Squid rocket science: How squid launch into air

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ABSTRACT

Squid not only swim, they can also fly like rockets, accelerating through the air by forcefully expelling water out of their mantles. Using available lab and field data from four squid species, *Sthenoteuthis pteropus*, *Dosidicus gigas*, *Illex illecebrosus* and *Loligo opalescens*, including sixteen remarkable photographs of flying *S. pteropus* off the coast of Brazil, we compared the cost of transport in both water and air and discussed methods of maximizing power output through funnel and mantle constriction. Additionally we found that fin flaps develop at approximately the same size range as flight behaviors in these squids, consistent with previous hypotheses that flaps could function as ailerons whilst aloft. *S. pteropus* acceleration in air (265 body lengths [BL]/s^2; 24.5 m/s^2) was found to exceed that in water (79 BL/s^2) three-fold based on estimated mantle length from still photos. Velocities in air (37 BL/s; 3.4 m/s) exceed those in water (11 BL/s) almost four-fold. Given the obvious advantages of this extreme mode of transport, squid flight may in fact be more common than previously thought and potentially employed to reduce migration cost in addition to predation avoidance. Clearly squid flight, the role of fin flaps and funnel, and the energetic benefits are worthy of extended investigation.

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1. Introduction

Optimal speeds for pelagic squid migration have been discussed for several species including the Humboldt squid *Dosidicus gigas* (Payne and O'Dor, 2007), which has lately extended its range along the western coast of North America (Brodeur et al., 2006; Zeidberg and Robison, 2007). O'Dor and colleagues also described fin flaps in *D. gigas*, an anatomical feature that likely plays a role in squid gliding both in and out of water by acting like the ailerons of airplanes (O'Dor et al., 2007). The size at which *D. gigas* fin flaps become distinct appears to be about 0.06 m mantle length (ML, Table 1 in O'Dor et al., 2007). The present report links migration speeds and fin flaps through some remarkable new observations that expand the potential roles of squids in ecosystems.

Squid not only swim, they also fly (Jabr, 2010), but the mechanics of this has not been well understood. Maciá et al. (2004) documented fourteen published reports of squid flight going all the way back to Rush (1892), who was likely describing (*Sthenoteuthis pteropus*). Another ommastrephid squid, *Illex illecebrosus*, was also reported to fly (O'Dor, 2012; O'Dor et al.,

1977; Webber and O'Dor, 1986), causing researchers to lower the water level in a 15 m diameter aquarium to avoid having squid fly onto the surrounding deck at night.

Despite documented flight in several squid species, we are only aware of one analysis of powered flight by squid (Cole and Gilbert, 1970) from an 8 mm movie of a *D. gigas* off Peru in 1964. Based on an estimated mantle length (ML) of 1.22 m, this squid accelerated in air during its 1.70 m flight. It was clear that water continued to be pumped out of the mantle while the squid was in the air, implying that the "jet" was the source of power for acceleration. This was also documented by Maciá et al. (2004) for other pelagic species.

However, with high-speed photographs of squid flight, it is now possible to measure speeds and cost of transport in both water and air by knowing intervals between images and estimating animal size. This allows for improved analyses of how squid fly as well as increased understanding of how this behavior may benefit squid in their environment.

The literature on flight and swimming has become somewhat confused; for example penguins are often said to "fly" underwater because they use their wings to swim. In part this reflects the fact that both air and water are fluids, and the same fluid dynamic equations apply, although factors such a density and viscosity differ dramatically, so there are relatively few things that operate in both media. The definitions we will use are: (1) flying and flight

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happen in air, (2) swimming happens in water, (3) gliding can happen in either—it involves creating "lift" as a fluid moves over a surface, typically called a wing, while the object maintains momentum by falling in a gravitational field, (4) soaring can happen in either—lift is created by a moving fluid interacting with an essentially stationary wing, (5) launching is the process of gaining altitude in air that allows squid to fly using a combination of gliding and soaring—it requires a transfer of momentum from a fluid going in one direction to a squid going in the other, for example, a jet. Lift is the result of differential rates of fluid flow over the upper and lower surfaces of a "wing" creating a partial vacuum on the upper surface that exerts an upward force. Squid fins and arms both appear to function as wings creating lift.

