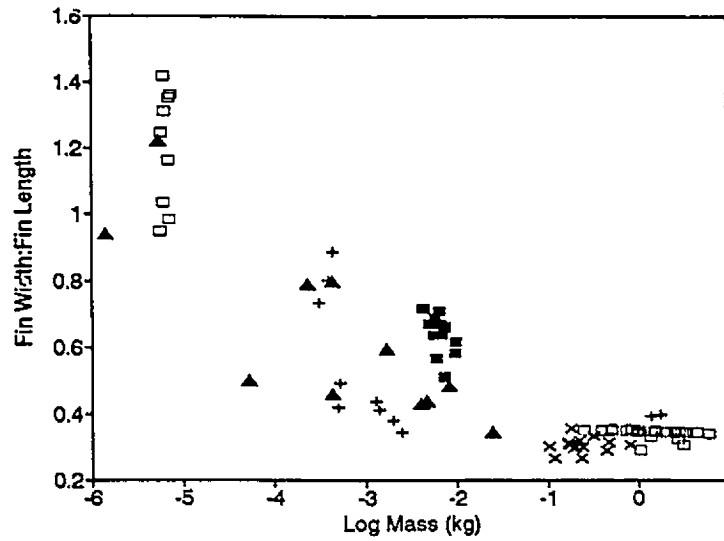


Figure 3.3. The relationship between log mass (kg) and the ratio of fin width to fin length. The squid species represented are *Loligo forbesi* (□), *L. opalescens* (▲), *L. vulgaris* (×), *Sepioteuthis lessoniana* (+) and *Lolliguncula brevis* (■).

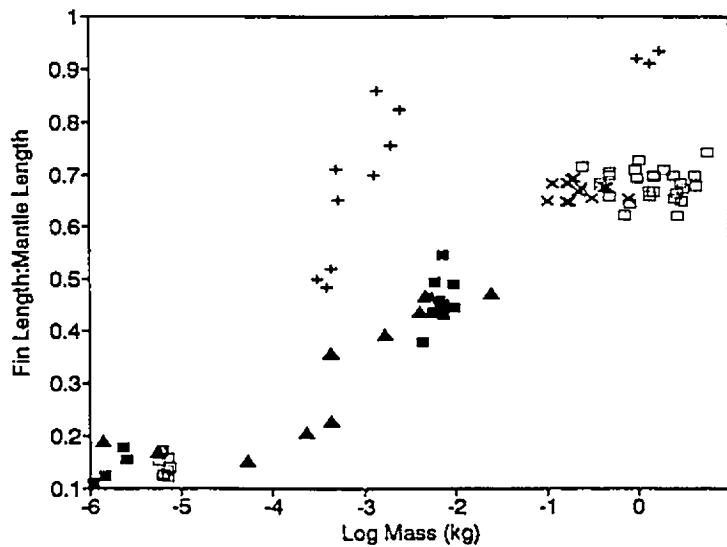


Figure 3.4. The relationship between log mass (kg) and the ratio of fin length to mantle length. The species represented are *Loligo forbesi* (□), *L. opalescens* (▲), *L. vulgaris* (×), *Sepioteuthis lessoniana* (+) and *Lolliguncula brevis* (■).

show ratios that range from 0.5 (*L. brevis* and *L. opalescens*) to 0.7 (*L. forbesi*).

For animals that are aquatic flyers (as squid are), the aspect ratio of the fins, which indicates one aspect of the flight performance of a flyer (Azuma, 1992) is an important consideration and is calculated as:

$$AR = FS^2/FA \quad (FS \text{ is the fin span or total fin width})$$

and decreases with increasing mass (Figure 3.5) so that the large squid all have low aspect ratio (less than 10) fins and the small squid have high AR (above 10) fins. As a comparison with actual fliers, Figure 3.6 is a graph of the Reynolds Number acting on the squid, as well as some representative birds and insects.

As mentioned in the previous chapter, drag is a fluid-dynamic force that acts on a body moving in a fluid and since the squid's fins are part of the animal and, therefore, are moving through the fluid, the drag forces acting upon them were calculated to add to the model. Minimal drag coefficients for the fins (C_f) were calculated using the equation for flat plates parallel to laminar water flow, multiplied by 2 to take account of the two fins on the squid.

$$C_f = 2(1.33/R_f^{0.5})$$

The effect of the addition of the drag caused by the fins (D_f) is shown in Figure 3.7 of D_b , D_f and total drag, D_t and although D_b is clearly the largest component of the total drag, D_f has an appreciable effect. When D_t for all speeds is graphed with T_{je} (Figure 3.8), the change can be compared with those in Figure 2.12. As expected, the crossover of D_t and T_{je} shifts up the curve with increasing speed, from 1×10^{-6} kg at $0.5BLs^{-1}$ to 5×10^{-6} kg at $1BLs^{-1}$ and 5kg at $2BLs^{-1}$, indicating that below these masses,

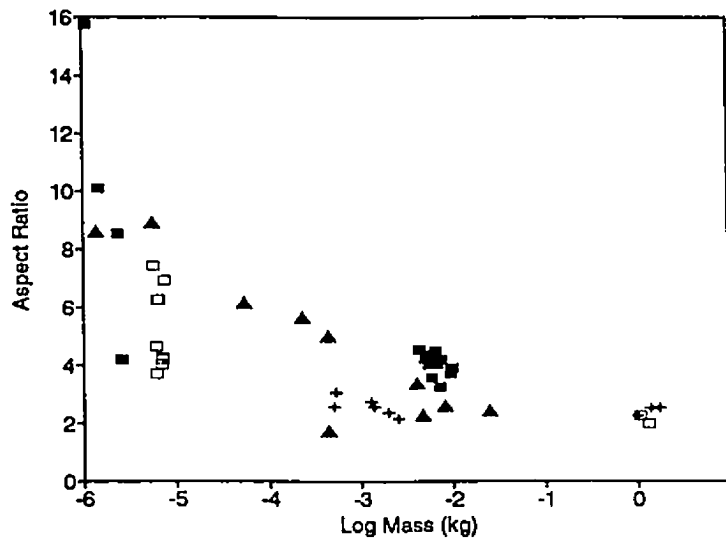


Figure 3.5. The relationship between log mass (kg) and the aspect ratio of the fins for the following squid species *Loligo forbesi* (\square), *L. opalescens* (\blacktriangle), *Sepioteuthis lessoniana* (+) and *Lolliguncula brevis* (\blacksquare).

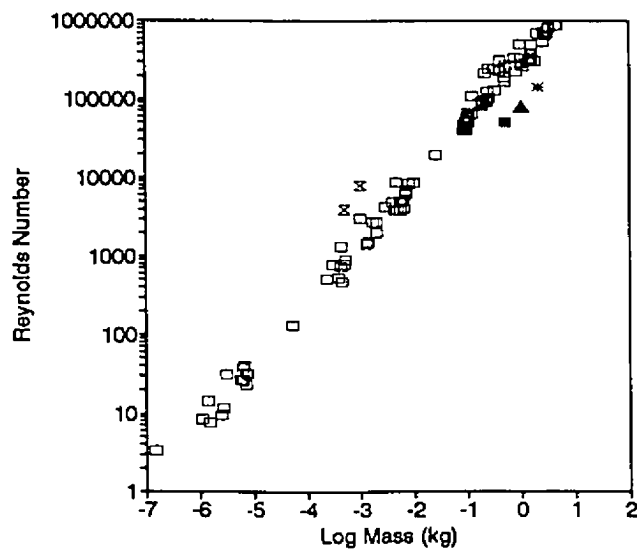


Figure 3.6. The relationship between log mass (kg) and Reynolds number for long-finned squid (\square), petrel (\blacksquare), falcon (\blacktriangle), condor (\times), vulture ($*$) and 2 insects (X).

model squid should not be able to move at these speeds due to the drag acting on them.

This model did not include the effect of any thrust produced by the fins, although it is likely that they produce thrust over some part of the velocity range. This model considers only the detrimental effects of the presence of fins on the jet thrust, although the fins may be producing net thrust (i.e. more thrust produced than drag acting on them).

To study the effect of changing the shape of squid fins on drag forces, the ratio of FL:ML (0.12 & 0.72) and FA:ML (6×10^{-6} & 0.04) for the smallest and largest loliginids respectively were taken as base ratios for "small" and "large" fins. The model was then manipulated so that all squid either had "small" fins or "large" fins from hatchling to giant squid size. Figure 3.9 shows the effect of a change in fin length on D_f . The "small" line is for squid over the entire size range if they maintained relatively tiny fins, rather than increasing in relative size. The "large" line is similar, but it represents squid with relatively large fins from hatching throughout ontogeny. The normal D_f is also graphed for comparison showing that the possession of large fins causes more than a 1000 fold increase in fin drag for the smaller squid. Figure 3.10 shows the changes to total drag associated with having either "large" or "small" fins throughout ontogeny. Retaining small fins merely reduces the required jet thrust in larger squid, but the possession of large fins causes a significant increase in D_t at small sizes, an increase that would be very detrimental in small squid. When the crossover of these different D_t 's with T_{je} are compared at $1BLs^{-1}$, the changes are magnified. This crossover occurs at 1.5g with "small" fins, 11g with "real" fins and 5kg for squid with "large" fins throughout ontogeny, indicating that most squid would have difficulty swimming due to the drag

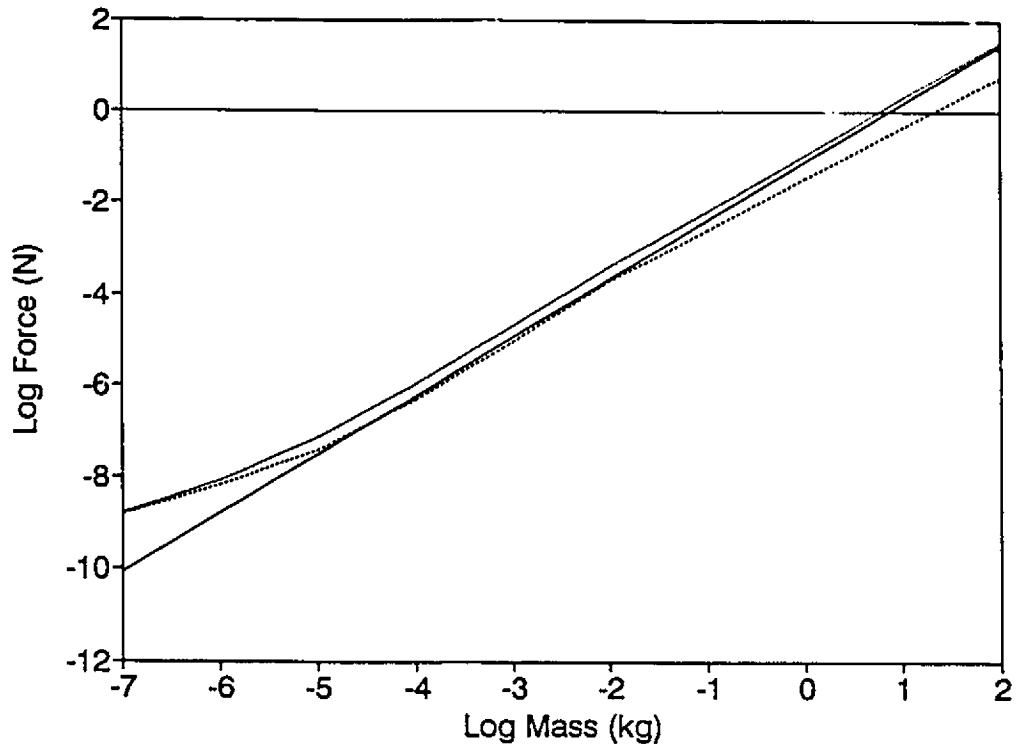


Figure 3.7. The relationship between log mass (kg) and the drag forces (N) acting on the squid at 1BLs^{-1} ; body drag (D_b ; dashed), fin drag (D_f ; solid) and total drag (D_t ; dotted).

