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Studies on Acoustic Target Strength of Squid

V. Effect of swimming on target strength of squid

I Nyoman ARNAYA* and Noritatsu SANO*

Abstract

The effect of swimming movement on dorsal aspect target strength of squid was investigated through controlled experiments in a water tank with special reference to surume ika (*Todarodes pacificus*). These mesurements were conducted by moving the squid in the sound beam of a transducer (beam angle of 36°, ensonifying frequency of 50 kHz and pulse repetition rate of 150 pings/min). The different speeds of the movement were based on the results of the swimming speed measured in the aquarium. The average swimming speed was 0.28 m/s, and for comparison other swimming speeds of 0.12 m/s (slow swimming) and 0.40 m/s (fast swimming) were also employed. Results of the target strength measurements are expressed through the probability density function and mean target strengths.

It is found that, contrary to bladder fish, swimming movement significantly effects squid target strength. The two major factors which influence swimming speed, body volume (or shape) and body tilt angle, have a significant effect on dorsal aspect target strength. This is because squid swim mainly by jet-propulsion : when swimming quickly the external diameter of their mantle changes by about 30%, but when swimming slowly it changes by only 10%. Furthermore, as swimming speed increases, tilt angle decreases. The average tilt angle typically decreases from about −30° when hovering to near −3° at high speed. For the present study in which the average swimming speed was 0.28 m/s and the normal speeds was not higher than 0.40 m/s, the average tilt angle was not more than −10°.

Introduction

The success of hydroacoustic survey techniques in providing a quantitative measure of fish size or density almost always depends on what is known about the target strength distribution of the fish being surveyed. Much of the early controlled target strength measurements focused on establishing a relationship between fish length or weight and target strength. Variations due to position in the beam and fish behaviour were removed by immobilizing a specimen on the acoustic axis of the beam.

Evidence for the effect of the swimming movement on fish target strength is scant and conflicting. According to OLSEN[1], the effect on the dorsal aspect target strength is substantial, involving a degree of variation of the order of 3-10 dB for gadoids of 50-70 cm in length. CLAY[2,3] has found a similarly distinct effect on the lateral aspect target strength. This is supported by both measurement and by theoretical computation based on an acoustic model of a fish as a linear array of point scatterers. More recent computations based on FOOTE's model[4,5] predict only a negligible effect on the dorsal aspect. These computations are compatible with

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CLAY's in lateral aspect, and have also been confirmed by direct measurements in dorsal aspect performed by controlled and *in situ* measurements. This modelling may be the most successful one, but it requires careful measurements to determine the bladder shape and is limited to rather high frequencies.

Recently, FOOTE(6) has investigated the influence of the swimming movement on "bladder fish" target strength through a modelling exercise. In this, several gadoid specimen were represented as acoustic scatterers through their triangulated swimbladder surfaces, assumed to be perfectly pressure-releasing. The swimming movement was described as periodic deformation in swimbladder shape consistent with actual measurements of whole-body movements of swimming gadoids. The conclusion was immediate: the swimming movement does not significantly affect the dorsal aspect target strength. Therefore, NAKKEN and OLSEN(7) and others, whose work is based on large amounts of data collected about this kind of immobilized-single-fish target strength, did not expect their data to be effected by swimming movement. This is also supported by SANO's experiment(8) and FURUSAWA's model(9). Using his prolate spheroidal models, FURUSAWA concluded that most backscattered energy is attributable to the bladder; the variability of the target strength of bladder fish with respect to their orientation distribution is smaller than that of bladderless fish. And in addition he suggested that contrary to bladder fish, when we measure target strength of bladderless fish, we must sufficiently take into account the orientation, composition of body, surroundings, bubbles and noise.