Squid locomotion is normally referred to as jet propulsion because the mantle alternately fills with and ejects water while the squid is underwater. However, squid in air cannot refill the mantle with water, so their "launch" into air is technically rocket propulsion. By mixing opportunistic photographed observations with established energetics this report explores the potential roles of squid flight.

2. Methods

Flight through air was analyzed using sixteen photographs of squid, likely *S. pteropus*, off the coast of Brazil (Lat. 24–28.0 S, Lon. 041–02.5 W) on 30 October 2009, recently provided by amateur photographer Bob Hulse (Fig. 1). The photos were taken in "burst" mode with a Canon 1D MIII camera and a 100–400 mm lens, so that individual images were 0.15 s apart, allowing detailed analysis of squid flight dynamics. In analyzing these *S. pteropus* rockets we encountered similar problems to those Cole and Gilbert (1970) had faced: we needed to estimate the size of the squid, as there were no visible references other than the rolling waves. Our primary size calibration was an assumption that the *S. pteropus* mantle lengths (ML) were equal to a specimen *Sthenoteuthis oualaniensis* collected (Young, 1975) and measured as 0.06 m ML that was observed to fly horizontally onto the deck of the 48 m R/V Kana Keoki in Hawaiian waters, nearly 3 m above the ocean surface (Richard Young, personal communication). We tried using Rayleigh instability (de Gennes et al., 2002) to independently estimate drop size and link it to squid size in photographs, but decided the ML assumption was a safer basis for calculations. However, using the equation in Fig. 2 for *Loligo opalescens* (O'Dor, 1988a), we were able to calculate the ejected mantle volume for a 0.06 m mantle length (ML) squid, which was consistent with the observed stream size.

To increase the value of such opportunistic observations, we encourage nature photographers in air to equip themselves with the same sort of parallel laser beams used routinely by cameras on remotely-operated underwater vehicles to provide reference distances. Such systems have recently been tested in air (Rothman et al., 2008) and would help deliver a lot more hard data from photographs of flying squid and many other creatures.

