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Oceanic squid do fly

K. Muramatsu · J. Yamamoto · T. Abe ·
K. Sekiguchi · N. Hoshi · Y. Sakurai

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Abstract Using powerful jet propulsion, some squid species are able to exit the water and become airborne; this is a common behavior seen throughout the world's oceans. However, direct scientific observation is rare, with most studies relying on anecdotal evidence and limited photographic documentation. Here, we examine the flying behavior of young oceanic squid (Ommastrephidae) observed in sequential photographs taken in the Northwest Pacific (35°34.0′N, 146°19.3′E) on July 25, 2011. We define four phases in the flight process: launching, jetting, gliding and diving. During flight, squid actively change their aerial posture and attitude depending on the flight phase and their distance from the water. The present study demonstrated that flight of squid is not simple gliding after incidental exit from the water, but involves jet propulsion, generation of lift force and control of different body postures in different flight phases, which have evolved to enhance escape from predators.

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K. Muramatsu · Y. Sakurai
Graduate School of Fisheries Sciences, Hokkaido University, 3-1-1 Minato, Hakodate, Hokkaido 041-8611, Japan

J. Yamamoto (✉)
Field Science Center for Northern Biosphere, Hokkaido University, 3-1-1 Minato, Hakodate, Hokkaido 041-8611, Japan
e-mail: yamaj@fish.hokudai.ac.jp

T. Abe · N. Hoshi
Faculty of Fisheries Sciences, Hokkaido University, Hakodate, Hokkaido 041-8611, Japan

K. Sekiguchi
Graduate School of Arts and Science, International Christian University, 3-10-2 Osawa, Mitaka City, Tokyo 181-8585, Japan

Introduction

The evolution of a buoyancy mechanism released shelled mollusks from the benthos, thereby allowing the descendant cephalopods to adopt a pelagic existence (Boyle and Rodhouse 2005). Modern squids have swimming capability similar to fishes. In addition to undulating fin movements, squids have jet propulsion. They take water into the mantle compression chamber through a wide inlet and force it out through a narrow funnel that can direct the jet through a wide range of angles (Packard 1969). Free-swimming squids and cuttlefishes commonly jet away from predators in a rapid secondary defense mechanism (Hanlon and Messenger 1996). During an escape response, squid produce powerful jet propulsion backward by sharply contracting the mantle (Gosline and Demont 1985) and the process sometimes ejects the animal out of the water (Hanlon and Messenger 1996). Squid "flight" is not unusual and has been reported previously (Rees 1949; Arata 1954; Murata 1988; Macia et al. 2004). However, since it is usually unanticipated, accurate descriptions are often lacking or anecdotal. Although a sequence of photographs of a large squid exiting the water using jet propulsion (Cole and Gilbert 1970) and a recent quantitative analysis showing squid accelerating through the air (O'Dor et al. 2012) are available, it is not clear whether the behavior is actual "flight" or a jet-propelled jump. Azuma (2006) has analyzed the aerodynamics of gliding *Sthenoteuthis oualaniensis* (based on a photograph) and identified the existence of lift force. This study (*loc. cit.*) suggests that squid do indeed have flight capability, refer to, that is, "biomechanical flight," which is defined as locomotory behavior in the air involving active control of aerodynamic forces (Dudley et al. 2007). Thus, to confirm flight, it is necessary to demonstrate propulsion while in the air in combination with some additional lift. To date, information on squid airborne behavior involving the escape jet mechanism and subsequent aerodynamic processes is still limited. We postulate that squid flight is active and intentional behavior, as suggested by Macia et al. (2004), rather than simple gliding after incidental exit from the water by jet propulsion. The objective of this study was to investigate in detail the process of "squid flight"; we aimed to test whether our postulate is robust.