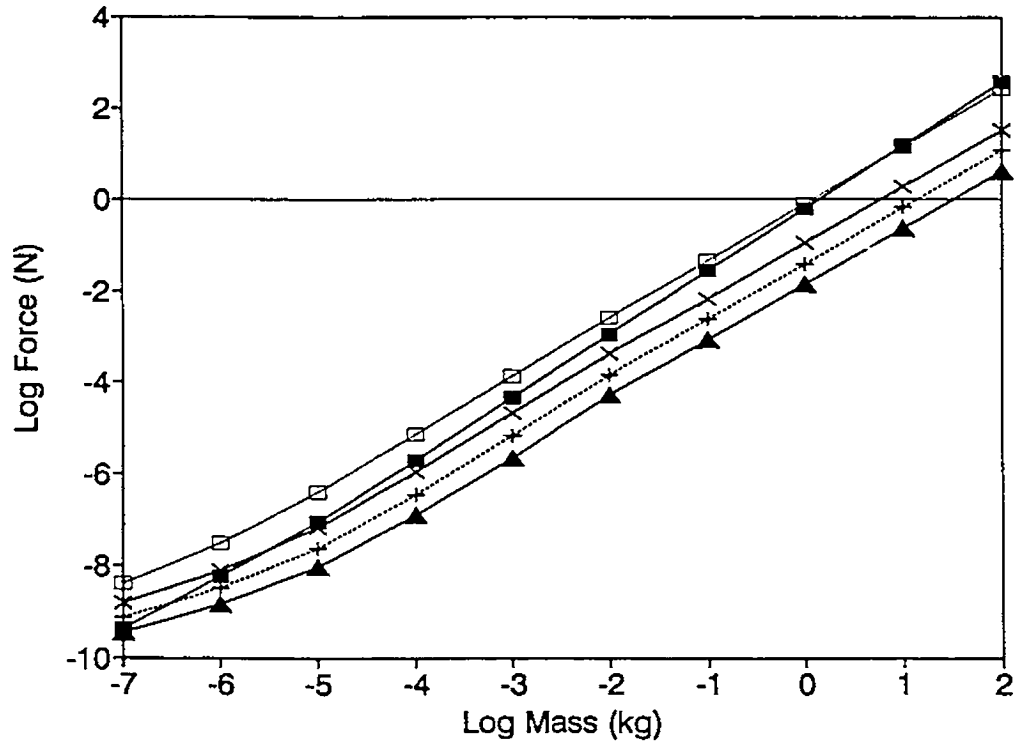


Figure 3.8. The relationship between the log mass (kg) and the log transformed model data for the effective thrust (■;N) and the total drag (N) on the squid at different speeds; $0.25BLs^{-1}$ (solid), $0.5BLs^{-1}$ (dashed), $1.0BLs^{-1}$ (solid), $2.0BLs^{-1}$ (dotted).

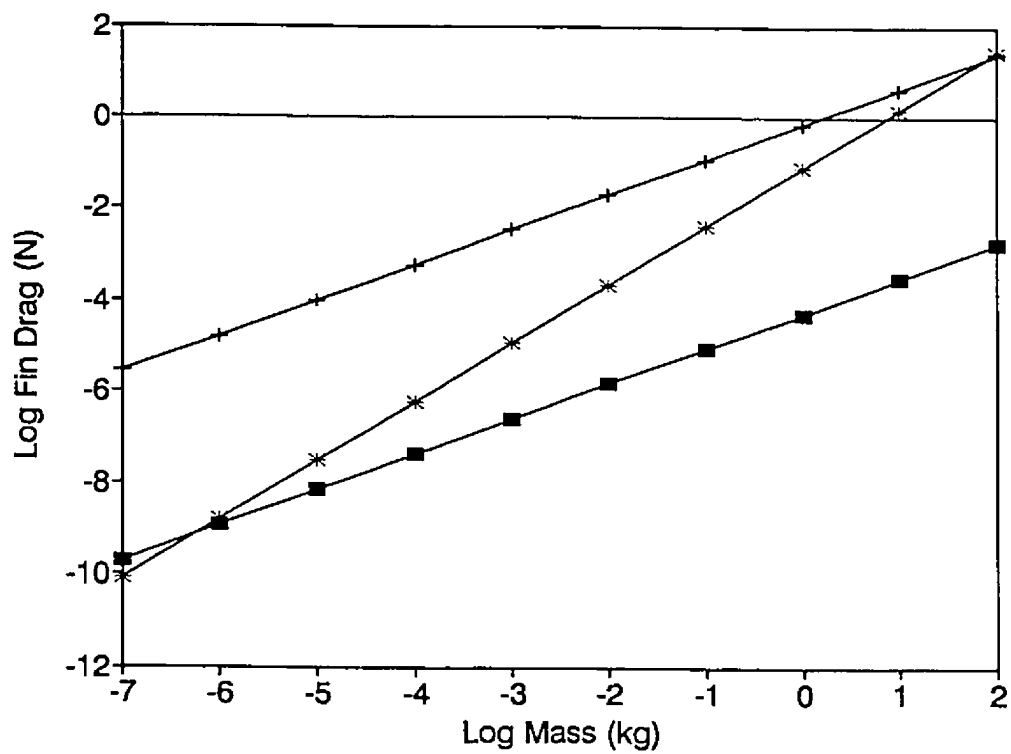


Figure 3.9. The relationship between log mass (kg) and the log transformed model data for fin drag (D_f) for squid with "small" fins (■), "large" fins (+) and "real" fins (*) moving at $1.0BLs^{-1}$.

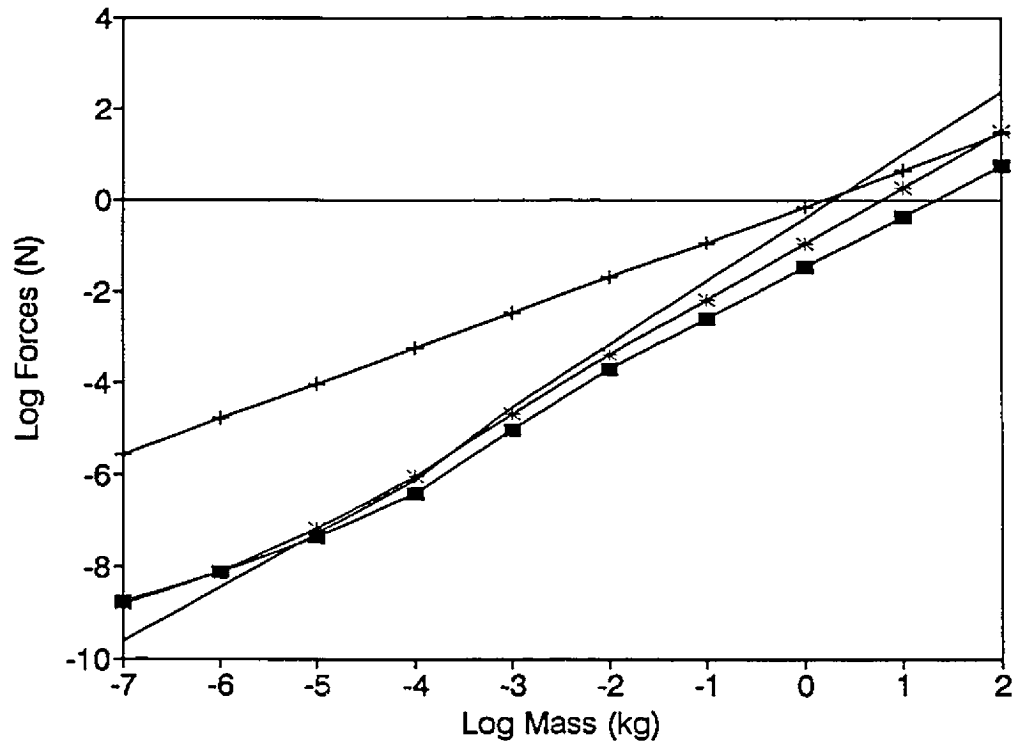


Figure 3.10. The relationship of log mass (kg) and the log transformed model data for the effective thrust (N; solid; as calculated in Chapter 2) and the total drag (N) on squid with "small" (■), "large" (+) and real (*) fins at 1BLs^{-1} .

forces, if they carried "large" fins throughout growth. Figure 3.11 illustrates the effect of "large" fins on the total drag for squid over a range of speeds (from $0.25\text{--}2.0\text{BLs}^{-1}$) and there is a shift in the drag-thrust crossovers up from 100g at 0.25BLs^{-1} , to 800g at 0.5BLs^{-1} , 5kg at 1.0BLs^{-1} and 11kg at 2.0BLs^{-1} so that animals below these points would not be able to move at these speeds, due to the drag on their large fins. Figure 3.12 is the same comparison but for "small" fins and there is no appreciable difference in crossover points (other than a slight increase at 2.0BLs^{-1}), since the body is the major component of drag in these squid, not the small fins.

3.4. Discussion

Given the large effect of fin size at small squid size (due to skin friction drag), the relative size of fins can be an important indicator of the squid's hydrodynamic lifestyle. Figure 3.4 shows the increase in FL:ML ratio with increasing mass and the clumps of points indicate a cluster of measurements for different species of squid. Those animals belonging to the *L. opalescens* growth series have an increasing FL:ML ratio with increasing mass (from 0.2–0.5ML) and this is also apparent from the juvenile and adult *S. lessoniana* (from 0.65 to 0.95ML respectively). Overall, the larger the loliginids get, the longer the fins in relation to mantle length, and the smaller adult animals (ie. *L. opalescens* and *L. brevis*) have ratios that fall on a continuum from the hatchlings towards the large *L. forbesi*, possibly indicating that the size of fins on an adult squid is more a function of body size than of the species itself. When adults of the smaller species are compared with the same size juvenile/subadults of larger species, the body shapes are

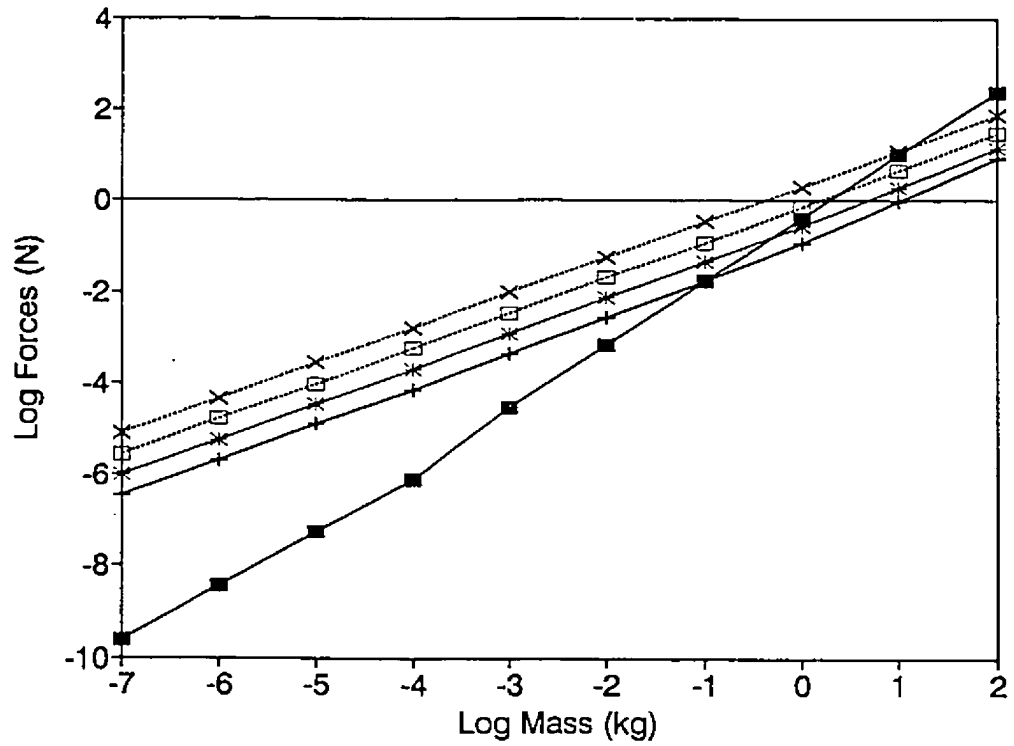


Figure 3.11. The relationship of log mass (kg) and the log transformed model data for effective thrust (N; ■) and total drag on squid with "large" fins swimming at various speeds; $0.25BLs^{-1}$ (+), $0.5BLs^{-1}$ (*), $1.0BLs^{-1}$ (□) and $2.0BLs^{-1}$ (x).

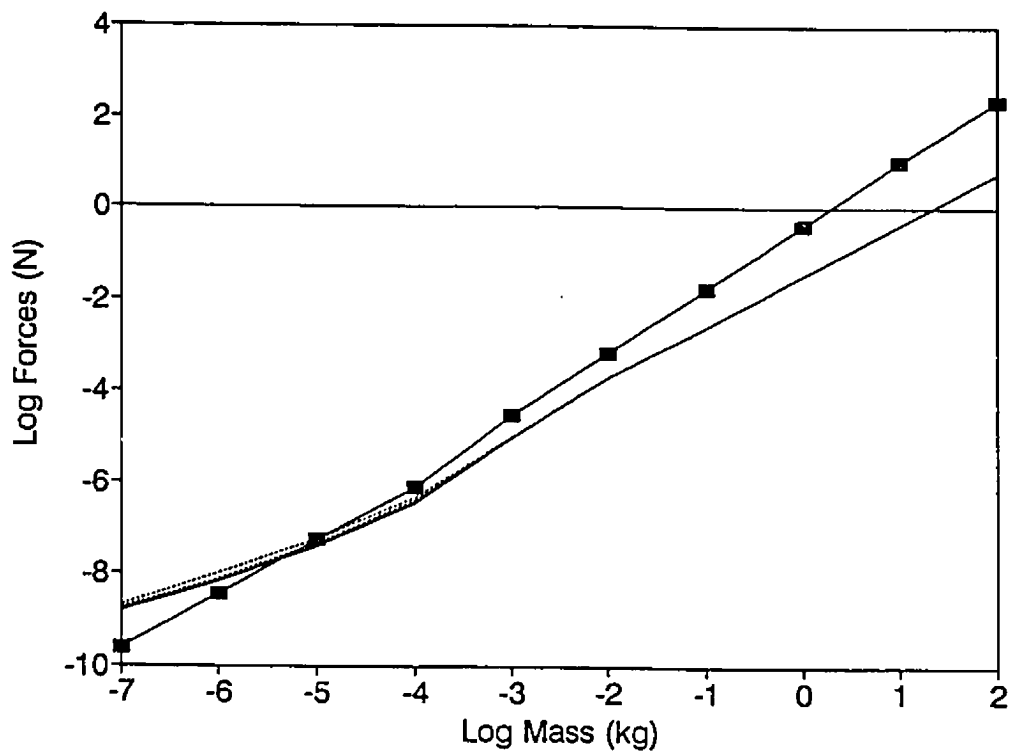


Figure 3.12. The relationship of log mass (kg) and the log transformed model data for effective thrust (N; ■) and total drag on squid with "small" fins swimming at various speeds; 0.25BLs^{-1} (solid), 0.5BLs^{-1} (dotted), 1.0BLs^{-1} (dashed) and 2.0BLs^{-1} (centre-line).

remarkably similar, so one can speculate that if *L. opalescens* grew to 5kg, they would be morphometrically very similar to *L. forbesi*, with the same general fin ratio. As these loliginid species have similar slow-moving lifestyles, this similarity in body form could be expected; they must all deal with similar complex environments and need the manoeuvrability gained from the large fins. Also, it is possible that in their niches, the loliginids contend with slower moving prey and, therefore, high speed generation is not as important as lower speed manoeuvring.