Additionally, we compared Hulse's photographs of *S. pteropus* in three different ways: (1) with comparisons to observations of flying *S. oualaniensis*, (2) examining preserved specimens of *Loligo* and *Illex* species and (3) by revisiting old literature on *D. gigas* flight. *S. oualaniensis* is a Pacific congener of about the same size as *S. pteropus* and has fin flaps, and therefore provides a valuable comparison. Richard Young (personal communication) also examined specimens of *Loligo* and *Illex* species at the Smithsonian Museum of Natural History in order to confirm the presence of fin flaps in them. Because there have been quantitative laboratory studies on 30 g *L. opalescens* (O'Dor, 1982, 1988a), this species is the best available for energetic comparison for 4 g *S. pteropus*.
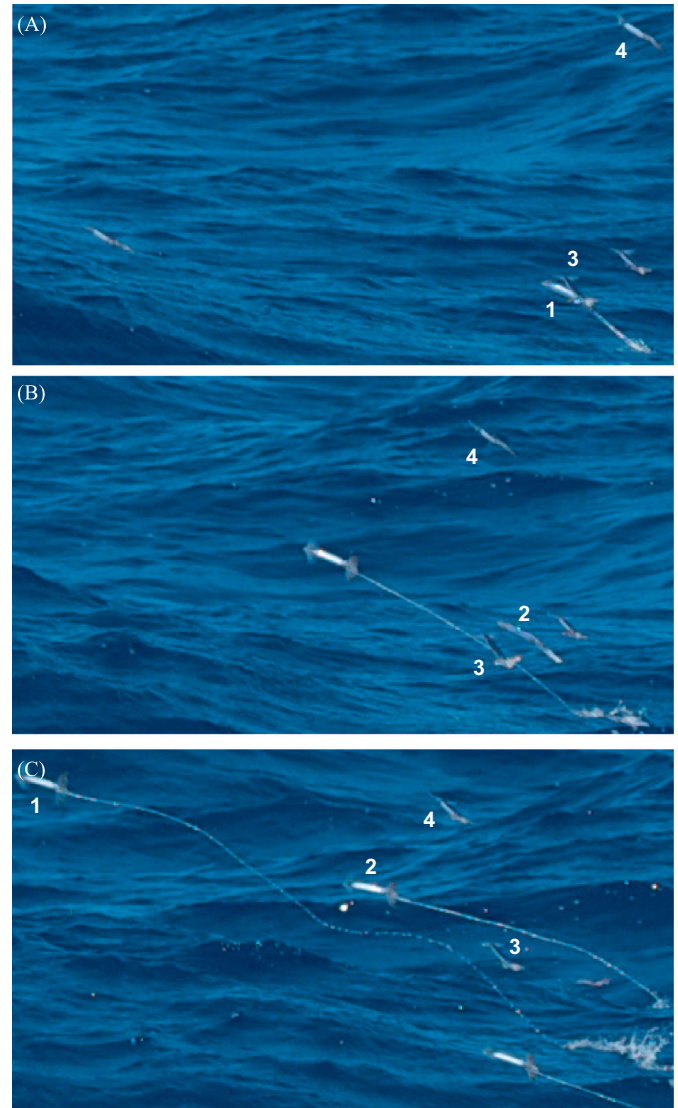
Fig. 1. Rocket powered flight by *Sthenoteuthis pteropus*. Frames (A–C) are sequential at intervals of 0.15 s, displaying four numbered individuals. Squids #1 and #2 are launching and water from the funnel is seen in white, streaming behind each squid out of water in (C). The white area of the squid mantle is estimated to be 0.06 m long. Both squid fly through the air with fins first and arms splayed in similar shapes, although Squid #2 shows a different pattern in its initial launch in (B). Squids #3 and #4 appear to be soaring in the wind without power and seem comparatively motionless and more variable in posture. We unfortunately lack data on wind at the location to analyze their motion.
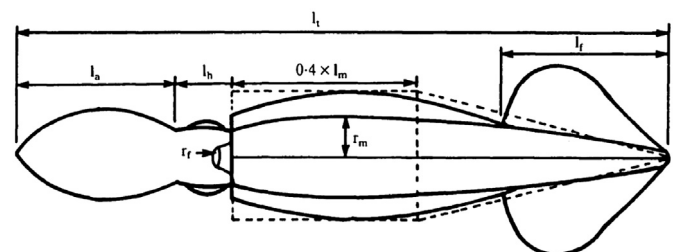
Fig. 2. Diagram showing the working parts of a squid used to pump water through the funnel which regulates stream diameter and thrust, with the measurement used to calculate mantle volume and stream diameter. $V_w = [r_m^2 - (r_r - x)^2](0.4\pi l_m) - (0.12\ M/d_s)$ (Modified from O'Dor, 1988a).

We also reviewed the references to flying squid landing on the deck of the Norwegian Kon-tiki raft on its three-month trip from Peru to Raroia (French Polynesia) from 28 April to 7 August 1947

(Heyerdahl, 1950). Unfortunately, the English translation from Heyerdahl's report is not very clear as to when and where which species of cephalopods appeared. While passing through the Humboldt Current off Peru, there were accounts of flying cephalopods landing on the Kon-tiki's deck, that were used as bait for fishing. Reanalysis of the details suggests that at least some of these squid probably were *D. gigas* and/or *S. oualaniensis* of about 0.06 m ML. *D. gigas* in this size range also flies and are routinely seen to launch at night when pursued from below by larger adults (Rui Rosa, personal communication).

Equations for generic muscular squids based on standard measurements (Fig. 2) were used to convert ML to estimate total body length (BL, in meters) and mass (M, in kg): $BL = ML/0.65$; $M = 20\ ML^3$ (O'Dor, 1988b). Frame intervals were used to calculate the average velocity and acceleration of each species over the duration of an event as well as the maximum velocity and acceleration during a single frame. Velocities and accelerations were converted to BL/second for comparisons across sizes and reports in the literature.