Materials and methods

We observed airborne squid and succeeded in taking a sequence of photographs of the entire flight process in the Northwest Pacific (35°34.0′N, 146°19.3′E) at 14:25 local time (05:25 Greenwich Mean Time) on July 25, 2011 from the *T/S Oshoro Maru* (72.9 m length and 1,792 gross tonnage) operated by Hokkaido University, Japan. The sea surface temperature was 24.7 °C, and salinity was 34.1, with a wave height of approximately 1 m. The vessel was heading east at a speed *ca.* 22.8 km h^{-1} (12.8 knots), and schools of squid exited the water on the starboard side on two occasions. The series of photographs captured for each school (6 and 15 frames respectively) were taken with a digital SLR camera (Canon EOS 7D with a Sigma APO DG 135–400-mm lens) in action mode (frame interval 1/8 s) from the upper deck *ca.* 12 m above the sea surface. Two additional frames of the second school were captured with another digital SLR camera (Nikon D300S with a Nikon AF VR 80–400-mm lens) from the same deck.

Results

Squid exited simultaneously from the sea surface, heading in the same direction while jetting water (Fig. 1). From the photographic record, the duration of each airborne behavior was determined to be 3 s. The photographs indicated at least 121 and 92 animals of similar size in the two schools. The squid had cylindrical mantle and transversely rhomboidal fins. The schools were chased by a red-footed booby (Fig. 1). Judging from the wing length of the red-footed booby (typically 383 mm, Nelson 2005), mantle length was estimated to be ~122–135 mm. Analysis of these 21 frames showed that the process of airborne behavior was almost synchronous. We classified the behavior into four phases (total numbers of observed squid in each step are in parentheses): launching (1), jetting (14), gliding (1,355) and diving (89). We have only one photograph of a launching squid (Fig. 2a, a′) since the animals emerged suddenly and unexpectedly, breaking the sea surface at a shallow angle by jetting water backward while folding the fins against the mantle and folding the arms. During jetting (Fig. 2b, b′), the fins and arms were spread and a stream of water was continually expelled from the funnel. No squid undulated its fins or flapped its arms. We were able to estimate speeds of three jetting squid from two contiguous frames (interval 1/8 s); a large wake of bubbles on the sea surface provided a baseline (Fig. 3). The mean mantle length of the airborne squid was 60.1 % (SEM = 0.4, $n = 30$) of body length (BL), and the speed of jetting squid ranged from 8.8 to 11.2 m s^{-1} or 43.4 to 49.7 BL per second. Thus, distance travelled was estimated to be ~26.4–33.5 m. After water jetting had ceased, behavior shifted to the gliding phase (Fig. 2c, c′). Squid started to glide keeping arms and fins spread. A "wing" consisting of spread arms and fully spread protective membranes between them was clearly visible in the photographs. The outermost arms were spread almost perpendicularly to the body axis. The outermost protective membranes were slightly brown, suggesting the presence of chromatophores. Inner arms were more curved than outer arms, but the space between them was also covered by membranes. The fins were slightly curved upward, and body attitude had a slightly upward pitch overall in relation to the sea surface. Finally, on the approach to the sea surface, fins were closely held against the mantle and the arms were folded (Fig. 2d, d′). The squid entered the water in a downwardly pitched attitude with very small splashes and minimal surface disturbance. None of the animals were bounced across the surface.

Fig. 1 Squid in flight. Squid mantle length was estimated to be 122–135 mm based on the typical wing length of a red-footed booby (383 mm, Nelson 2005)