It is the purpose of the present study to investigate the swimming movement characteristics of squid and the effect of that swimming movement on squid target strength. Squid, which lack a gas-filled swimbladder (bladderless fish), have a very directive acoustic backscattering pattern, and consequently it is suggested that the variability of the target strength with respect to swimming movement or orientation is higher than that of bladder fish which have a broad backscattering pattern and have no prominent side lobes.

Swimming Movement Characteristics of Squid

1. *Hydrodynamics of squid*

Squid, which live and compete in the open ocean with fish and mammals use a propulsive system totally unlike that of their predators and competitors. Jet propulsion is the mode of locomotion typical of common squid. Like fish the squid body is designed for suspension, the stiff supporting member being placed dorsally and the viscera hung below. Squid have a rounded cross-section and stream-lined form. They have a single pair of caudal fins projecting from the mantle and they vary in shape according to the size and way of life, from paddle-shaped in larval stages, suggesting a propeller action capability, to the triangular shape typical of fast-swimming(10) squid.

Strikingly different from fish is the absence of fins on the dorsum and the presence of a single pair of fins away from the middle of the body in squid. The pectoral and pelvic fins of fish near the middle of the body are used in left/right turning, providing lift, and acting as brakes. In squid these three functions are taken over by the funnel which is capable of directing the jet of water from the mantle downwards, sideways or backwards. In view of its multiple functions, the control of funnel direction and intimately connected thrust control of the jet, must be rather sophisticated and should be worth experimental investigation especially in relation to forces acting on the statocyst and to visual influences. Some general features of design are clear[11]:

(1) Its turning function explains why the funnel aperture, like the fish pectoral fins, is placed a little forward of the mid-vertical line and not precisely on it so as to provide a turning couple when the jet is directed sideways. A sideways-directed funnel acting from the middle would cause the body to drift not turn. On the other hand, since the funnel aperture is not located too far from the center of gravity, squid, which are heavier than waters, are better suited to carry out their function of counteracting sinking.

(2) The most squid are 2-4% heavier than water. The passive sinking tendency is counteracted while swimming by a dynamic lift component contributed by fins and funnel. ZUEV's analysis[10] of their actions explains: (a) why the fins lie in the horizontal plane and towards the posterior end of the body, (b) why they are generally located well above the long axis of the body (a position not common for lateral fins in fish, though found in flying fish), and (c) why the relative size of the fins in many squid increases as the weight of the body to be lifted increases.

(3) A number of deep-water squid have fins that do not increase in size relative to the rest of the body. On these grounds alone such forms might be assumed to be those of bottom-living or floating creatures.

The motion of a jet-propelled squid body travelling through a fluid medium is governed by the equation of motion[12] which, in the direction of thrust, is

$$G+\frac{1}{2}C\rho A U^2+m\left(\frac{dU}{dt}\right)+q\left(\frac{dm}{dt}\right)=0 \tag{1}$$

where G is component of gravity force acting in the direction of thrust, C is drag coefficient, A is frontal area of body, m is instantaneous mass of body and contents, U is instantaneous velocity of body, ρ is density of fluid, and q is the velocity of jet relative to body.

The derivation of this equation allows for the fact that the total mass of the body and its contents decreases as fluid is ejected.

The four terms of this equation are, respectively, the forces associated with gravity, drag, acceleration and jet thrust.

(1) Gravity force

The resultant of body weight acting vertically downwards and buoyancy force acting vertically upwards will have a component G in the direction of thrust. If the body and fluid have equal density, or if the thrust is horizontal, the gravity force (G) in the direction of thrust will of course be zero.

(2) Drag

The drag force will depend upon the densiy (ρ) of the fluid, the frontal area (A) which probably decreases as the creature discharges the contents of its mantle cavity, the velocity (U) of the body and upon the drag coefficient (C). The latter depends upon the instantaneous shape of the body and the nature of the fluid flow around it, which in turn is a function of the velocity (U).

(3) Inertia force

The third term of Equation (1) is familiar from NEWTON's Second Law of

Motion, from which the whole equation may be derived. This term depends upon the total mass of the body together with the mass of the fluid at an instant in the mantle cavity and upon the instantaneous acceleration (dU/dt) of the body.