3. Results

Assuming the *S. pteropus* off Brazil were the same size as *S. oualaniensis* off Hawaii, we estimate that the first squid to launch in Fig. 1A flew a total of 1.04 m under power. This analysis was also consistent with the stream diameter and drop size reported below. This powered flight is less absolute distance, but 12 times further in body lengths (BL, Table 1) than a much larger *D. gigas* flew off Peru. It is also clear from several other squid pictured (Fig. 1A and B) that once powered flight ends, these squid can continue to glide or soar with their bodies in fixed postures, often with the arms held so as to mirror the shape of the fin. Fig. 1 identifies two launching squid and two gliding squid. Unfortunately, the motion of the gliding squid was difficult to analyze as we lacked information on local wind conditions. Table 1 quantitatively compares *S. pteropus* flight to that of

D. gigas (Cole and Gilbert, 1970) and to the well documented underwater jetting of intermediate sized *L. opalescens* (O'Dor, 1988a), reporting estimates of BL and mass. Although we cannot be certain about the ML of the *S. pteropus*, our estimate is conservative and it is important to recognize that if the ML is greater, it can only make the launch calculations more impressive. The example quoted in Table 1 for *L. opalescens* is at its maximum sustainable velocity (0.6 m/s, O'Dor, 1988a) in a swim-tunnel and the maximum acceleration value is for a single maximum escape jet and is in no sense sustainable. However, we think that such a maximum jet would be comparable to the work done as squid launch.

The panels in Fig. 1 are only about 2% of the total area of the photographs, and we were able to analyze the flights of five squid in the 16 photographs. The individual squid (#1 in Fig. 1) representing *S. pteropus* in Table 1 is typical and provided the most accurate start and stop times and distances traveled. The others were comparable: squid #2 that appears at the bottom right of Fig. 1B made a slightly longer flight, but launched before the photo burst started, so calculation of rates was less accurate. A second interesting feature of this squid is its launch. Its attitude, posture and color are initially different from the other squid in powered flight but become similar in 1C. This change supports the concept that these squid do not just wind up in the air by accident, but have a behavioral program to insert themselves into the glide zone and coordinate chromatophore activity. Table 1 also compares the net cost of transport (COT) in air and water, assuming *S. pteropus* has similar maximum and standard rates of oxygen consumption as *L. opalescens* has at 17.5 °C (O'Dor, 1982). COT is calculated from swim-tunnel respirometry, as the difference between maximum aerobic scope at the highest sustainable speed and the extrapolated standard metabolic rate at zero velocity (See Table 1). The lower COT reflects the greater distance flown per unit time based on size-adjusted data.

Although the sixteen photographs are of high resolution, we were unable to identify fin flaps in *S. pteropus*. However, the resolution allowed analysis of stream diameter. The estimated

Table 1
Comparing four squids in air and water (*S. pteropus*, this analysis; *D. gigas*, Cole and Gilbert, 1970; *L. opalescens*, O'Dor, 1982; *I. illecebrosus*, Foyle, and O'Dor, 1988).

	Air		Water		
	S. pteropus	**D. gigas**	**L. opalescens**	**I. illecebrosus**	**I. illecebrosus**
				Head first	**Fin first**
Mantle length (m)	0.060	1.219	0.121	0.273	0.273
Total length (m)	0.092	1.876	0.182	0.42	0.42
Mass (kg)	0.00432	36.25	0.032	0.407	0.407
Frame interval (s)	0.15	0.063	0.0555	0.0333	0.0333
Duration (s)	0.45	0.69	0.83	0.4 v (0.1a)	0.4 v (0.1a)
Distance (m)	1.06	1.71	0.50	6	7.8
Average velocity (m/s)	2.37	2.48	0.6	2.4	3.1
Average velocity (BL/s)[a]	25.68	1.32	3.30	5.7	7.4
Maximum velocity (m/s)	3.43	7.20	2	2.6	3.9
Maximum velocity (BL/s)	37.16	3.84	10.99	6.19	9.3
Average acceleration (m/s²)	16.54	7.86	1.13	10.0	18.0
Average acceleration (BL/s²)	179.2	4.19	6.19	23.8	42.9
Maximum acceleration (m/s²)	24.48	49.94	14.41	12.0	37.0
Maximum acceleration (BL/s²)	265.2	26.6	79.2	28.6	88.1
Current (m/s)			0.6		
Maximum O₂ 17.5C (mg/kg-h)	1144		1144		
Std. O₂ 17.5C (mg/kg-h)	448		448		
Net COT[b] (J/kg-m)	1.13		5.67		

[a] BL is body lengths.