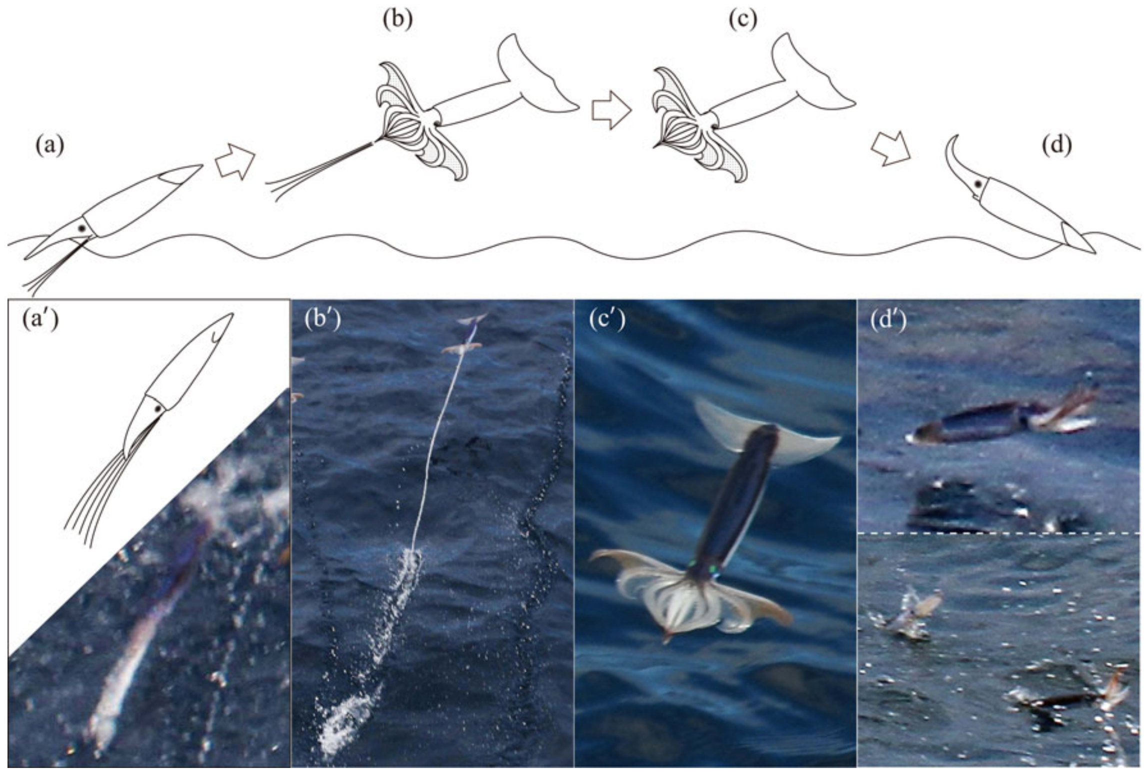

Fig. 2 Schema of the flight process (*upper panel*) based on photographic observation (*lower panels*). Launching (**a**, **a**′): squid break the surface under jet propulsion, rolling down their fins against the mantle and folding their arms. Jetting (**b**, **b**′): squid spread the arms and fins and continue jetting until in the mantle is exhausted. Gliding (**c**, **c**′): squid spread the fins and arms. Diving (**d**, **d**′): approaching the sea surface, squid coil fins around the mantle and fold arms upward, and streamlining the shape to minimize disturbance on water entry

Discussion

Although no specimen was collected from the schools observed, we identified them as ommastrephid squid, very likely young of *Ommastrephes bartramii* or possibly *S. oualaniensis* on the basis of habitat and morphology (Roper et al. 2010). Squid of this family have well-developed body muscles and are powerful jet swimmers (Boyle and Rodhouse 2005); some species are commonly called “flying squid.” Airborne behavior has been reported in both *O. bartramii* (Murata 1988) and *S. oualaniensis* (Azuma 2006).

Our observations suggest that squid were probably escaping vessel disturbance. Several previous studies have reported similar airborne escape mechanisms for avoiding boat and fishing net contact (Arata 1954; Murata 1988; Macia et al. 2004). We do not have photographs of animals before they exited the water, but we believe squid probably approach the sea surface at increasing speed propelled by escape jets. The rolled-back fin posture (Fig. 2a, a′), which minimizes drag, indicates high-speed swimming (Webber and O’Dor 1985).