If fins are important for the large adult loliginids for manoeuvring, then why don't small squid have relatively large fins too? One of the major problems that the small (hatchling) squid have to contend with while living at low Reynolds numbers is skin friction. Skin friction is caused by the viscosity of the fluid in the boundary layer and exerts force parallel to local fluid flow. Skin friction is more significant in more viscous situations (i.e. low Re), but occurs at all Re. Animals living in the viscous world of low Reynolds numbers decrease the amount of "skin", or surface area, exposed to the fluid, and thereby decrease the skin friction component of drag. Therefore, the streamlining seen in animals at high Reynolds numbers (i.e. large squid, sharks, whales, etc.) is not useful for animals at low Reynolds numbers. A sphere has less surface area than an ellipse of the same volume and causes less skin friction drag. Thus hatchling squid are shorter and rounder than the more inertia dominated adults, for whom streamlining is the most important factor (especially at high speeds), and this is also why the small squid have small fins (Figure 3.1), to decrease the skin friction until they reach a size where the balance of drag and thrust is more favourable.

Undulation of the large, paired fins produces movement similar to that of balistiform swimming in triggerfishes (turned on their sides; Lighthill & Blake, 1990) or skates (Daniel, 1988) and is an economical method of moving forward (Lighthill & Blake, 1990). Lighthill & Blake (1990) also theorized that a relatively low ratio of fin width to body width actually enhanced the force produced by fin movements and, therefore, the fins of squid should be relatively slender (i.e. low FW:FL ratio, or low aspect ratio). Large fins might be able to produce more thrust, but they also cause more drag and so, there should be a width:length ratio that has an optimal thrust:drag ratio for big fins. Figure 3.3 demonstrates this for loliginids. Although small squid have very "square" fins (FW:FL=1), as the squid grows and the fin length increases faster than fin width, this ratio decreases. The round fins of the small squids minimize the skin friction component of drag at low Re and small size, while still allowing them to steer and manoeuvre in the water when undulation may be less efficient. As the squid grow from the viscous-dominated, low Re world, the fins elongate and change shape into slender fins, like those used in balistiform fishes. For animals above about 5g (the smallest adults measured), the ratio of FW:FL is about 0.35 over a 1000-fold increase in mass (Figure 3.3), which indicates that 0.35 may be an optimal ratio for adult loliginid squid fins. A non-loliginid, oceanic squid with large, complete fins is *Thyrianoteuthis rhombus*, whose FW:FL ratio is about 0.32. Therefore, even these large squid have fins that are similar in shape to the loliginid ones, probably because the drag on such large, rhomboid fins is very considerable and, even with the extra thrust that these fins can produce, *T. rhombus* would need an exceptionally strong jet to move around at high speed. Since *T. rhombus* is an

epipelagic, panoceanic squid, known to be a powerful swimmer (Roper *et al.*, 1984), one could expect smaller fins to decrease the drag associated with swimming quickly. Unfortunately, not enough is known about *T. rhombus* ecology for the functional significance of its large fins to be understood.

Aspect ratio (AR) is a measure of the wingspan to wing chord and indicates the flight performance of a flyer (Azuma, 1992), and in general, soaring birds have high AR wings (above 10) and flapping birds have low AR wings (less than 10). The hydrodynamics of movement in the ocean are not that different from the aerodynamic forces in the air, although the change in the fluid means a 15-fold change in the dynamic viscosity of the fluid. Figure 3.6 is a comparison of the Reynolds number for some representative birds and insects and the loliginid squid. The petrel's AR is about 10, while the other birds in the figure are about 4–7 (Azuma, 1992). For batiform rays, Daniel (1988) predicted that high AR fins/wings would have slow undulations and there would be relatively few propulsive waves along the wing, while low AR wings would have fast undulations and more propulsive waves. Blake's (1983b) work on knife-fishes and electric fishes, with very low AR dorsal or pectoral fins, showed multiple propulsive waves while Daniel's (1988) work on higher AR skate "wings" showed few waves present, indicating that, at least for fish, the range of fin shapes in nature is consistent with the hydrodynamic theory. Figure 3.5 shows the AR for a million-fold range of squid and there is a general decrease in AR with increasing size. Since the small fins of juvenile squid have a small area, to keep the skin friction low, the high AR is expected, and, due to their short length, they do little more than flap (i.e. 1 wave on the fin at a

time), as expected from Daniel's (1988) predictions. The longer, low AR fins of the larger, adult squid can flap at high swimming speeds, but usually produce multiple waves along their length, also as predicted. Squid fins are highly flexible, since they have no rigid structural support (such as the fin rays in fish fins) and Daniel (1988) also predicted that this type of highly flexible fin would have a low AR, while more rigid wings and fins would have high ARs. Therefore, the behaviour of squid fins follows Daniel's (1988) predictions for animals with low aspect ratio "wings" and it is apparent that the high AR of the fins of young loliginid squids is merely a step on the way towards the low AR fins of the adults, an ontogenetic step made necessary by hydrodynamic drag constraints.

So, squid have small, high AR fins as hatchlings and develop large, low AR fins as adults, but how would their locomotion be affected in this did not happen? Figure 3.9 shows the dramatic changes to fin drag that occurs when squid have either "large" or "small" fins throughout growth. The presence of "large" fins causes a 1000 fold increase in fin drag at 1BLs^{-1} at hatchling size, a change which would cause the squid to decelerate at that speed due to the drag. Figure 3.10 shows the effect of different speeds on the total drag for squid with "large" fins throughout growth. Even at 0.25BLs^{-1} , only squid over 100g would be able to swim with their jets due to the high drag from the large effect of skin friction at small sizes and Reynolds numbers. "Small" fins, on the other hand, cause a decrease in fin drag from the real values throughout growth (Figure 3.9) and a slight decrease in total drag at 1BLs^{-1} as well (Figure 3.10). When different speeds are taken into account (Figure 3.10), there is little effect on the total drag of larger squid, where the body is such a large component of the drag. The drag on this "small"

finned squid is similar to what we would expect to find for the short-finned squid (such as *Illex illecebrosus*) which have small/short fins throughout their growth, and at adult size the fins are only 0.2ML, marginally larger than those of a hatchling long-finned squid (0.14ML).

CHAPTER 4. The Scaling of Fin Use in Long-Finned Squid.

4.1. Introduction

The previous chapters referred to fin growth and the effect of shape change on a squid model, but how do the squid actually use their fins when swimming?

Internally fins are tightly packed three-dimensional muscular arrays with associated connective tissue fibres known as muscular hydrostats (Kier, 1989). Since there can be no volume change in this system, a change in one dimension will cause a concomitant change in another and the energy of that movement may be stored as elastic energy, much like the system in the mantle during jetting (Gosline & Shadwick, 1983). Kier *et al.* (1985) also found mechanoreceptors in cuttlefish and squid fins oriented in three mutually perpendicular directions, allowing the fine control over fin movement witnessed in squid. Although the presence of these mechanoreceptors indicates a mechanism for neural control of fin movement, there has been little study of the control of the fins since Boycott's (1961) early work, even though there is a vast body of work on cephalopod neuroanatomy and neurophysiology, particularly that of the giant axons (Mackie, 1990; Otis & Gilly, 1990).

Fin undulations are more mechanically efficient than jet propulsion, because momentum can be produced at all times, unlike the periodic jet. The periodicity of the jet cycle also leads to energy loss from the acceleration reaction, which is a force that resists changes in the animal's velocity (Batchelor, 1967). As stated before, it is also more mechanically efficient to propel a larger mass of water slowly, than a small mass

quickly (Alexander, 1977) and the undulations of the fins not only propel water constantly, but also propel more water than the jet by increasing wave amplitude to an optimum (Johnsen & Kier, 1993). The fins actual role in squid locomotion has only been studied cursorily, beyond noting that squid roll the fins against the mantle at high speed (Webber, 1985; O'Dor, 1982; Bradbury & Aldrich, 1969; Zuev, 1965a). *Illex illecebrosus* (Williamson, 1965), *Symplectoteuthis oulaniensis* and *Illex coindetti* (Zuev, 1966) were all incapable of translational movement following fin amputation and had difficulty maintaining both a linear path in the water and their vertical position in the water column. This indicates that the fins not only have a function in steering, but also have an important function in lifting the negatively buoyant squid.

Although cephalopods use their fins for undulatory propulsion, they have also maintained the jet, suggesting that the combination of the two systems is more energetically efficient than fins alone and enhances their escape and/or predatory abilities. The only direct evidence of this is Webber's (1985) note that individual *I. illecebrosus* that used their fins less than others at low velocity generated higher mantle pressures than those that used their fins more at the same speed. Also, both Webber (1985) and Packard (1969) noted that squid use a strong fin beat during mantle refilling, probably to smooth out the velocity curve produced by the periodic jet alone.

Squid fins can be used in many ways; producing thrust from undulations at low speed (Aleyev, 1977), manoeuvring, flapping during the refilling stage to smooth out thrust production, decreasing drag by being rolled against the mantle at high speed, and even producing a small jet by the action of rolling the fins around the mantle at moderate

speed (Clarke, 1988). The velocity of the fin waves also varies with the velocity of the squid, from Zuev's (1966) 4–5 beats per minute during immobile hovering in *Illex coindetti* to O'Dor & Balch's (1985) observation of 90 beats per minute for a spawning female *I. illecebrosus* unable to utilize her jet. The squid fins can also be synchronized with the jet to maximize the total thrust production during escape movements, as noted by Williamson (1965).

Williamson's (1965) study of an *Illex illecebrosus* unable to use its mantle for jetting demonstrated the production of thrust by the fins, as the squid continued to move slowly. O'Dor & Balch's (1985) spawning female *I. illecebrosus* also continued to move while unable to use her jet, although in both cases, the squid sank slowly without the added lift from the jet.

In his study of the very low aspect ratio fins of eels, Gray (1933) found that fin undulations that moved slower than the speed that the animal was swimming could not produce drag-based thrust. The wings of birds, however, can produce lift-based thrust through a range of speeds (Azuma, 1992) and Daniel (1988) modelled flapping skate fins as a system using lift-based thrust. Since loliginid squid fins are similar in shape to skate fins, they could be using both the lift- and drag-based thrust production.

O'Dor's (1988a) studied the forces acting on swimming *Loligo opalescens* and described at least three different modes of fin action correlated with swimming speed; multiple propulsive waves at low speed, single waves synchronized with the refilling cycle at moderate speeds, and no waves when the fins are wrapped around the mantle at high speeds. This study looked at the fin action in different species of squid (Figure 4.1),

over a wide size range and as large a swimming speed range as possible, to see if these different fin "gaits" were common to loliginids with different fin shapes and to take a detailed look at fin movements in squid.

4.2. Materials and Methods

4.2.1 *Loligo forbesi*

After capture as described in Chapter 2, *Loligo forbesi* of both sexes (0.84–3.1kg) used for swimming studies were maintained at 15°C in a 3m diameter, 1m deep recirculating tank as described in Porteiro *et al.* (1990). The freely swimming squid were videotaped from overhead with sufficient resolution to calculate animal speed, mantle diameters and fin wave speed with a Panasonic WV-D5000 camera (30 frames/sec) and an AG-2400 recorder with a 0.1s time base superimposed. Squid also carried neutrally buoyant acoustically telemetering differential pressure tags (V3D-1L-R, Vemco Ltd., Shad Bay, Nova Scotia, Canada), as used in *Nautilus* (O'Dor *et al.*, 1990), mounted internally in the mantle cavity (Webber & O'Dor, 1986). Signals from the tags were monitored with a Vemco V-10 hydrophone and VR-15 receiver and were recorded on a Toshiba T-1000 laptop computer.

L. forbesi were also swum from 0.2–0.3ms⁻¹ in a 0.3m diameter Blazka-style swim tunnel respirometer (Beamish, 1978) constructed of flexible 0.2mm transparent vinyl, for ease of portability. Animals were placed in the inner tube of the "swim-bag", which was closed with a 0.01m mesh removable acrylic grid. The outer tube was then sealed and filled to constant volume under constant pressure. The grid closure at the end

of the inner tube is partially blocked to create a back pressure that inflates the tube when the motor is running. A grid upstream of the squid in the swimming tube maintains microturbulent flow in the chamber. The apparatus retains the temperature of the water surrounding it, but shows no significant uptake of oxygen when run for 1h with half-air saturated water. Oxygen depleted water is replaced by opening valves in the motor housing, unzipping the outer bag and running the motor. Oxygen is measured in a recirculating loop that passed an Orion oxygen electrode. When submerged, the optical quality of the vinyl is adequate to allow video recordings of mantle and fin movements. (Figure 4.2, from O'Dor *et al.*, 1994).