[b] COT is cost of transport. Net COT for *L. opalescens* is calculated from O'Dor, 1982 following Brett (1964, 1972) from swim-tunnel respirometry, as the difference between maximum aerobic scope at the highest sustainable speed and the extrapolated standard metabolic rate at zero velocity. One mL of oxygen at Standard Temperature and Pressure is assumed to yield 19 J of work. Wells and O'Dor (1987) and more recently Rosa and Seibel (2010) found little evidence of metabolic size scaling in squid, so we assume that the inherent correction for body mass in calculating COT per kilogram-meter is adequate for this estimation and comparison of the costs of swimming and flight. The alternative assumption that smaller animals require more oxygen would only make flight even more economical, comparatively.
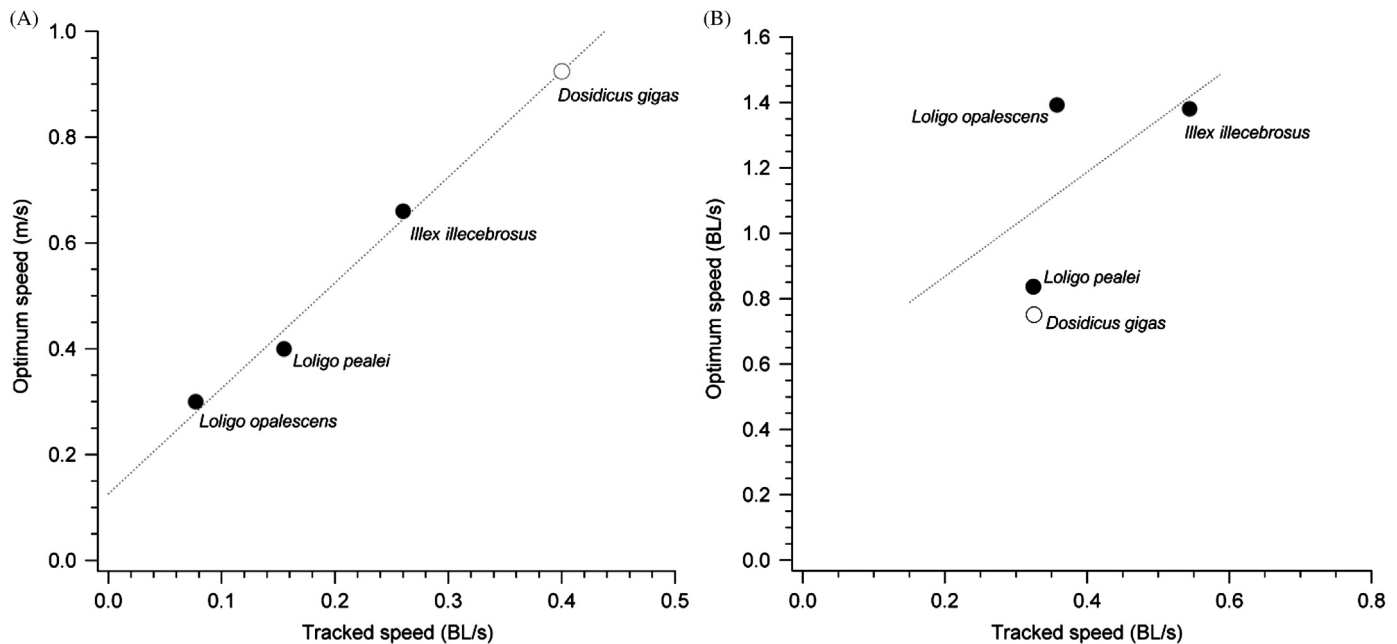
Fig. 3. (A) An extension of Figure 3 from Payne and O'Dor (2007) comparing speeds in nature from tracked animals to optimum speeds estimated to minimize COT from swim-tunnel respirometry. It includes a new tracking data on *Dosidicus gigas* (Stewart et al., in review) that has been fitted on the dotted line. (B) The same data from (A) re-plotted in BL/s shows that body length is the dominant determinant of swimming speeds in squid. The other correlate that might be important may be fin length, which is larger in *Loligo* spp. The dotted line in (A) shows Optimum Speed$=2.00 \times$ Tracked Speed$+0.126$ with a Pearson's $r=0.986$. For (B) OS$=1.61 \times$ TS$+0.128$, $Pr=0.601$.