(4) Jet thrust

The jet thrust developed by the jet of water is given by the product of jet velocity (q) and the rate of mass flow (dm/dt) through the funnel. We shall show later that it can also be determined from the shape and size of the funnel together with a knowledge of either the jet velocity of the fluid pressure inside the mantle cavity or the shape and properties of the mantle material.

If the drag and gravity forces are neglected, Equation (1) reduces to

$$mdU = -qdm \tag{2}$$

or

$$dU = -q\left(\frac{dm}{m}\right), \tag{3}$$

and if the jet velocity is assumed constant, Equation (3) can be integrated to give the following well-known expression for the increase in the velocity (ΔU) which will occur as the total mass decreases from m_0 to m:

$$\Delta U = U - U_0 = q\ ln\ (m_0/m). \tag{4}$$

If it is assumed that a squid having a body mass (m_b) expels the entire contents of its mantle cavity (m_c), then Equation (4) can be rewritten as

$$\begin{aligned} \Delta U &= q\ ln\ \{(m_b + m_c)/m_b\} \\ &= q\ ln\ (1 + m_c/m_b) \end{aligned} \tag{5}$$

Thus Equation (5) gives a simple expression for calculating the increase in velocity resulting from a single jet pulse. However, particular notice should be paid to the assumptions that (i) gravity forces are negligible, (ii) drag forces are negligible, and (iii) jet velocity is constant.

Assumption (i) may not be unreasonable as squid are only about 4% more dense than sea water; however, hydrodynamic drag forces may be considerable and the jet velocity is unlikely to be constant throughout the pulse.

2. *Buoyancy mechanism*

A useful way of thinking of the buoyancy of an animal is to draw up what might be described as a buoyancy balance sheet, putting on one side those components which are denser than sea water and which will, therefore, tend to "sink" the animal, and on the other side the components which are less dense than sea water and so will tend to "float" it. The sinking components of animals are those whose specific gravities are greater than that of sea water (i.e. about 1.025 g/cm^3). These components are principally the proteins of their tissues, especially muscles, and their skeletons. On the other side of the balance sheet the principal floating components of animals are those whose densities are less than that of sea water and these can be fats, certain body fluids and chambers filled with gas[13].

In order to achieve neutral buoyancy therefore the proportion of floating components in an animal must be increased and this usually involves some special buoyancy mechanism. In recent years two such buoyancy mechanisms have been reported in cephalopods[13]. The first is concerned with certain body fluids, the second with chambers filled with gas. In several families of pelagic oceanic squid, such as *Ommastrephes* and *Todarodes*, which have no obvious buoyancy mechanism, squid are about 4% denser than sea water (so the density of the body must be 1.064 g/cm^3), and like the mackerel, must swim all their life if they are to avoid sinking. The detailed buoyancy balance sheet is not known but its principal sinking component is certainly protein of its muscles (about 5% denser than sea water or a density of 1.075 g/cm^3). Its shell is reduced to the very thin, transparent "pen" which has a weight of only 0.6% of that of the whole animal and which, since its specific gravity is only 1.2 g/cm^3, weighs very little in sea water. There squid, like some very active fish, e.g. tunny fish, need to stay in mid-water by swimming.

3. *Jet-propulsion swimming mechanism*

Squid swim by rapidly expelling water from the mantle cavity. The mantle contains both radial and circular muscle fibers[14]. During the inhalant phase of water circulation, the circular fibers relax and the radial muscles contract. This action increases the volume of mantle cavity, and water rushes in dorsally, laterally, and ventrally between the anterior margin of the mantle and the head. When the mantle cavity is filled, the action of the mantle muscles is reversed.