4.2.2 *Sepioteuthis lessoniana* and *Lolliguncula brevis*

Juvenile *Sepioteuthis lessoniana* of both sexes of 0.45–2g wet weight (1.2–2.6cm ML) from the population cultured at the Marine Biomedical Institute, University of Texas Medical Branch, Galveston, Texas were swum from 0.03–0.15ms⁻¹ in a 2.5cm diameter swim tunnel constructed of clear acrylic (Figure 4.3). Oxygen levels were measured through a recirculating loop that passed an Orion oxygen probe. The swim tunnel was submerged in a 10 gallon fish tank and, therefore, retained the temperature of the surrounding water (18–24°C). The water in the tank was changed with each experiment and oxygen saturated water was flushed through the respirometer between runs.

Adult *Lolliguncula brevis* of both sexes of 4–10g wet weight (39–55 mm ML) were caught by bottom trawl in Galveston bay or in the Gulf of Mexico immediately offshore from Galveston and maintained in 1.5m diameter by 1m deep tank. The squid

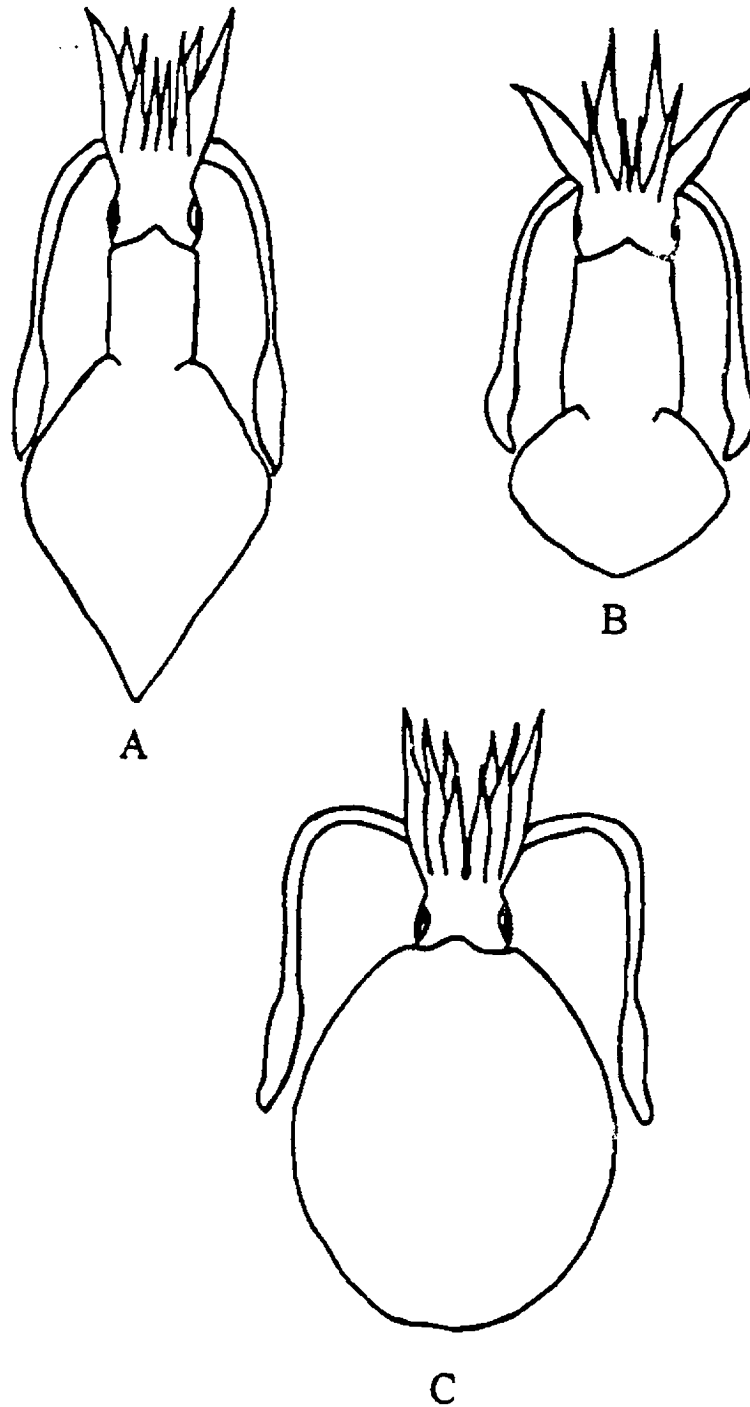


Figure 4.1. Adult fin shapes for the three squid species swum in the swimming experiments. (A) *Loligo forbesi* (B) *Lolliguncula brevis* (C) *Sepioteuthis lessoniana*. Redrawn after Roper *et al.* (1984)

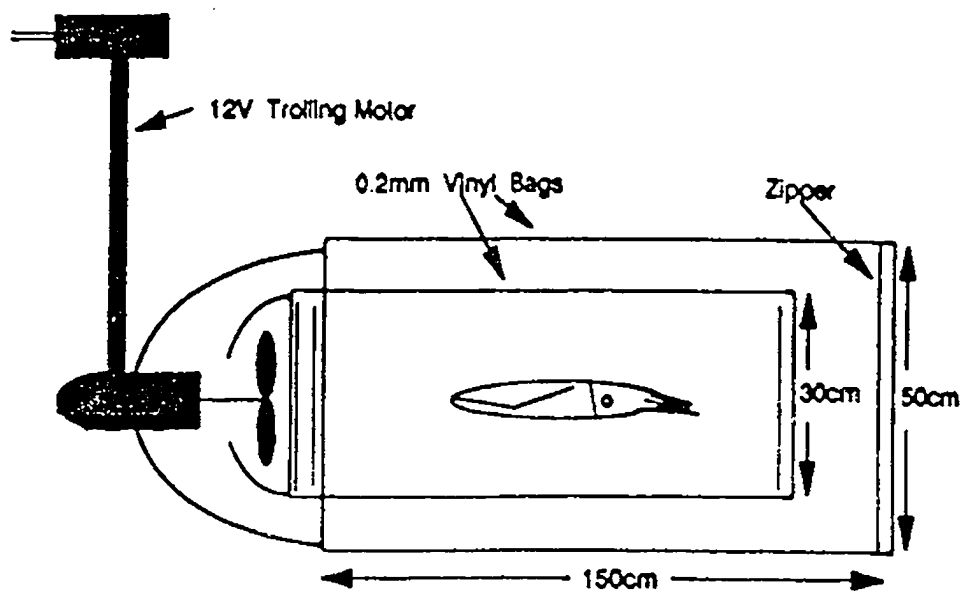


Figure 4.2. The design for the swim-tunnel respirometer used in the Azores for the studies of *Loligo forbesi*. The dotted lines represent 1cm mesh grid used to produce micro-turbulent water flow (From O'Dor *et al.*, 1994).

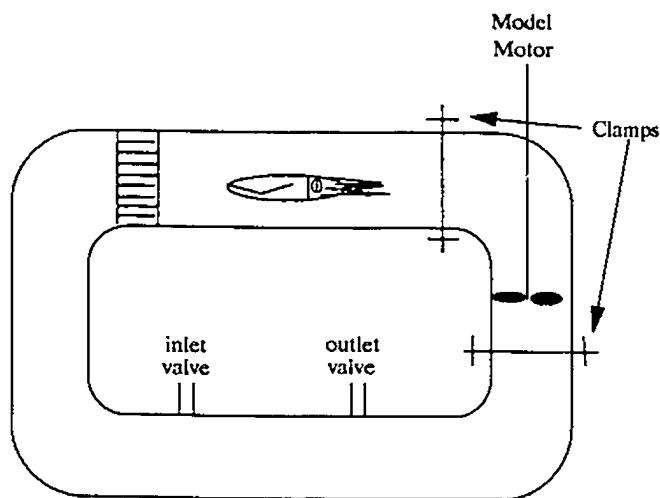


Figure 4.3. The design for the swim-tunnel respirometer used in Galveston, Texas for studies of juvenile *Sepioteuthis lessoniana*. The clamps delineate the part of the system that could be opened and the short horizontal lines represent the small tubes used to ensure micro-turbulent water flow.

were swum at speeds of $0.03\text{--}0.21\text{ms}^{-1}$ in a Brett-style respirometer (Brett, 1964) with a 15cm diameter swimming chamber. This swim tunnel (as described in Wells *et al.*, 1988) uses recirculating water, and, to maintain oxygen saturation, air was bubbled through the holding tank. Oxygen was measured via a recirculating loop passing an Orion oxygen probe, and the tank was checked regularly to ensure that ammonia levels remained low, and the water was flushed periodically.

Fin and mantle movements for both species were recorded on Hi8 video tapes with a Sony TR-81 camera with a 0.01s time base superimposed and then transferred to VHS for later analysis in Halifax. Natural light was supplemented with a 650-W photography light and the squid were allowed to adjust for 30 minutes to both the swim tunnel and the light source. Analyses of the videos were done by viewing the tapes on a Panasonic Time Lapse VCR (model AG-6750). Fin beat frequencies were counted over 5s periods, were repeated no less than 6 times for each speed and then the rates averaged. These fin beat frequencies were used to calculate fin wave speed when multiplied by the length of the fin, since all waves travel the full length of the fin.

Fin wave speeds for *Sepioteuthis lessoniana*, *Lolliguncula brevis* and *Loligo forbesi* were collected from videotapes and the mode of fin waves noted (whether continuous waves or flaps), which reflected O'Dor's (1988a) findings of three modes of fin usage. Also fin wave speeds for *Loligo pealei* from the studies of Sims (1986) and Hoar & Freedman (in prep.) were included for comparison with the loliginids studied.

4.3. Results

For the large *L. forbesi*, there were generally multiple fin waves produced at low swimming speeds and fewer waves at medium speed (the decreased number of waves translates into decreased speed at $0-0.3\text{BLs}^{-1}$, Figure 4.4). There is a wide variation in speed between 0.4 and 1BLs^{-1} , related to the presence of either single or multiple waves being produced along the fin. At very high speed ($\geq 0.8\text{ms}^{-1}$ or 1BLs^{-1}) the waves were not produced in synchrony with the refilling of the mantle and the fins were usually wrapped around the mantle (or against the tunnel wall in some unused swimming sequences) and used in conjunction with a strong jet to regain swimming position in the respirometer. *L. forbesi* had difficulty maintaining their position or swimming at high speeds (1BLs^{-1} or higher), and when swimming freely in the tank, maintained very low speeds except when chased (e.g. for use in a swim tunnel experiment).

The small *L. brevis* also did not swim well at high speeds, as indicated by the large variability in fin speeds, particularly at high speeds (Figure 4.5). Low fin speeds at high swimming speed occurred when a squid rolled its fins against the mantle; occasionally an animal would try to flap its fins at high speeds, producing the high fin wave rates, but these animals did not maintain position very well. At low speeds, *L. brevis* produced waves at high frequency, but due to their small fin size (0.47ML), only produced 1 wave at a time along the fin. *L. brevis* never produced fin wave speeds greater than 0.1ms^{-1} , so swimming above 0.1ms^{-1} , the waves should not be producing any drag-based thrust (Gray, 1933); however, at swimming speeds above 1BLs^{-1} or 0.08ms^{-1} the squid synchronized the fin flapping with the refilling stage of the jet cycle.

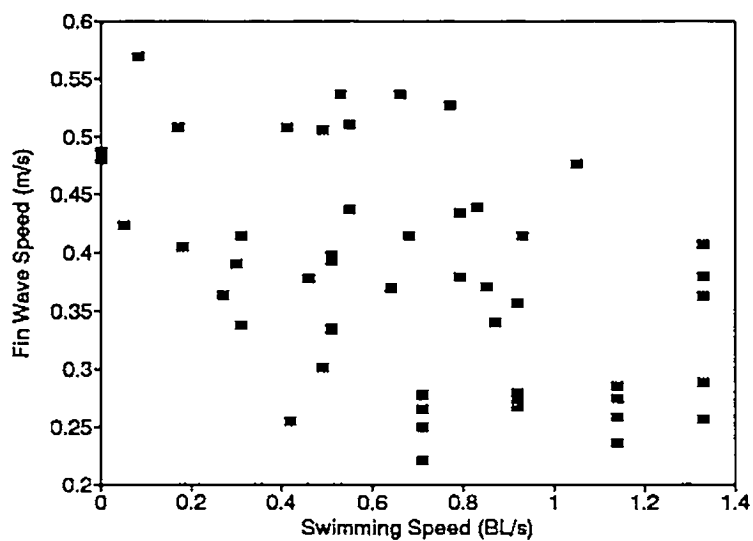


Figure 4.4. The relationship of swimming speed (BLs^{-1}) and fin wave speed (ms^{-1}) for 5 adult *Loligo forbesi*.