mantle volume of *S. pteropus* of the assumed size was about 4 ml and would produce the stream of about 2 mm diameter for the 1 m distance traveled by squid #1, which appears consistent with the stream diameter in Fig. 1 and with the size of the droplets falling from the stream.

Fig. 3, which expands on Payne and O'Dor (2007) shows that when speeds are expressed in meters per second (m/s) there is a high correlation between measured swimming speeds in nature and measured optimum speeds from swim-tunnels (Fig. 3A). This correlation collapses when speeds are expressed in body lengths per second (BL/s) (Fig. 3B), suggesting that, as in fish (Weihs, 1973), body size is likely the driver of the tight correlation in Fig. 3A. Big fish and big squid swim faster as a rule, although design features like fin size also play a role.

4. Discussion

Making advances with rare and difficult-to-observe phenomena requires analysis of opportunistic field data and comparison with quantitative laboratory studies. Squid behavior and skin delicacy limit laboratory studies to only a few species. Brett (1972) defined the approach to quantifying locomotor costs for aquatic animals using swim-tunnel respirometers, and, while dozens of fish species have been analyzed to his exacting standards (Blake, 1983a), we are aware of only three species of pelagic squid with comparable data: *L. opalescens*, *Loligo pealei* and *I. illecebrosus* (O'Dor, 2002). Although Bartol (2001) presents extensive swim-tunnel data on *Loliguncula brevis*, it is a specialized nearshore squid, not directly comparable to other more pelagic squids. The aim of this report is to compare between pelagic species in order to bridge gaps in our understanding of their flight and migration. Trueblood and Seibel (2013) provide additional new data on *D. gigas* metabolic rates.

The tradeoffs between power and efficiency in jet propulsion are extremely complex (O'Dor, 1988a), and comparing performance between media that differ as significantly as do air and water in density and viscosity is an additional challenge. To compare *S. pteropus* to *D. gigas* it is necessary to understand that squid have a high degree of control over the two factors that generate jet thrust: the rate of mantle muscle contraction and the diameter of the funnel orifice that focuses and directs the jet (Fig. 2). Escape jets maximize both contraction rate using anaerobic muscle and funnel diameter by relaxing funnel muscles (O'Dor, 1988c). This maximizes thrust production and acceleration over a single cycle. In contrast, slow contraction forcing the same volume of water through a funnel orifice constricted by muscle contraction can deliver thrust over a long period maximizing the power output.

In absolute terms, in air *D. gigas* achieves maximum acceleration and a velocity of 7.2 m/s compared to a maximum velocity of 3–4 m/s in water (Gilly et al., in press; Gilly et al., 2006), presumably reflecting the lower drag in air. *L. opalescens* manages a maximum velocity of 2 m/s in water, but unfortunately we have no direct comparison in air. The lower volume of water ejected over a longer time from *S. pteropus* does not produce as much average or maximum velocity or acceleration, but the accumulated effect of lower drag in air is quite dramatic in terms of body lengths. A rule of thumb in biological hydrodynamics is that the routine cruising speed of fishes is 1 BL/s (Weihs, 1973). As shown in Fig. 3, squid manage about half of this in the real world, although their predicted optimum speeds are often a bit higher. Large bodied fishes like basking sharks do worse at 0.3 BL/s (Sims, 2000).