The contraction of the circular muscles not only increases the water pressure within the cavity but also locks the edges of the mantle tightly around the head. Thus water is forced to leave through the ventral tubular funnel. The force of water leaving the funnel propels the animal in the opposite direction. The funnel is highly mobile and can be directed anteriorly or posteriorly, resulting in either forward or backward movement. The rapidity of movement depends largely on the force with which water is expelled from the funnel, but the movements are beautifully controlled. The fastest movement is achieved in backward escape swimming, when powerful contractions of the mantle eject water from the anteriorly directed funnel.

A more detailed description of the water jet propulsion mechanism of squid was reported by GOSLINE and DEMONT[15] (see Fig. 1). As shown in this Figure, the jet cycle begins with hyperinflation (1), in which the outside diameter of the mantle increases by approximately 10 percent compared with the relaxed state and the volume of the internal cavity rises by about 22 percent. Water flows into the cavity through large openings on each side of the head, passing over the surface of the funnel (see horizontal section, part (B) of Fig. 1), a tissue structure that projects back from the head. After expansion reaches its peak, the mantle contracts to about 75 percent of its relaxed diameter (2). Pressure in the cavity rises sharply, forcing the funnel against the mantle wall and sealing the water inlets. Nearly all the water (equivalent to about 60 percent of the relaxed mantle volume) is expelled through the narrow funnel tube in a powerful jet. The mantle then refills to the relaxed level (3), further contraction might damage soft internal organs. A single escape-jet cycle lasts for about a second and may be repeated six to 10 times. When the squid is swimming slowly, its mantle contracts, without hyperinflating, to about 90 percent of its relaxed diameter.

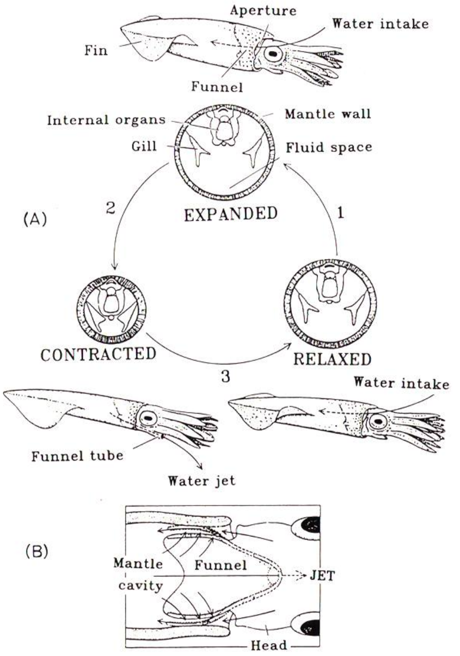

Fig. 1. Jet cycle of the squid is shown in side (A) and cross-sectional views (B).

Fig. 2. Experimental set-up for squid swimming speed observation. The major radius, minor radius, and depth of the oval-shaped aquarium tank are 1, 0.5, and 1 m, respectively.

Materials and Methods

1. *Preliminary experiment*

For the present study it is important to analysis the "backward" or jet-propelled swimming of the squid (the most common mode of free-swimming squid which we observed in the aquarium tank) and to measure their swimming speed in relation to tilt angle.

Squid, *Todarodes pacificus*, swimming movement and swimming speed observations were conducted in a small oval-shaped aquarium tank of about 2 m^3 volume (see Fig. 2), containing sea water at 8°C and water current speed of 0.2 m/s. The width and depth of the tunnel inside the aquarium were 0.4 m and 1 m, respectively, to make squid swimming as free as possible. Body weight and dorsal mantle length of the 25 squids used range from 300–360 g and 20–25 cm.

Video recordings of the swimming animals were made using a color video camera Victor GX-V7 from the side of the aquarium at a distant of 45 cm from the window of 30 cm × 30 cm size. To determine swimming speed, a 5 cm reference grid was marked on the inside wall of the aquarium ; then the swimming speeds in the aquarium were calculated using the change in horizontal distance per unit time, and since the video analysis did not detect vertical displacement, they may be slightly underestimated.

