# RESEARCH NOTES

## New observations on airborne jet propulsion (flight) in squid, with a review of previous reports

Silvia Maciá[1,6], Michael P. Robinson[1,2], Paul Craze[3], Robert Dalton[4] and James D. Thomas[5]

[1]*Hofstra University Marine Lab, PO Box 90, St Ann's Bay, Jamaica;*
[2]*Department of Biology, University of Miami, Coral Gables, FL 33124, USA;*
[3]*School of Biological Sciences, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK;*
[4]*Applied Ecology Research Group, Division of Health Design and Science, University of Canberra, Bruce, ACT, Australia;*
[5]*Nova Southeastern University Oceanographic Center, Dania Beach, FL 33004, USA*
[6]*Present address: Barry University School of Natural and Health Sciences, 11300 NE 2 Ave, Miami Shores, FL 33161, USA*

Cephalopod molluscs are among the strongest and most agile invertebrate swimmers, using both undulation of fins and jet propulsion to move through the water and, occasionally, through the air. Among cephalopods, the squids in particular have evolved the most effective means of jet propulsion.[1–3] The mantle is hyperinflated and water is taken in through the collar flaps between the anterior margin of the mantle and head, followed by a rapid contraction of the mantle that pushes the water out through a flexible narrow funnel.[1,4,5] The funnel can direct the jet of water forwards or backwards, thereby propelling the squid in the opposite direction to the movement of the water.[4]

Jet propulsion in squids is used primarily as an escape response and most often occurs entirely under water. In many species of squid, however, the propulsive force is sufficient to launch the squid completely out of the water, after which it may fly or glide for some distance. Some researchers do not use the term 'fly', but prefer the term 'gliding'.[7] In this paper, however, we will refer to this airborne jet propulsion as flight based on observations of squid posture and movement that suggest to us a more active behaviour than simple gliding. We report new observations of flying behaviour in a species of squid (*Sepioteuthis sepioidea*) previously thought to be too heavy for long-distance flight,[7,8] as well as an observation of squid flight from a geographic area in which such behaviour has not previously been reported. We also review previous reports on flying behaviour in other species of squid.

The Caribbean reef squid, *Sepioteuthis sepioidea*, has been observed to jump briefly out of the water when disturbed, but was thought to be too heavy or otherwise incapable of flying for any considerable distance.[7,8] On the north coast of Jamaica, two of us (S.M. and M.P.R.) observed a single individual of this species to fly for a horizontal distance of approximately 10 m, reaching a maximum height of 2 m above the surface of the water (Table 1). We estimated the total length of the squid to be 20 cm, therefore its horizontal flight was 50 times its body length. As the squid moved forward through the air, it extended its fins and flared its arms into a radial pattern. The proximal half of each arm was angled at 45° relative to the longitudinal body axis. The arms were bent so that the distal half was parallel to the body axis. The squid appeared to have been startled by the noise from our outboard engine. Based on the formula $v^2 = 2gh$, used by Cole and Gilbert,[9] where $h$ = height, the initial velocity of this squid is estimated at 6.3 m s$^{-1}$.

Two additional observations of flying in solitary individuals of *S. sepioidea* were made by one of us (J.D.T.) in Belize (Table 1). In both cases the squid again appeared to have been startled by the oncoming boat, and each squid reached a height of 2 m above the water. While airborne, both squid rapidly undulated their lateral fins. The arms were folded together and extended posteriorly in line with the body, giving a streamlined appearance. After approximately 4 s of flight, both squid rapidly flared their arms downward. This posture acted as an airbrake and immediately terminated horizontal movement. One of the squid flew approximately 7 m in the air. In the other instance, the speed of the airborne squid closely matched that of the boat, which was approximately 9–10 m s$^{-1}$.

One of us (P.C.) also observed an unidentified solitary squid flying through the air in the north Caribbean, 300 m off the coast of Grand Turk. This squid flew approximately 15 m in the air and attained a height of 1.5 m. The speed of the squid matched that of the boat from which it was observed (approximately 10 m s$^{-1}$), and its initial velocity is calculated at 5.5 m s$^{-1}$.

The final new observation reported here occurred 370 km off the coast of Sydney, Australia. Flying squid have not been previously reported from this area (Table 1). In this case one author (R.D.) observed a school of hundreds of unidentified, but probably red arrow squid, *Nototodarus gouldi* (McCoy), being chased by skipjack tuna (*Katsuwonus pelamis* L.). These squid were approximately 10–15 cm long. At least some of the squid were observed jetting water while airborne and, once this jetting ceased, they dropped rapidly back into the water. Some of the squid reached a height of 3 m above the water and flew at least 8–10 m horizontally. While in flight, the squid took on a red and green coloration that reverted to a dull translucence after landing on the deck of the ship. The arms of squid that landed on the ship were covered in a thin layer of mucus. Given $h$ = 3 m, we calculate the initial velocity of these squid at 7.8 m s$^{-1}$.