Squid we observed may have increased speed by jet propulsion after exiting the water, as in another species of squid (Cole and Gilbert 1970; O’Dor et al. 2012). While the initial lift for launching speed presumably comes from continual water discharge through the funnel (Packard 1972), the speed we calculated in our study seemed beyond the swimming capability of squid. Although there are no data on the swimming performance in either *Ommastrephes* or *Sthenoteuthis*, propulsion of squid is inefficient compared with fish because the backward thrust by jet propulsion of squid is much less than that of tail propulsion used by fish due to the low Froude efficiency of squid swimming (Alexander 1977). Therefore, squid must accelerate less water to a much higher speed to achieve the same thrust as a fish (Alexander 1977; Webber and O’Dor 1985). In fish, the upper limit of swimming speed relative to BL is up to 25 BL per second (Wardle 1975), which is much slower than in jetting squid (43.4–49.7 BL s^{-1}). Jetting water while airborne can generate propulsion, and there is much less drag in air than in water. Moreover, jetting water from the mantle cavity promotes acceleration as a consequence of weight loss.

To travel further, squid generate aerodynamic forces by conversion of the gravitational potential energy stored during an increase in altitude in the jetting phase. At the termination of jetting, squid start gliding with a slightly

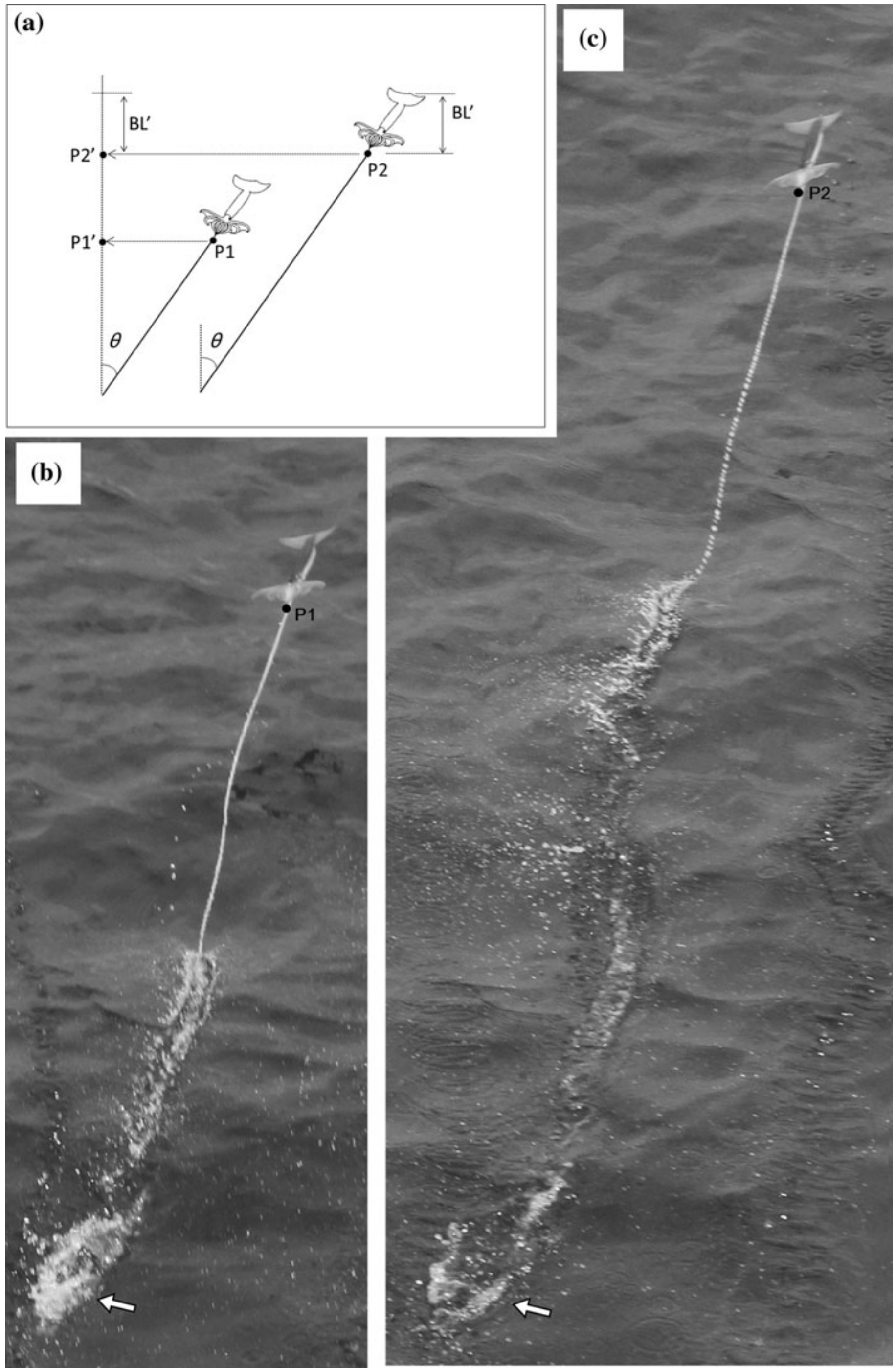

Fig. 3 Schema for calculating jetting squid speed (**a**) using two contiguous photographic frames (**b**, **c**). Tips of the arranged arms move from P1 (**b**) to P2 (**c**) in the frame interval (1/8 s) judged from the wake the squid left behind at the launch site (*arrow* **b**, **c**). Because the direction of travel was maintained, we were able to set the angle θ between the travel direction and the shooting direction of camera which was almost perpendicular to the travel direction of the vessel. P1, P2 and BL were projected to P1′, P2′ and BL′ (=BL cosθ), and speed was calculated as P1′P2′/BL′

pitched-up attitude (Fig. 2c, c′). Azuma (2006) showed that the aerodynamics of gliding *S. oualaniensis* indicate the existence of a lift force that pushes the front edge of the fin slightly upward. The squid fin we observed was similar in shape, likely due to work of the lift force. Additionally, Azuma (2006) pointed that the arrangement of arms and membranes as observed in our study provides a higher lift force than the fin. Moreover, squid are able to maintain balance with the pitched-up moment because the center of gravity is located in the rear part of the