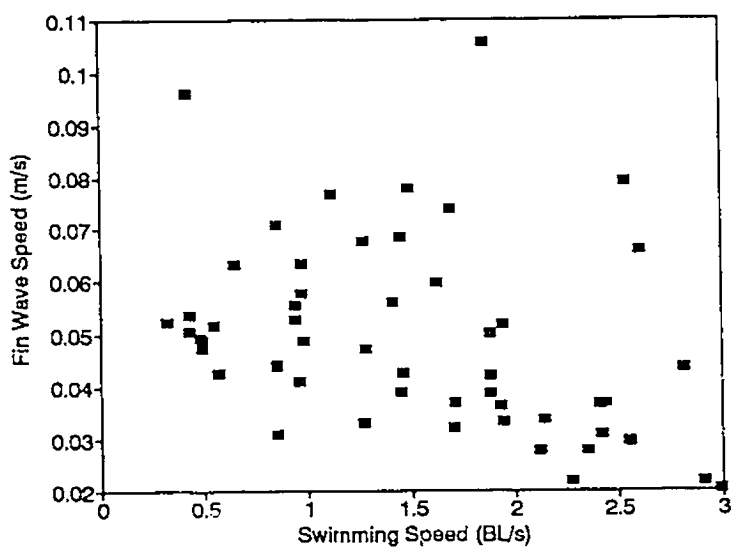


Figure 4.5. The relationship of swimming speed (BLs^{-1}) and fin wave speed (ms^{-1}) for 10 adult *Lolliguncula brevis*.

Therefore, since the squid produce jet thrust unevenly, causing speed to oscillate, this is the one time during high speed swimming where the fins could produce significant thrust and help maintain position while swimming.

Juvenile *S. lessoniana* did not appear to be very strong swimmers and reproducible speeds in this swim tunnel were not well matched with observed squid behaviour (Figure 4.6). Since the mini-swim tunnel was limited in its ability to produce low speed currents, the speeds that the squid were made to swim were not speeds at which they could swim well. Therefore, the data were unreliable and much of it could not be used for finwave counts. The culture tanks in which these animals were maintained have low-speed currents in them, which I was unable to reproduce in the swim tunnel. At speeds of approximately $2BLs^{-1}$ ($0.06ms^{-1}$) the squid were observed synchronizing the fins with the jet cycle, just as the adult *L. brevis* did. *S. lessoniana* have very thin fins at this size (mean ML $1.99\pm 0.25cm$), and, at high speeds did not appear to have the same degree of control that the adult squid have as they did not consistently roll their fins against their mantles to decrease drag.

Figure 4.7 shows wave speed versus swimming speed for *S. lessoniana*, *L. forbesi*, *L. brevis* and *L. pealei* from Hoar & Freadman (in prep.) and Sims (1986) for comparison. Both *S. lessoniana* and *L. brevis* show little change in wave speed with increasing swimming speed, which is probably due to the small size of both the animals and their fins (eg. the fins reach maximum velocity quickly). There is wide scatter in the *L. forbesi* data as they were all swimming at fairly low speeds, relative to fin length, compared to those of the other species. Sims' (1986) *L. pealei* data is very clustered,

since it was all from one animal and at only three speeds, but there is still a fair amount of scatter in the data. Only Hoar & Freadman's (in prep.) *L. pealei* data show any trend towards increasing wave speed with increasing swimming speed, although again there is scatter in the data.

Since only those waves travelling faster than the squid is swimming can produce drag-based thrust (Gray, 1933) the relationship between these fin waves and the fin length were compared. Figure 4.8 is a comparison of the logs of the highest wave speeds gathered for each squid size that fall to the left of the 1:1 line in Figure 4.7 versus the log of the squid fin length ($b < 1$).

Figure 4.9 shows hydrodynamic propulsion efficiency for *L. forbesi*, *L. brevis*, *S. lessoniana*, and Sims (1986) and Hoar & Freadman's (in prep.) *L. pealei* against swimming speed in BLs^{-1} . Since hydrodynamic propulsion efficiency is calculated according to Cheng & Blickhan (1994; modified from Lighthill 1971) as

$$\frac{1}{2}(1+u)/v \quad (u=\text{swimming speed, } v=\text{wave speed}),$$

and wave speed is variable, the efficiency is also variable and ranges above 1, indicating greater than 100% efficiency, which is impossible. These unlikely efficiencies are an artefact of the combination of fin and jet propulsion and may actually reflect the relative importance of the two at various speeds. There is a dearth of research into jet assisted finning (JAF) and more appropriate equations are needed to describe it.

Figure 4.10 shows the simultaneous records of jet pressure, efficiency and animal and fin-wave velocity for a 2kg *L. forbesi* performing a reversal from fins-first to head-first to fins-first swimming (Hoar *et al.*, 1994). In (C) the polarity of the fin wave

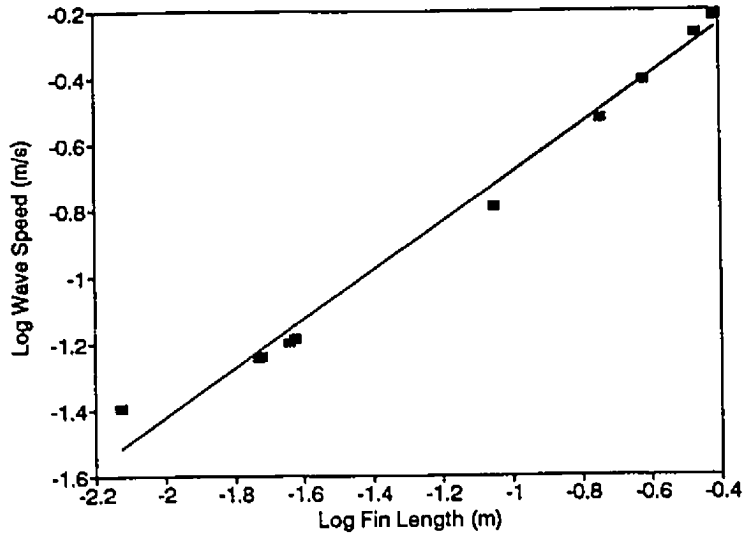


Figure 4.8. The relationship between the log fin wave speed (ms^{-1}) and log fin length for wave speeds to the left of the 1:1 relationship in Figure 4.7 ($r^2=0.99$).

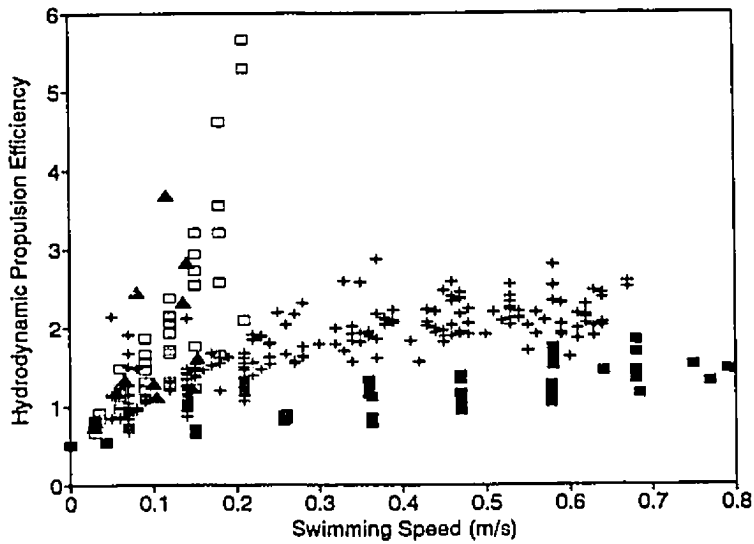


Figure 4.9. The relationship between swimming speed (ms^{-1}) and hydrodynamic propulsion efficiency for various long-finned squid species; *Loligo pealei* (+), *Loligo forbesi* (■), *Sepioteuthis lessoniana* (▲) and *Lolliguncula brevis* (□).

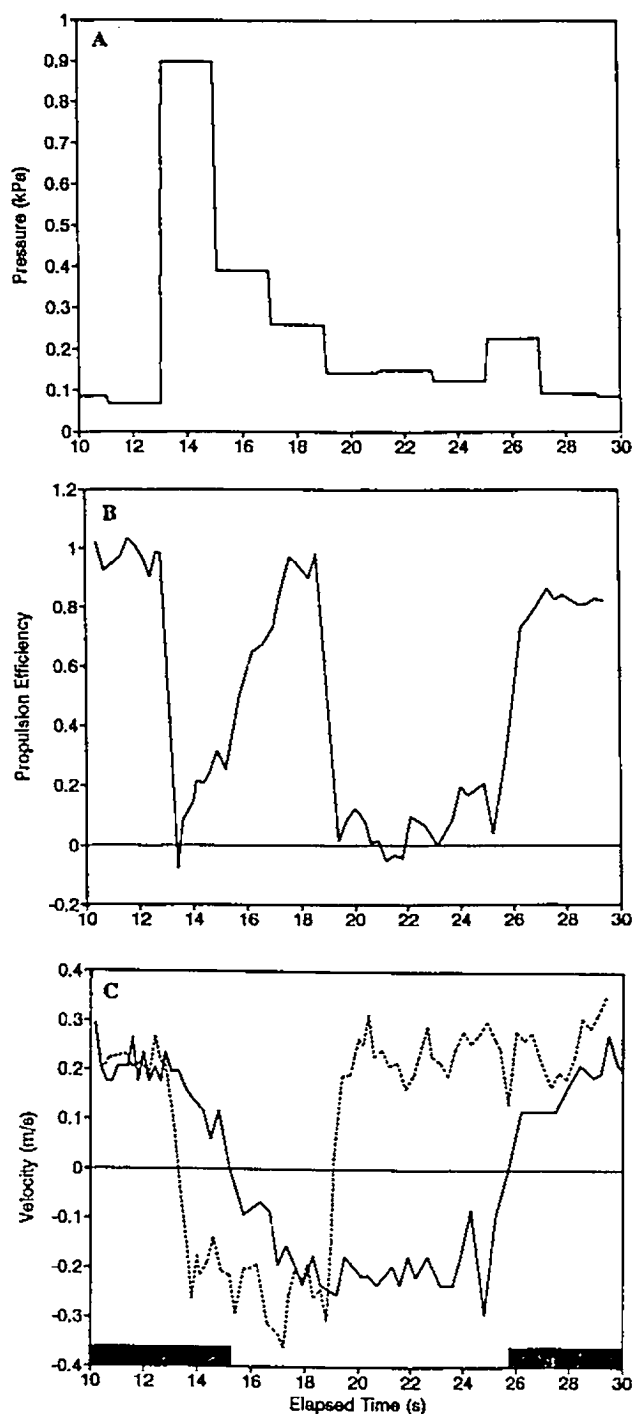


Figure 4.10. Simultaneous records of jet pressure, animal velocity and fin wave velocity during a cycle of reversals by a *Loligo forbesi* in a 3m diameter tank. (A) indicates average pressures over intervals of about 2s. (B) is the efficiency and (C) is animal velocity (solid) and fin wave velocity (dashed), black bars indicate that the animal is swimming fins-first (From Hoar *et al.*, 1994).

velocity is reversed, as is customary for dealing with fish, where motion is only possible when waves produce momentum in one direction by pushing water in the opposite direction. (B) shows the efficiency calculated as in Figure 4.9 for undulatory swimming and is included here since the squid is moving slowly and using the synergistic thrust of both fins and jet (Aleyev, 1977), or JAF. The squid swam fins—first with both fins and animal travelling at similar speeds and in an apparently efficient way, then the fins reverse coincident with a finward jet, which slows the animal and changes the swimming direction until the fins and animal reach the same speed in the opposite direction, and efficiency returns. Halfway across the tank the fins reverse again, with no change in animal speed and, with this calculation, an efficiency of 0. As the squid nears the tank side, a small headward jet ($\frac{1}{4}$ the pressure of the earlier one) reverses the animal's direction and accelerates the animal quickly to 0.2ms^{-1} where the fins are again effective. As with the earlier efficiency graph, the calculated numbers seem unlikely, since the efficiency ranges from below 0 to 1, however, the equation does give some indication of what is occurring; low efficiency when the animal and fin waves are in two different directions and very high when the two systems act together to produce JAF.

4.4. Discussion

4.4.1 Finning

Until now, the only quantitative studies of fin movement with swimming speed were O'Dor's (1988a) study of *Loligo opalescens* and Freadman *et al.*'s (1984) abstract on *L. pealei*. O'Dor (1988a) found a pattern in the fin waves produced by low aspect

ratio *L. opalescens* fins which is consistent with maximizing thrust while keeping drag at a minimum. These squid produced multiple waves along the fins at low swimming speeds when they were moving slowly enough to remain in laminar flow regimes. As the squid were swum faster and drag increased, the squid changed to flapping their fins in synchrony with the refilling stage of the jet cycle, possibly to contribute some thrust during the one time when the squid was losing momentum and, thus decrease the variability of thrust production to some extent. At very high speeds, such as escape jets, the squid rolled their fins against their mantles, thereby decreasing drag and gaining an optimal body profile which is more efficient for movement at high speeds. Fin waves, in the loliginids studied here, followed the same patterns seen for *L. opalescens* (Figures 4.4, 4.5 & 4.6), except for juvenile *S. lessoniana*, which did not seem to have the same control over their fins at high speeds that the adult squid had and therefore, did not roll their fins against the mantle as well as the adult squid. This fin use pattern, resembling gaits, may be a general one for squid, since other workers (Webber, 1985; O'Dor, 1982; Bradbury & Aldrich, 1969; and Zuev, 1965a) all noted fins being rolled against the mantle at high speeds for ommastrephid squid species. *Sepioteuthis sepioidea* also synchronizes fin flaps with refilling at fairly high speeds (personal observation; Forsythe & Hanlon, pers. comm.).