The flying behaviour of squid has been known for some time. Several instances of this behaviour have been reported, with individual flights as long as 55 m and as much as 6 m above the surface of the water (Table 1). The number of squid in flight varies from solitary individuals to schools of hundreds. Our observations, as well as those of others, indicate that flight appears to be most commonly an escape response to disturbances such as predators or boat engine noise.[10,11] Flight may also occur when squid are chasing prey, as was observed in a small school of *Loligo pealeii* Lesueur chasing fish in Long Island Sound, New York, USA.[9] While submerged jet propulsion is a common method of locomotion among all squid, jet propelled flight is not common and does not occur in all situations where it might be expected. In a school of thousands of *Illex illecebrosus* (Lesueur) being chased by a pod of common dolphins (*Delphinus delphis*), no squid were observed exiting the water, despite much evasive swimming behaviour.[12]

Jetting by squid while underwater produces the initial force that propels the animal out of the water. Jetting of water while the squid is airborne has been observed on at least five occasions in at least two genera (Table 1). Analysis of film of one instance of flight indicated that the force generated by the continued jetting of water while airborne produced acceleration from an initial speed of 1.8 m s$^{-1}$ to a maximum speed of 7.2 m s$^{-1}$.[9] If applied at the proper angle, this force could produce lift and, ultimately, flight in squid. The squid we observed off the coast of Australia fell to the water as soon as jetting ceased. This

Correspondence: S. Maciá; e-mail: smacia@mail.barry.edu


© *The Malacological Society of London 2004*

Downloaded from http://mollus.oxfordjournals.org/ at Northern Arizona University on June 27, 2015

**Table 1.** Recorded observations of airborne jet propulsion in squid.

| Date | Location | Species | Size (cm) | No. of individuals | Max. height (m) | Horizonal distance (m) | Notes | Ref. |
|---|---|---|---|---|---|---|---|---|
| Aug 2003 | Jamaica, Caribbean (18.5°N, 77.2°W) | *Sepioteuthis sepioidea* | 20 | 1 | 2 | 10 | Tentacles flared into radial pattern | This paper |
| Mar 2001 | Belize, Central America | *Sepioteuthis sepioidea* | – | 1 | 2 | 7 | Squid matched speed of boat (9–10 m $s^{-1}$); two separate observations of single individuals | This paper |
| Jul 1998 | Northern Caribbean | Unidentified | – | 1 | 1.5 | 15 | Squid matched speed of boat, 10 m $s^{-1}$ | This paper |
| Mar 1976 | 370 km east of Sydney, Australia | *Nototodarus gouldi* | 10–15 | Hundreds | 3 | 10 | Jetted water while airborne; tentacles covered in thin layer of mucus | This paper |
| Jul 1984 | NW Pacific (37.0°N, 160.3E–175.0°W) | *Ommastrephes bartramii* | 15–19 | 10–hundreds | 1–2 | 10–20 | Eight separate observations of schools of squid | 11 |
| Summer 1936 | Long Island Sound, USA | *Loligo pealeii* | 25 | A few | 0.2 | – | Squid were chasing prey | 9 |
| 1964 | Montemar, Chile | *Dosidicus gigas* | 120 | 1 | – | – | Jetted water while airborne | 9 |
| 1947 | Pacific | *Onychoteuthis banksi* | – | 1–3 | – | 45–55 | Various observations by Thor Heyerdahl in his *Kon-Tiki* voyage | 4 |
| – | Atlantic | Unidentified | – | Dozens | – | – | Observed by E.C. Allcard in his *Temptress* voyage | 4 |
| Jul 1953 | Central Atlantic (36.7°N, 79.3°W) | Unidentified | 15 | 1 | 1.8–2.4 | 12–15 | Jetted water while airborne; no wind | 10 |
| Jul 1953 | Central Atlantic (26.3°N, 76.8°W) | *Stenoteuthis bartrami* or *Ommastrephes sagittatus* | – | 1 | 2.4 | – | Jetted water while airborne; chased by shark | 10 |
| Jan 1953 | Central Atlantic (27.0°N, 79.3°W) | Unidentified | – | 1 | – | 6 | Jetted water while airborne; squid was'quartering to the wind' | 10 |
| Aug 1924 | East central Atlantic, off coast of N. Africa | *Onychoteuthis banksi* | 17 | 1 | 6 | – | Several other possible instances reported from museum records | 17 |
| Mar 1892 | 480 km off Brazil (30°S, 45.5°W) | Unidentified | Various sizes | Hundreds | 3.6 | – | – | 15 |

Max. height = greatest distance above the surface of the water; horizontal distance = horizontal distance from point of exit from the water to point of re-entry.

sequence of events seems to support the role of jetting while airborne in aiding flight.