body. Ommastrephid squids have strong arms with a well-developed protective membrane (Roper et al. 2010), and the "wing" thus formed presumably has the capability of sustaining the primary lift force. Furthermore, the stiffened mantle (stiffening results from muscle contraction during jetting; Gosline and Demont 1985) plays a role as the principal axis connecting the spread fins and arms; it also stabilizes aerial attitude. Before re-entry, squid wrap the fins around the mantle and fold the arms (Fig. 2d, d′). This streamlined posture results in a smooth water entry, minimizing the potential for drag. During this rearrangement of the fins and arms, the change in animal attitude is caused by retention of lift at the trailing end (generated by the "wing") and loss of lift at the leading end (generated by the now folded fins). These changes suggest that squid are aware that they will shortly re-enter the water, although we were not able to discern this from photographs. Squid may measure the distance from the sea surface visually, they may have an internal mechanism that measures posture or speed changes, or they may simply have a fixed pattern with no feedback from the environment.

This study confirms that airborne behavior of squid is highly active, and the animals can indeed fly. We propose that flight of squid involves jet propulsion, generation of lift force and control of different body postures in different flight phases. Such systematic flight behavior differs from unsystematic escape responses known as protean behaviors (Driver and Humphries 1988) that are seen in cephalopods (Hanlon and Messenger 1996; Staudinger et al. 2011) and other taxa (Edut and Eilam 2004; Domenici et al. 2008; Royan et al. 2010). However, the flight behavior has effects similar to protean behaviors that inhibit detailed predator prediction of position and actions of prey (Driver and Humphries 1988); predators will lose the squid when they enter the atmosphere because of the refractive differences between the water and air, as is the case for flying fish when they exit the water (Davenport 1994). Squid probably do not use flying behavior to facilitate energy saving (O'Dor et al. 2012) in the way that dolphins do when they leap into the air during high-speed swimming (Au and Weihs 1980). This is because jet propulsion before exiting the water and the maintenance of muscle tone in air are intensively energy demanding as in flying fish (Davenport 1994). There should be further investigations of the potential benefits of flight and the new risks encountered by marine animals moving in the atmosphere.

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