At low speeds, the squid swam against the current using JAF and were fairly good at maintaining their position in the water column. None of the three loliginids studied, however, swam well at high speeds and all tended to collapse fairly quickly against the swim tunnel screen. In all cases, the squid continued to exhibit fin waves at speeds

slower than the speeds at which they were swimming (Figures 4.4, 4.5 & 4.6), even though the fin waves must move at a speed faster than the animal moves to produce drag-based thrust (Gray, 1933). At higher speeds, the fins may be pushed by the water when they are not tight against the mantle, causing them to flutter, increasing the drag on the animal. In most cases, when the squid fins were moving slower than the squid, they were synchronized with the jet, so that the fin wave (usually more of a flap at these moderate speeds) occurred during the refilling part of the jet cycle. Therefore, the fin could be producing some "useful" drag-based thrust at the low point in the velocity curve, smoothing the variable thrust production curve that would occur if the squid used solely the jet to swim and decreasing the acceleration reaction. The speed at which the squid start to synchronize their fins with the jet is not consistent between species or even individuals and is not easily discernible from the figures (4.4, 4.5 & 4.6), but was observed with *L. forbesi* starting at about 0.7BLs^{-1} (Re is about 130 000), *L. brevis* at about 1BLs^{-1} (Re about 1 500) and the juvenile *S. lessoniana* at about 2BLs^{-1} (Re about 750). It is possible that this synchronizing speed may be related to the size of the squid, since increasing speeds (in BLs^{-1}) are seen with decreasing size, but a wider spectrum of different sized squid is needed to determine this accurately.

There are also some high fin wave speeds at high swimming speeds for these squid, which may be artefacts caused by the fins fluttering with the fast water flow but could be powered. The difference is difficult to deduce from ordinary video at high speeds, particularly with small squid. For squid with trapezoidal fins, these high speed waves, as well as the flaps at moderate speed, may be producing lift-based thrust in the

same manner as bird wings during flight (Azuma, 1992; Daniel, 1988). Unlike drag-based thrust, lift-based thrust can be produced by waves advancing slower than the animal is swimming. Although I am unable to analyze this component in my data, it may be a factor in the animal's locomotion, and must be considered in future analysis of changing gaits with speed.

Field experiments in the Azores indicated that *L. forbesi* were slow moving animals ($<1\text{BLs}^{-1}$), tending to maintain their horizontal position for hours, possibly through "soaring" in upwelling currents, with only vertical diel movements (O'Dor *et al.*, 1994). This low swimming speed in the field was consistent with laboratory data where the squid were less excitable (i.e. less high speed swimming into tank sides) when a slow current (up to 0.5ms^{-1}) was introduced to the tank and readily swam at low speeds in the swim tunnel. The fastest speed recorded either in the swim tunnel, or on video after startling, was 0.8ms^{-1} , less than 1BLs^{-1} for that animal (O'Dor *et al.*, 1994), suggesting that this is a generally slow-moving squid, which may be true for other long-finned squid which have not been studied in the field.

The remaining graphs include some unpublished data on *Loligo pealei* fin speeds (Hoar & Freadman, in prep.; Sims, 1986) because this species lies in the large gap between the small *L. brevis* and large *L. forbesi*. The graph of wave versus swimming speeds (Figure 4.7) implies that there is little relationship between the two, since Hoar & Freadman's (in prep.) data show a trend of increasing wave speed with increasing speed, which is inconsistent with the decreasing number of waves seen with the gaits. The lack of any relationship in *S. lessoniana* probably results from the lack of information at very

low speeds (i.e. less than $1BLs^{-1}$) and conversely, in *L. forbesi*, to lack of high speed data. The *L. brevis* data have a slight decreasing trend, which would be consistent with the three gaits observed in these animals and is the only obvious evidence for this. Since the data from Sims (1986) are all from the same animal, but at three different swimming speeds, they illustrate the wide variation that can occur at lower speeds, where the squid can either produce multiple or single waves along the fins, but can not address the issue of gaits due to its small range.

Gray's (1933) analysis of undulating eel fins indicated that only those fin waves travelling faster than the animal swims can be producing drag-based thrust. The exponential relationship in Figure 4.8 relates fin wave speed to fin length for this kind of thrust and indicates that there is a decrease in wave speed for larger fins. This relationship may indicate that as the animal gets bigger, the drag-based thrust production is limited by the force that can be applied to the fluid during undulation and, therefore, the squid have to move to lift-based thrust, which does not require waves to move faster than the squid is swimming (Azuma, 1992). A change from drag- to lift-based thrust production is a form of gait change and likely also involves a change in the mechanics of muscle movement. There are two types of muscle within the fin, fibres with large mitochondrial cores (oxidative fibres) which only occur in the outer layers of the transverse muscle, and fibres with small mitochondrial cores which occur in the dorsoventral, longitudinal and transverse muscles (Kier, 1989). Measurements of muscle activity during gentle fin beating in *Sepia* indicate the use of only the oxidative fibres, while the other muscle groups become active during vigorous fin beating (Kier *et al.*,

1989). It is likely that at the lower swimming speeds, when the fin waves produce drag-based thrust, the squid are using only the oxidative fibres (in combination with a connective tissue fibre array; Johnsen & Kier, 1993) but that the shift to faster waves and higher amplitudes involves different muscles in a changing gait. The fins of squid also vary in thickness from base to tip and it is possible that this may cause some change in the muscle mechanics of the fin. This factor, although noted, was not measured due to technical difficulties, but should be taken into account in future studies.

4.4.2 Jet Assisted Finning

There is, as yet, no system for calculating the mechanical efficiency for an animal that utilizes two systems of propulsion simultaneously. The Froude Efficiency equation as used in Chapter 1 is effective for the jet system and, therefore, hydrodynamic propulsion efficiency (Cheng & Blickhan, 1994) was tried as an approach to understanding the importance of the fins (Figure 4.9). This calculation, however, yields impossible results, since it implies that some *L. brevis* were capable of over 500% efficiency. This is partly a result of the equation lacking a term for the jet propulsion. There are data for a large group of animals whose efficiency lies below 1, virtually all of which occur at less than $1BLs^{-1}$. Since the use of the fins is more pronounced at low speeds (i.e. the multiple waves; Aleyev, 1977), it may be that these efficiencies at low speed are closer to the actual efficiencies of fins in JAF. At higher speeds the hydrodynamic propulsion efficiency equation may be indicative of the jet component of JAF (i.e. 500% indicates fins account for less than one fifth, or 20%, of thrust).

In nature, squid perform a unique movement when they reverse swimming direction without turning. This movement is very useful to the squid, increasing the element of surprise, since they can overtake a school of fish by swimming fins-first and then reverse into the school head-(and more importantly, arms-)first, as described in Foyle & O'Dor (1988). Also, when kept in a 15m diameter pool, long-finned squid maintained vertical position through repeated horizontal reversals, while short-finned squid bobbed up and down while jetting (Webber & O'Dor, 1986), which indicates that short-finned squid are more dependent on the jet for lift production. The Azorean *Loligo forbesi*, when kept in a 3m diameter tank, quickly learned to adjust their behaviour to avoid hitting the sides by slowly reversing back and forth across the tank. Figure 4.10 shows simultaneous velocity and pressure records along with calculated efficiency for a reversing squid and shows the expected change in direction of fins just prior to the initial jet. There is a strange change in fin direction after this, however, when the animal is only halfway across the tank, which does not seem to affect the velocity at all, as the squid does not reverse again until after a headward jet. This change in fin direction could be acting as a sort of braking system for the animal, once it has seen the other side. There would, however, be a decrease in animal speed, so it must serve some other, as yet undefined, purpose or perhaps be a relic of the original behaviour pattern. The fin waves may be used by the squid to produce lift and, therefore, the change in direction may be related to their negative buoyancy.

The loliginid squid studied seem to rely on their fins to a great extent, since they produce fin waves constantly, at all but the highest speeds (i.e. escape velocity), in a

manner similar to that described by Aleyev (1977). Since squid are negatively buoyant, the use of constant fin waves may not only be a thrust producing, but also a lift producing action. Drag-based thrust can only be produced at lower speeds, where the fin undulations can be produced faster than the swimming speed, but lift-based thrust can be produced over a wide range of speeds independent of fin undulations, which may be indicated by the presence of gaits in the squid studied.

CHAPTER 5. General Discussion

This thesis investigated the changes in morphometrics that occur with growth of long-finned squid and the effect of these on swimming. Changes in the allometry of the squid over a billion-fold mass range were then incorporated into a model of jet propulsion that predicts the thrust and drag acting on the animals. The effect of the fins was included in this model and the effect of changes in fin length studied for the first time in squid. The use of the fins in swimming for squid of three different sizes was also compared to the scant published data to gain insight into the concept of fin gaits (O'Dor, 1988a) and the synergy of fins and jet.

5.1 Mechanisms

In response to the changing forces acting on the squid as they grow from a tiny hatchling in a viscosity-dominated world to a large adult in our inertia-dominated world, they not only become more slender, with an optimal body profile for high Reynolds number locomotion, but also develop larger fins. Both changes can occur because of the decrease in the relative importance of skin friction drag acting on the larger squid, along with a concomitant increase in the importance of pressure drag and, therefore, streamlining. Fin growth shows the most positive allometry relative to mass of all morphometric measurements (i.e. the fastest relative growth). Across the adult range (5g–5kg), and regardless of length, the fins have a similar width to length ratio of 0.35 that

implies an optimal shape for producing thrust and minimizing drag for their preferred form of locomotion, jet assisted finning (JAF). Not only does there seem to be an optimal shape for the fins, but the relationship between the length of the fins and the size holds regardless of final adult size, at least for these long-finned loliginids. This means that it may only be the final size of the adult (above 5g) that dictates the maximum relative fin length and not the species. This suggests that if a *Loligo opalescens* could be grown to the size of a large *L. forbesi*, the relative fin size (and shape) would be virtually indistinguishable from the latter. This may, in fact, be the mechanism that leads to the larger relative fin size of the Azorean *L. forbesi* compared with the smaller individuals of the same species along the coast of Europe (Martins, 1982). Although of different species and even genera, all the squid in the study were long-finned, shallow, coastal-dwelling species with similar lifestyles and niches and would require fins similar in form. Thus the phenotype/genotype question is not really resolved for this group and the question remains as to why *Thysanoteuthis rhombus*, a pelagic squid, would have large loliginid-like fins. Perhaps this shape optimizes the smooth transition from drag- to lift-based thrust generation with increasing speed. As well, it is possible that this type of physically rather than phylogenetically constrained fin shape and size may also occur in the short-finned ommastrephid squid. However, these squid are less dependent on the economies of low speed undulations, and have shapes specialized for flapping.

The loliginid squid swum in this study all performed better at relatively low speeds, and, when kept in tanks with slow currents, all maintained very low speeds. These low speeds are consistent with the use of multiple propulsive fin waves for JAF,

which cannot be used at high speeds, since the fin waves must move faster than the animal to produce undulatory thrust (Gray, 1933). As the squid were made to swim faster, they synchronized the wave/flap with the refilling of the mantle during the jet cycle, to smooth out the periodic thrust production curve created by the jet, as previously shown in *L. opalescens* (O'Dor, 1988a). That these squid prefer to move slowly is consistent with their lifestyle as localized coastal species. Where information is available, their spawning migrations are short (100s of kilometres) compared with those of ommastrephids like *Illex* or *Todarodes*, both of which travel 1000s of kilometres from feeding to spawning grounds, and this may also be related to the better high-speed swimming capabilities of the ommastrephids.

The finning of squid in this study seemed to indicate the use of different modes at different speeds, outside of the "gaits" mentioned. The analysis of the highest wave speeds attained by the fins of all species yielded an exponential relationship that may be related the restriction of drag-based thrust to slower swimming speeds. At faster swimming speeds, when the waves are being produced slower than the squid is swimming lift-based thrust may be produced, but unfortunately, analysis of this mode requires measurement not possible in available videos. The switch from drag- to lift-based thrust production may be related to the anatomy of the fins and may be indicated by the different gaits observed. Therefore, it is the changing use of the different fin muscle systems that must be better understood before the cause of these gaits and an understanding of the different types of thrust production can be explained. The complexity of the nervous system required to control these gaits, particularly as they

change with scale, must occupy a large component of the ample brains of cephalopods.

When studying locomotion, some method of assessing the efficiency of the animal is generally used as an indication of how well it swims. The mechanical efficiency of squid is particularly hard to understand or quantify, since there is no published method for calculating the efficiency of an animal that uses two completely distinct but synergistic methods of propulsion. The Froude efficiency equation used here for the model is applicable only to the jet and not the fins, and therefore, hydrodynamic propulsion efficiency was applied to the fin waves. Each form assesses only one of the two propulsion methods, which lead to the former producing particularly low efficiencies and the latter highly variable ones (up to 500% efficient). Until a method is developed to quantify the efficiency for squid utilizing JAF, there will remain a distinct gap in the information on swimming squid.