Although the fins of squid are not as well adapted for gliding or flying as those of flying fishes,[7,13] many squid have certain morphological and behavioural characteristics that appear to aid flight. In flying squid, the initial lift is provided primarily by the force of the expulsion of water through the funnel.[14] Based on examinations of photographs and specimens, Azuma hypothesized that some squid might develop a temporary sheet of mucus between their arms that can provide lift while in flight.[13] He argued that, although the fins and body provide some lift, this alone is not sufficient, and the additional planing area provided by the temporary mucus sheet is necessary for flight. Although we observed mucus on the arms of *Nototodarus gouldi* immediately after flight, we did not observe an actual sheet of mucus spread between the arms during flight. The validity of this hypothesis remains uncertain.

Other morphological and behavioural characteristics may also provide the lift needed for flight. *Onychoteuthis banksi* (Leach) has membranes along the edges of some of its arms, as well as relatively wide fins.[5] Certain squid, while in flight, spread their fins and arms horizontally and undulate their fins,[10,11,13] as also reported here. Arata reported that flying squid arranged their arms so as to form 'a sort of hood to add to the supporting elements needed for flight'.[10] This posture appears similar to that observed in one of the flying individuals of *Sepioteuthis sepioidea* reported here.

Although *S. sepioidea* was previously thought to be too heavy for 'effective long-distance gliding',[8] our observations of this squid indicate that it can, in fact, travel for distances approximately 50 times its typical body length of 20–25 cm. Relatively large individuals of other squid species have also been observed in flight, including a 25 cm *Loligo pealeii* and a 120 cm *Dosidicus gigas* (Orbigny).[9] Rush reported that a school of hundreds of flying squid included individuals of 'various sizes,' although no length measurements are given.[15]

In eight separate observations of schools of flying squid, *Ommastrephes bartramii* (Lesueur), consisting of 10 to hundreds of individuals, no squid larger than 18 cm in length (170 g weight) were ever observed in flight.[11] Larger individuals were common, but were geographically segregated from the smaller squid and were found only at higher latitudes where water temperatures were lower. Although Murata suggests that the larger squid were incapable of flight, their lack of flying



Downloaded from http://mollus.oxfordjournals.org/ at Northern Arizona University on June 27, 2015

behaviour could be a result of water temperature and not individual size.[11] The squid *Loligo opalescens* Berry, however, is able to compensate for the slowing effect of colder temperatures on neuronal and muscular aspects of submerged escape jetting so that its maximum water jet velocity and distance travelled are actually greater at colder temperatures.[16] If *Ommastrephes bartramii* is similarly capable of temperature compensation, the suggestion by Murata that flight ability in this species is limited by size and not temperature is likely to be correct.[11]

While there is some question as to the exact nature of airborne jet propulsion in squids, we believe use of the term 'flight' is not wholly inappropriate. Morphological traits such as broad fins and arm membranes, as well as airborne behaviours including jetting and changes in arm posture suggest that flight has evolved in squid, most likely as an anti-predator behaviour. Such traits also suggest that flight represents a more active and intentional escape behaviour than simply gliding after an incidental exit from the water during escape jetting. Whether considered flight or gliding, however, this behaviour appears to be more widespread than previously thought.

## ACKNOWLEDGEMENTS

Many thanks to C. Albrecht, R. Anderson, P. Callomon, R. Cipriani, H. Saito and M. Vecchione for assistance in gathering information and publications relating to flying squid, to K. Yano for translating Azuma (1981), and to two anonymous reviewers for very helpful comments. This is contribution no. 7 of the Hofstra University Marine Laboratory.