Squids fly using their fins, arms and probably their fin flaps to create lifting surfaces that act as wings and allow them to glide for considerable times and distances (Azuma, 1992) as they ride air currents over waves like flying fish and albatross (Wilson, 1975). We have previously demonstrated that squid dynamically "soar" in

water currents to save energy (O'Dor et al., 1994), and doing so in air would require similar neurophysiological controls. Given this, squid systems may be pre-adapted to flight. As Maciá et al. (2004) indicate, seeing whole schools of squid gliding is fairly common and photographs are not unusual, but until Hulse's photos became available there was no direct quantitative evidence of how these squids actually launched themselves into flight.

Similar to the situation for porpoises (Blake, 1983a,b), the cost of transport (COT) for squid in air is one fifth of that in water because of lower drag (Table 1). Like porpoises, squid may be able to use flight to reduce their migration costs in addition to using it to escape from predators. Hertel (1966) reports that flying fish (family Exocoetidae) emerge from the water at 10 m/s at an angle of 30° and can further accelerate to 20 m/s using their caudal fin which remains in contact with the water before becoming airborne. Flying fish flights can be as great as 50 m. Our evidence suggests that while squid only reach about 3.5 m/s, once they are aloft their glide and soaring times and distances may be on the order of those reached by flying fish. Heyerdahl (1950) reports 50 m squid flights in the Humboldt Current region.

It may be premature to attempt to develop a general theory of squid rocket propulsion based on extrapolations from 4 g to 40 kg squids. However, flight could be a form of migration, although this was not suggested from any of the cases reported by Maciá et al. (2004), perhaps because flight is more common at night in most species. It seems clear that the high energetic cost to launch squid, rules out porpoising or other continuous active forms of flight, but squids #3 and #4 in Fig. 1 remain in the air gliding for long periods and could easily be carried by the wind or perhaps even take advantage of local air currents generated by waves as do albatrosses. Size drives the correlation between empirical and optimal swimming speeds (Fig. 3), as in fish (Weihs, 1973). *S. pteropus* of about 0.06 m ML seem to launch in large numbers and are probably physiologically programmed to maximize power output and flight time by slowly delivering a very fine jet. Individual *D. gigas* of 120 cm ML are among the flyers (Maciá et al., 2004), but they have never been seen in schools, so it seems likely that the flight by adults could be a relatively rare occurrence related to predator avoidance. However, recent tracking studies along the US Pacific coast, included in Fig. 3A, show 10 kg *D. gigas* traveling at an average of 0.4 m/s (Stewart et al., in review). Respirometry data is lacking to calculate an optimum speed for *D. gigas*, but Fig. 3 of Payne and O'Dor (2007) projected an estimate from the regression for smaller species based on the then fastest recorded migration of *D. gigas*. The recent results continue to increase, elevating predicted optimal speeds. Perhaps they really do spend part of their time flying!

5. Conclusions

Flight has a clear energy benefit that would aid horizontal migration in addition to being an escape mechanism. The best estimate of cost of transport (COT) that we can make is by assuming that the maximum and standard metabolic rates for *S. pteropus* are scalable to those of *L. opalescens* at 17.5 °C (O'Dor, 1982). Because of the much lower drag in air, the distance traveled per unit time is five times more in air, which reduces the net COT to 20% of that in water. Fin flaps clearly have the potential to act like ailerons in airplanes altering lift characteristics and controlling roll. Given the relatively low-mass construction of squid < 0.1 m ML, these jet-propelled animals may be more effective in less dense air than in water. Flexible wing designs, not unlike fin flaps, have been tested by NASA in F-18

jets to decrease drag and reduce weight (NASA, 2009). Although no studies have been made to look at this specifically, it is certainly possible to record fin flap behavior filming from below in many swim-tunnels. Getting squid to fly in a wind tunnel seems more problematic, but perhaps not impossible. An alternative may be to employ acoustic accelerometer tags (Payne et al., 2011) to monitor a variety of squid over significant periods and quantify how much time may be spent flying. It is clear that accelerations in air can exceed those in water several fold.

Acknowledgment

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