In all species studied, the squid continued to produce waves when swimming at speeds faster than those that their fins could maintain which, according to Gray (1933) can produce no drag-based thrust for the animal. The fins may be producing lift-based thrust, but there are also other potential uses for the fin waves. The waves could act as a braking system for the squid when applied opposite to the squid's direction of movement, but the implication from Figure 4.10 is that the fins alone have limited capacity to slow the squid. It is likely, however, that the fins are used effectively to slow down the squid over larger distances. Classic experiments demonstrating that drag is reduced when dead fish are made rigid, show that passive undulations clearly absorb energy very effectively (Brett, 1963), suggesting that the squid could use fin undulations

for dynamic braking and steering.

Since many squid travel in schools, particularly the coastal loliginid species, even passive fin waves may not be totally wasteful. Energy is transferred from the moving fins to the water around the squid at all wave speeds, whether drag- or lift-based thrust is being produced. Since the squid school moves in formation through the water, this energy transfer may actually accelerate the water between the squid and augment the swimming of those behind the leaders. If not by actually moving the water mass, at least by making the water less turbulent or microturbulent, thereby increasing their swimming efficiency. This may be another way of shifting power between the jet and the fins and is another area needing further research.

5.2 Life History

The life histories of many squid, both loliginid and ommastrephid are tied to current systems (Coelho, 1985; O'Dor, 1992). Those of some ommastrephid squid, such as *Illex* or *Todarodes*, are tied to along-shore current systems involving larval drift to feeding grounds and adult countercurrent swimming to spawning beds (O'Dor, 1988b). Loliginid squid, however, are usually associated with inshore and offshore currents, such as *Loligo vulgaris reynaudii*, which move offshore as juveniles to feed and migrate back to the inshore as adults to spawn (Augustyn *et al.*, 1992). During both these types of life histories, the changing circumstances around the squid as they travel currents may require a change in the animals themselves. Juvenile squid invest heavily in growth to attain minimum sub-adult size quickly and avoid the energetic costs and dangers of being small

(Forsythe & van Heukelem, 1987). This growth in total size of the squid leads to large changes in the overall shape of the fins and, therefore, how the squid can use them to move. As a result, studies of free-swimming loliginid squid can be better understood by the inclusion of knowledge of the use of the fins by these animals. O'Dor *et al.*'s (1994) work on *L. forbesi* showed a squid that seemed to minimize horizontal movements. The laboratory studies on these animals showed them to be preferentially slow swimmers content to swim in slow currents. In the field, these squid concentrated for long periods near sea mounts, implying their use of "soaring" techniques on upwelling currents to hold vertical position (since the jet pressures produced was quite low; O'Dor *et al.*, 1994), much like gulls soar on updrafts near cliff-faces. Recent work on *Loligo vulgaris reynaudii* on South African spawning beds has indicated a unique cephalopod mating strategy involving small "sneaker" males and leks. Also, these different sized squid appear to have average swimming speeds related to size; the largest males generally moving the slowest ($0.3BLs^{-1}$), and the smallest "sneaker" males the fastest ($0.8BLs^{-1}$, but up to $2BLs^{-1}$), with the females in between ($0.6BLs^{-1}$; Hanlon, 1995; O'Dor *et al.*, in press). This pattern is consistent with the notion that moving quickly is very costly for large finned squid due to the increased drag.

Not all squid use currents to soar or to assist their life cycles, in the Cayman Islands, schools of the reef squid, *Sepioteuthis sepioidea*, have been observed holding position in steady high current zones produced by surf "run off" (Hanlon *et al.*, 1992 & pers. comm.), which would be very costly energetically for the animals. So, why do they do this? During the night, these squid move over the inner reef hunting for prey, but then

return during the day to the currents. The schools maintain position facing fin-first into the current and may gain an advantage in that fish moving into the current to catch them will be swept downstream, where they can be easily watched, and are visible to the squid if they try to swim upstream to catch dinner. So, the advantage of being a difficult-to-catch prey item must outweigh the energetic costs of swimming in the current, but even so, they do keep those costs as low as possible, by wrapping their fins around the mantle with only the occasional flap during refilling, a swimming style vastly different from their nightly use of the fins to manoeuvre over the reef.

Each of these long-finned squid have found ways in which to utilize their fins to an effective advantage in their niche environments, but what do they do as hatchlings, when the fins are so much smaller than as adults? Most squid have life histories that also involve changes in niche, from planktonic paralarvae to nekto-benthic, nektonic or pelagic adults and the changes in fin-form with growth mirror these (Vidal, 1994; Perez, 1995). The planktonic life of the various squid is quite similar and the small fins contribute not only the low drag mentioned previously, but also some steering and possibly lift to the squid (although the work on the juvenile *S. lessoniana* indicates that their control over the fins is not yet perfected). Hatchling squid swim vertically through the water column and it is not until they have grown (both in total length and fins) that they begin to swim horizontally. The thrust supplied by the fin waves is primarily useful for horizontal swimming (Aleyev, 1977), so this change in lifestyle and fin form may be closely tied. It is only those squid that inhabit complex, coastal niches (aside from the poorly understood *Thysanoteuthis rhombus*) that grow the large, long fins studied in this

thesis, while pelagic squid have the small, short fins, not unlike those of young hatchling squid.

Although general patterns for the scaling of JAF locomotion are emerging, this thesis seems to have raised more questions than it answered: how are the squid controlling the funnel orifice during a jet cycle, how does the thickness of the fin relate to the use of different muscles during high speed finning versus low speed finning, and how best to calculate the swimming efficiency for an animal that may use three separate but synergistic modes of locomotion? Given the diversity of squid designs and lifestyles the scope for research on the locomotion of these fish competitors is at least as broad as that for fish themselves.

APPENDIX 1

Summary of the morphometric data for the different species of long-finned squid used for the analyses and model. Abbreviations used for species names are *Loligo opalescens* (Lopal), *Lolliguncula brevis* (Lbrev for the Smithsonian provided hatchlings and gunc for the Texan animals), *Loligo forbesi* (Lf# for the Smithsonian-provided hatchlings, Lf(B) for squid caught and measured on the Baia da Horta, Lf90-# for squid used in the laboratory, where numbers identify the animals), *Sepioteuthis lessoniana* (SepII for the 3 adult squid, Sep# for the juveniles used in the laboratory), *Loligo vulgaris reynaudii* (Lvulg), *Architeuthis sp.* (Arch) and *Illex illecebrosus* (illex).

	mass (kg)	funnel circ.	mantle diam.	mantle thick.	mantle length	total length (m)	fin width	fin length	fin area
Arch	70.79	3.0E-01	3.3E-01	4.5E-02	1.5E+0	4.7E+0	4.1E-01	2.5E-01	5.2E-02
Illex	1.5E-07		9.8E-04	3.0E-05	1.1E-03	1.8E-03		1.0E-04	
Illex	5.0E-01	3.5E-02	7.0E-02	7.0E-03	2.8E-01	4.9E-01	6.5E-02	1.2E-01	
Lopal	4.3E-04	2.8E-03	5.9E-03	5.0E-04	2.4E-02	3.6E-02	3.9E-03	8.4E-03	1.6E-05
Lopal	1.7E-03	3.9E-03	8.6E-03	1.1E-03	3.4E-02	5.2E-02		1.3E-02	
Lopal	4.3E-04	3.4E-03	6.5E-03	6.2E-04	1.7E-02	2.7E-02	3.1E-03	3.9E-03	6.0E-06
Lopal	5.3E-05	8.5E-04	3.1E-03	3.1E-04	8.0E-03	1.1E-02	6.1E-04	1.2E-03	3.7E-07
Lopal	2.3E-04	1.6E-03	4.6E-03	6.2E-04	1.4E-02	2.2E-02	2.3E-03	2.9E-03	3.4E-06
Lopal	5.6E-06	7.2E-04	1.7E-03	9.6E-05	3.2E-03	5.1E-03	6.6E-04	5.4E-04	1.8E-07
Lopal	4.7E-03	6.2E-03	1.3E-02	1.1E-03	5.9E-02	9.4E-02	1.2E-02	2.7E-02	1.6E-04
Lopal	4.1E-03	4.7E-03	1.1E-02	1.4E-03	4.5E-02	7.0E-02	8.5E-03	2.0E-02	8.4E-05
Lopal	1.4E-06	2.7E-04	1.1E-03	5.6E-05	2.2E-03	3.8E-03	3.9E-04	4.2E-04	8.2E-08
Lopal	2.5E-02	8.2E-03	1.6E-02	2.8E-03	9.5E-02	1.4E-01	1.5E-02	4.5E-02	3.4E-04
Lopal	8.3E-03	6.4E-02	1.4E-02	2.2E-03	5.8E-02	9.2E-02	1.3E-02	2.6E-02	1.7E-04
Lf(B)	3.0E+0	5.5E-02	1.0E-01	1.1E-02	5.7E-01	8.3E-01		3.9E-01	
Lf(B)	2.8E+0	4.7E-02	9.9E-02	1.0E-02	5.7E-01	8.1E-01		3.5E-01	
Lf(B)	6.0E+0	6.7E-02	1.2E-01	1.4E-02	7.8E-01	1.1E+00		5.8E-01	
Lf(B)	2.0E+0	5.8E-02	1.0E-01	1.0E-02	5.5E-01	8.3E-01		3.9E-01	
Lf(B)	5.0E-01	2.9E-02	6.0E-02	6.0E-03	2.7E-01	4.1E-01		1.9E-01	
Lf(B)	4.0E-01	2.8E-02	6.7E-02	8.0E-03	3.1E-01	4.7E-01		2.1E-01	
Lf(B)	4.0E-01	3.5E-02	8.0E-02	8.3E-03	3.8E-01	5.5E-01		2.6E-01	
Lf(B)	7.5E-01	4.3E-02	7.6E-02	7.6E-03	3.7E-01	5.7E-01		2.3E-01	
Lf(B)	5.0E-01	3.7E-02	7.0E-02	6.2E-03	3.3E-01	5.2E-01		2.3E-01	
Lf(B)	5.0E-01	3.8E-02	6.8E-02	8.3E-03	3.4E-01	5.0E-01		2.2E-01	
Lf(B)	2.5E-01	3.6E-02	7.0E-02	5.4E-03	3.2E-01	4.9E-01		2.3E-01	
Lf(B)	1.5E+0	5.1E-02	8.3E-02	9.0E-03	4.6E-01	7.0E-01		3.2E-01	
Lf(B)	4.3E+0	6.9E-02	1.1E-01	1.2E-02	6.6E-01	9.2E-01		4.6E-01	
Lf(B)	4.5E+0	6.3E-02	1.1E-01	9.9E-03	6.5E-01	9.3E-01		4.4E-01	
Lf(B)	9.5E-01	4.2E-02	9.2E-02	9.2E-03	4.8E-01	7.0E-01		3.4E-01	
Lf(B)	1.0E+0	4.4E-02	7.6E-02	8.5E-03	3.9E-01	5.7E-01		2.7E-01	
Lf(B)	3.2E+0	5.8E-02	9.9E-02	9.2E-03	5.8E-01	9.0E-01		3.9E-01	
Lf10	5.7E-06	1.0E-03	2.0E-03	4.5E-05	3.3E-03	5.2E-03	4.7E-04	5.0E-04	1.1E-07
Lf11	7.2E-06	9.1E-04	2.3E-03	3.5E-05	4.0E-03	5.6E-03	6.3E-04	6.4E-04	2.3E-07
Lf12	6.5E-06	9.4E-04	1.8E-03	3.5E-05	3.7E-03	6.3E-03	6.2E-04	4.7E-04	1.6E-07
Lf14	7.5E-06	8.7E-04	2.2E-03	4.2E-05	3.5E-03	5.6E-03	6.8E-04	5.0E-04	1.3E-07
Lf15	6.2E-06	7.0E-04	2.3E-03	4.5E-05	3.9E-03	6.0E-03	6.9E-04	6.7E-04	2.3E-07
Lf16	6.0E-06	8.0E-04	2.3E-03	3.5E-05	3.3E-03	5.1E-03	6.8E-04	5.5E-04	2.3E-07
Lf17	6.3E-06	8.5E-04	2.0E-03	4.4E-05	3.3E-03	5.1E-03	6.8E-04	4.2E-04	1.9E-07
Lf8	7.1E-06	1.1E-03	2.1E-03	4.2E-05	3.0E-03	4.8E-03	4.9E-04	3.6E-04	1.1E-07
Lf9	7.0E-06	8.8E-04	2.0E-03	5.6E-05	3.5E-03	5.7E-03	5.4E-04	4.7E-04	1.9E-07
Lf90-1	2.6E+0	6.0E-02	9.5E-02	8.0E-03	5.5E-01	8.5E-01		3.6E-01	
Lf90-1	1.1E+0	4.3E-02	7.0E-02	6.0E-03	3.3E-01	5.1E-01	7.0E-02	2.4E-01	6.1E-02
Lf90-2	1.4E+0	3.3E-02	6.7E-02	6.6E-03	3.8E-01	5.7E-01		2.5E-01	
Lf90-3	2.7E+0	4.2E-02	1.1E-01	9.4E-03	5.8E-01	8.5E-01	1.3E-01	3.9E-01	1.6E-01
Lf90-4	8.4E-01	3.3E-02	6.4E-02	6.2E-03	3.0E-01	4.7E-01		1.9E-01	
Lf90-5	3.1E+0	5.2E-02	1.1E-01	9.0E-03	6.0E-01	8.8E-01	1.2E-01	3.9E-01	1.7E-01
Lf90-6	1.5E+0	2.8E-02	7.3E-02	8.0E-03	3.8E-01	5.7E-01		2.7E-01	