## REFERENCES

1. PACKARD, A. 1969. *Nature*, **221**: 875–877.
2. WELLS, M.J. & O'DOR, R.K. 1991. *Bull. Mar. Sci.*, **49**: 419–432.
3. SHADWICK, R.E. 1994. *Mar. Freshwater Behav. Physiol.*, **25**: 69–85.
4. LANE, F.W. 1960. *Kingdom of the Octopus: the life history of the Cephalopoda*. Sheridan House, New York.
5. THOMPSON, J.T. & KIER, W.M. 2001. *Biol. Bull.*, **201**: 154–166.
6. THOMPSON, J.T. & KIER, W.M. 2002. *Biol. Bull.*, **203**: 14–26.
7. HANLON, R.T. & MESSENGER, J.B. 1996. *Cephalopod behaviour*. Cambridge University Press, Cambridge.
8. MOYNIHAN, M. & RODANICHE, A.F. 1982. *The behaviour and natural history of the Caribbean reef squid* Sepioteuthis sepioidea. Paul Parey, Berlin.
9. COLE, K.S. & GILBERT, D.L. 1970. *Biol. Bull.*, **138**: 245–246.
10. ARATA, G.F. 1954. *Nautilus*, **68**: 1–3.
11. MURATA, M. 1988. *Nippon Suisan Gakkaishi*, **54**: 1167–1174.
12. MAJOR, P.F. 1986. *J. Mammal.*, **67**: 769–770.
13. AZUMA, A. 1981. *Kagaku Asahi*, **41**: 81–85.
14. PACKARD, A. 1972. *Biol. Rev.*, **47**: 241–307.
15. RUSH, W.H. 1892. *Nautilus*, **6**: 81–82.
16. NEUMEISTER, H., RIPLEY, B., PREUSS, T. & GILLY, W.F. 2000. *J. Exp. Biol.*, **203**: 547–557.
17. REES, W.J. 1949. *Proc. Malac. Soci. Lond.*, **28**: 43–45.

*J. Moll. Stud.* (2004) **70**: 299–301

© *The Malacological Society of London 2004*

# A cytogenetic study of the periwinkle *Littorina keenae* Rosewater, 1978 (Gastropoda: Littorinidae)

Angelo Libertini[1], Renata Trisolini[1] and Suzanne Edmands[2]

[1]*CNR Istituto di Scienze Marine, Riva 7 Martiri 1364/A, I-30122 Venezia, Italy;*
[2]*Department of Biological Sciences, University of Southern California, Los Angeles, CA 90089-0371, USA*

Reid assigned 173 species to the gastropod family Littorinidae.[1] The systematics of this family has recently been revised and new genera and subgenera have been proposed on the base of phylogenetic analysis of morphological and molecular characters.[1–4] Cytogenetic studies may also contribute to phylogenetic analysis by providing additional characters for phylogenetic tree construction. Unfortunately, cytogenetic knowledge of littorinids is limited to a few species (Table 1). The chromosome number, and sometimes the karyotype morphology, has been investigated in nine species, and in two of them, *Melarhaphe neritoides* (Linnaeus, 1758) and *Littorina* (*Neritrema*) *saxatilis* (Olivi, 1792), sex chromosomes have been described.[5–8] The genome size (GS) has been determined only for six species.[9]

In the present study the chromosome number, karyotype morphology, GS and the percentage of adenine–thymine DNA in the genome (AT%) were investigated in *Littorina* (*Planilittorina*) *keenae* Rosewater, 1978. GS and AT% were also determined in *M. neritoides* for comparison.

Correspondence: A. Libertini; e-mail: angelo.libertini@ismar.cnr.it

About 100 specimens of *Littorina* (*Planilittorina*) *keenae* were collected on the rocks at high tide level in San Pedro and Malibu (southern California, USA) in August 2002. Twenty individuals of *Melarhaphe neritoides* were sampled along the stony shores in Venice (northeastern Italy) in August 2002. Taxonomic nomenclature for Littorinidae is according to Reid[1,2] and Williams *et al.*[4]

Chromosome preparations of *L. keenae* were obtained by air-drying from the male gonad, after an 18-h treatment in 0.01% w/v colchicine/filtered sea water solution.[7]

GS and nuclear AT DNA content were evaluated through flow cytometric assay performed on cell suspensions of the two periwinkle species obtained from deep-frozen gill and mantle, by means of a BRITE-HS cytometer (Bio-Rad Laboratories) equipped with a xenon-mercury lamp. Peripheral blood erythrocytes from chicken (2C GS = 2.50 pg, 2C AT DNA = 1.39 pg)[10] were added to the periwinkle cell suspensions as internal standard. The nuclei were stained with propidium iodide (40 specimens of *L. keenae* and 11 of *M. neritoides*) and Hoechst 33258 (34 specimens of *L. keenae* and 11 of *M. neritoides*) for GS and AT DNA evaluation, respectively. For each sample at least



Downloaded from http://mollus.oxfordjournals.org/ at Northern Arizona University on June 27, 2015