Lf90-7	1.5E+0	4.7E-02	7.8E-02	6.9E-03	3.9E-01	6.1E-01		2.6E-01	
Lf90-8	1.4E+0	4.6E-02	7.2E-02	6.5E-03	3.6E-01	5.7E-01	8.0E-02	2.4E-01	6.8E-02
Lf90-9	2.5E+0	5.6E-02	9.1E-02	8.5E-03	4.8E-01	7.3E-01		3.4E-01	
Lpeal	3.1E-01	3.2E-01	5.1E-02		3.3E-01	4.8E-01	1.9E-01	2.3E-01	5.4E-02
Lpeal	2.0E-03	5.7E-02	9.0E-03		3.1E-02	5.2E-02	2.1E-02	1.2E-02	3.1E-04
Lpeal	1.0E-03	1.0E-02	1.1E-02		3.0E-02	5.5E-02	2.2E-02	1.1E-02	3.0E-04
Lpeal	2.1E-01	2.6E-01	4.2E-02		2.9E-01	4.6E-01	1.8E-01	1.8E-01	4.2E-02
Lpeal	1.2E-01	2.0E-01	3.2E-02		2.1E-01	3.2E-01	1.3E-01	1.3E-01	2.2E-02
Lvulg	2.4E-01	3.1E-02	4.5E-02		2.2E-01	3.2E-01	4.2E-02	1.6E-01	3.4E-03
Lvulg	0.106	2.4E-02	3.3E-02	4.0E-03	1.8E-01	2.5E-01	3.5E-02	1.2E-01	2.6E-03
Lvulg	2.9E-03	9.3E-03	1.4E-02		3.7E-02	6.5E-02	7.2E-03	2.3E-02	8.3E-05
Lvulg	0.245	3.4E-02	4.6E-02	4.9E-03	2.3E-01	3.2E-01	4.7E-02	1.6E-01	3.6E-03
Lvulg	0.473	3.8E-02	5.6E-02	6.0E-03	3.2E-01	4.3E-01	6.8E-02	2.2E-01	7.3E-03
Lvulg	0.237	3.1E-02	4.5E-02	4.8E-03	2.6E-01	3.5E-01	4.6E-02	1.7E-01	3.9E-03
Lvulg	0.815	4.2E-02	6.7E-02	8.0E-03	4.0E-01	5.2E-01	8.1E-02	2.6E-01	1.1E-02
Lvulg	0.182	3.2E-02	4.0E-02	4.8E-03	2.1E-01	3.0E-01	4.3E-02	1.4E-01	3.0E-03
Lvulg	0.184	3.0E-02	4.5E-02	5.1E-03	1.9E-01	2.9E-01	4.4E-02	1.2E-01	2.7E-03
Lvulg	0.193	2.8E-02	4.3E-02	5.1E-03	2.2E-01	3.1E-01	4.5E-02	1.5E-01	3.4E-03
Lvulg	0.118	2.6E-02	3.8E-02	4.6E-03	1.8E-01	2.5E-01	3.2E-02	1.2E-01	1.9E-03
Lvulg	0.169	2.4E-02	4.1E-02	4.7E-03	2.1E-01	2.9E-01	4.3E-02	1.4E-01	3.0E-03
Lvulg	0.171	3.0E-02	3.8E-02	4.4E-03	2.1E-01	3.0E-01	4.3E-02	1.4E-01	3.0E-03
Lvulg	0.203	3.3E-02	4.5E-02	4.3E-03	2.0E-01	3.1E-01	4.2E-02	1.4E-01	2.9E-03
Lvulg	0.327	2.8E-02	4.6E-02	5.5E-03	2.5E-01	3.6E-01	5.5E-02	1.6E-01	4.5E-03
Lvulg	0.226	3.4E-02	4.0E-02	4.2E-03	2.2E-01	3.0E-01	4.7E-02	1.5E-01	3.5E-03
Lvulg	3.0E-06	1.1E-03	1.7E-03		2.5E-03	5.5E-03	5.7E-04	5.3E-04	1.5E-07
Sep	4.5E-04	2.7E-02	4.3E-03	5.2E-04	1.2E-02	2.2E-02		6.3E-03	
Sep1	3.9E-04	3.0E-02	4.8E-03	7.0E-04	1.6E-02	2.3E-02		7.5E-03	
Sep2	3.1E-04	3.0E-02	4.8E-03	5.0E-04	1.5E-02	2.8E-02	8.0E-04	7.5E-03	3.0E-06
Sep3	1.3E-03	4.1E-02	6.5E-03	9.2E-04	2.2E-02	3.8E-02	1.5E-02	1.5E-02	2.9E-04
Sep4	2.0E-03	5.5E-03	7.4E-03	1.2E-03	2.7E-02	4.4E-02	1.8E-02	2.0E-02	4.5E-04
Sep5	5.1E-04	3.6E-02	5.7E-03	6.8E-04	1.6E-02	2.8E-02	1.1E-02	1.1E-02	1.6E-04
Sep6	5.3E-04	3.2E-03	5.4E-03	7.3E-04	1.7E-02	3.0E-02	1.2E-02	1.1E-02	1.7E-04
Sep7	1.4E-03	4.1E-03	6.6E-03	8.8E-04	2.0E-02	3.9E-02	1.6E-02	1.7E-02	3.3E-04
SepI	1.4E+0	4.5E-02	8.8E-02	1.2E-02	3.3E-01	5.5E-01	2.2E-01	3.0E-01	8.1E-02
SepII	1.0E+0	3.9E-02	6.4E-02	8.2E-03	3.1E-01	5.3E-01	2.1E-01	2.9E-01	7.6E-02
SepIII	1.8E+0	6.1E-01	9.7E-02	9.7E-03	3.4E-01	5.6E-01	2.2E-01	3.1E-01	8.7E-02
gunc	7.4E-03	0.0E+00		1.5E-03	5.1E-02	8.0E-02	3.2E-02	2.8E-02	1.1E-03
gunc	7.5E-03	8.2E-03	1.1E-02	1.6E-03	4.9E-02	8.3E-02	3.3E-02	2.1E-02	8.8E-04
gunc1	6.9E-03	5.0E-03		1.6E-03	4.9E-02	7.7E-02	3.1E-02	2.2E-02	8.3E-04
gunc10	6.7E-03	5.3E-03	1.3E-02	1.5E-03	4.2E-02	6.4E-02	2.5E-02	1.9E-02	6.1E-04
gunc11	5.8E-03	5.8E-03	1.2E-02	1.5E-03	4.2E-02	6.2E-02	2.4E-02	1.8E-02	5.6E-04
gunc3	9.7E-03	6.1E-03	1.5E-02	1.5E-03	5.4E-02	9.3E-02	3.7E-02	2.4E-02	1.1E-03
gunc4	6.0E-03	5.7E-03	1.3E-02	1.5E-03	4.6E-02	7.1E-02	2.8E-02	2.3E-02	8.1E-04
gunc5	4.3E-03	5.1E-03	1.1E-02	1.4E-03	4.0E-02	6.2E-02	2.5E-02	1.5E-02	4.7E-04
gunc6	6.5E-03	5.9E-03	1.3E-02	1.7E-03	4.5E-02	7.1E-02	2.8E-02	1.9E-02	6.8E-04
gunc7	5.0E-03	5.5E-03	1.3E-02	1.5E-03	4.0E-02	6.2E-02	2.5E-02	1.8E-02	5.7E-04
gunc8	5.5E-03	4.3E-03	1.2E-02	1.4E-03	4.3E-02	7.0E-02	2.8E-02	1.9E-02	6.6E-04
lbrev1	2.4E-06	6.6E-04	1.6E-03	1.4E-05	1.9E-03	3.1E-03	4.1E-04	3.3E-04	9.9E-08
lbrev4	2.6E-06	7.4E-04	1.5E-03	1.6E-05	1.9E-03	3.4E-03	3.8E-04	3.0E-04	8.6E-08
lbrev5	1.1E-06	6.7E-04	1.5E-03	1.6E-05	1.8E-03	2.9E-03	2.6E-04	2.0E-04	2.6E-08

lbrev6	1.5E-06	5.2E-04	1.4E-03	2.1E-05	1.7E-03	2.8E-03	2.8E-04	2.1E-04	4.3E-08
Lp1-1	8.5E-02	1.8E-01	2.8E-02		1.4E-01	2.0E-01	5.6E-02	7.2E-02	2.0E-03
Lp1-2	9.2E-02	1.9E-01	3.1E-02		1.5E-01	2.1E-01	6.0E-02	7.6E-02	2.3E-03
Lp10-2	9.4E-02	1.6E-01	2.5E-02		1.4E-01	2.0E-01	5.5E-02	7.2E-02	2.0E-03
Lp11-2	9.5E-02	1.8E-01	2.8E-02		1.4E-01	2.1E-01	5.5E-02	7.0E-02	1.9E-03
Lp12-2	8.7E-02	1.9E-01	3.0E-02		1.5E-01	2.0E-01	5.4E-02	6.9E-02	1.9E-03
Lp13-2	9.8E-02	2.1E-01	3.4E-02		1.6E-01	2.3E-01	6.4E-02	8.2E-02	2.6E-03
Lp14-2	1.1E-01	2.2E-01	3.5E-02		1.8E-01	2.6E-01	7.0E-02	9.0E-02	3.2E-03
Lp15-2	1.0E-01	1.9E-01	3.0E-02		1.6E-01	2.3E-01	6.4E-02	8.1E-02	2.6E-03
Lp16-2	1.1E-01	1.9E-01	3.1E-02		1.6E-01	2.3E-01	6.2E-02	7.5E-02	2.3E-03
Lp17-2	1.00E-0	1.8E-01	2.8E-02		1.6E-01	2.2E-01	6.3E-02	7.9E-02	2.5E-03
Lp18-2	1.0E-01	1.8E-01	2.9E-02		1.6E-01	2.4E-01	6.1E-02	8.1E-02	2.5E-03
Lp19-2	1.0E-01	1.6E-01	2.5E-02		1.6E-01	2.2E-01	6.4E-02	7.9E-02	2.5E-03
Lp2-1	9.0E-02	1.7E-01	2.7E-02		1.6E-01	2.3E-01	6.2E-02	7.2E-02	2.2E-03
Lp2-2	1.1E-01	2.2E-01	3.5E-02		1.8E-01	2.4E-01	7.0E-02	8.9E-02	3.1E-03
Lp20-2	9.8E-02	1.6E-01	2.6E-02		1.5E-01	2.2E-01	6.3E-02	8.2E-02	2.6E-03
Lp21-2	1.00E-0	2.0E-01	3.2E-02		1.6E-01	2.3E-01	6.1E-02	7.9E-02	2.4E-03
Lp22-2	9.7E-02	2.1E-01	3.3E-02		1.7E-01	2.4E-01	6.6E-02	8.4E-02	2.8E-03
Lp23-2	1.0E-01	1.9E-01	3.1E-02		1.6E-01	2.4E-01	6.3E-02	8.2E-02	2.6E-03
Lp24-2	9.8E-02	1.9E-01	3.0E-02		1.6E-01	2.3E-01	6.5E-02	8.1E-02	2.6E-03
Lp3-1	8.9E-02	1.9E-01	3.1E-02		1.5E-01	2.2E-01	6.0E-02	7.9E-02	2.4E-03
Lp3-2	1.00E-0	2.1E-01	3.3E-02		1.7E-01	2.4E-01	6.6E-02	8.5E-02	2.8E-03
Lp4-1	1.1E-01	2.1E-01	3.3E-02		1.6E-01	2.3E-01	6.4E-02	8.3E-02	2.7E-03
Lp4-2	9.2E-02	1.7E-01	2.7E-02		1.5E-01	2.2E-01	6.0E-02	7.6E-02	2.3E-03
Lp5-1	1.1E-01	2.2E-01	3.5E-02		1.7E-01	2.5E-01	6.8E-02	8.7E-02	3.0E-03
Lp5-2	1.00E-0	2.1E-01	3.4E-02		1.6E-01	2.3E-01	6.4E-02	8.2E-02	2.6E-03
Lp6-1	9.4E-02	1.9E-01	3.0E-02		1.5E-01	2.1E-01	5.8E-02	7.4E-02	2.1E-03
Lp6-2	8.8E-02	1.8E-01	2.9E-02		1.5E-01	2.1E-01	5.8E-02	7.4E-02	2.1E-03
Lp7-2	1.0E-01	1.9E-01	3.0E-02		1.7E-01	2.4E-01	6.6E-02	8.4E-02	2.8E-03
Lp8-2	9.9E-02	1.6E-01	2.6E-02		1.5E-01	2.1E-01	5.8E-02	7.4E-02	2.1E-03
Lp9-2	1.0E-01	2.0E-01	3.2E-02		1.6E-01	2.3E-01	6.4E-02	8.2E-02	2.6E-03

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