Table 1. Body weight and dorsal mantle length of squid, *Todarodes pacificus*, used in experiments

Squid Do.	Dorsal Mantle Length (cm)	Standard Length (cm)	Body Weight (g)
1	20.5	35.5	235
2	21.8	36.7	256
3	23.0	38.0	338
4	24.2	39.2	420
5	25.5	40.5	441
Mean	23.0	38.0	338

2. *Main experiments*

2.1 *Materials*

The squid specimen used in these experiments were dead surume ika (*Todarodes pacificus*). The mantle length and body weight of these specimens are described in Table 1. As shown in the Table, the mean dorsal mantle length, standard length (the length from the root of the caudal fin to the tip of the longest arms excluding the two tentacles) and body weight are 23.0 cm, 38.0 cm and 338 g, respectively.

2.2 *Measuring methods*

These measurements were conducted in controlled experiments in a water tank. The complete measurements had two steps. The first step was measurement on a fixed target, and the second step was on a moving target. This target moving speed was selected to represent the actual swimming speed of squid relative to the fixed transducer.

Before the methods were applied on squid, measurements of the echo level (in this case, echo energy) from a standard steel ball with a diameter of 41 mm (target strength value of −39.96 dB) were conducted. Since this steel ball was used as a reference target, this was a measure of the echo level fluctuations in the system. After the calibration, measurements of the echo level or target strength of the squid were made.

The speeds of movement used were based on the results of the swimming speed observations in the aquarium as described above and were expected to represent the three types of behaviour which were identified and classified during preliminary measurements, i.e., (1) slow swimming (calm) behaviour (squid with very little visible movement, moving speed of 0.12 m/s), (2) active behaviour (squid with smooth and regular movement, moving speed of 0.28 m/s), and (3) wild behaviour (squid with fast or wild movement, moving speed of 0.40 m/s). The flexibility of the squid body and its motion so that aspect and body shape change from moment to moment during swimming movement, would cause the shape and amplitude of echoes from ping to ping to fluctuate. To measure these fluctuations of the target strength the probability density function (PDF) was used. Correspodingly, the sequence of echoes from the squid was expected to have a sequence of random echo energy and can be described by its PDF.

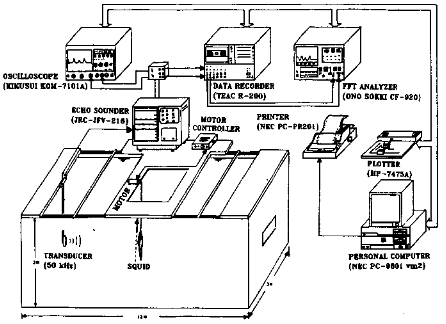

Fig. 3. Block diagram of data acquisition and processing system.

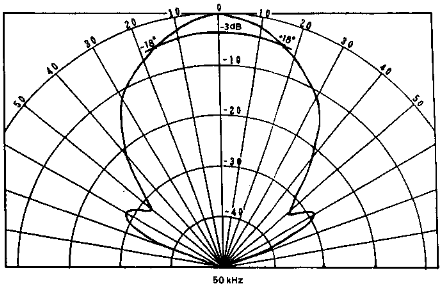

Fig. 4. Directivity pattern of transducer.

Other than PDF, averaging of target strength was also considered as an effective measure to investigate the effect of swimming on the target strength of squid. Consequently, the average target strength values of squid with respect to different swimming speeds were compared statistically to facilitate these comparisons.

2.3 *Experimental set-up*

The measurements were conducted in the $12 \times 3 \times 3\ \mathrm{m}^3$ anechoic water tank of Faculty of Fisheries, Hokkaido University. To move the squid at the desired speeds, a motor with a speed controller was used. Received echo signals from the echo sounder (JRC JFV-216), with an ensonifying frequency of 50 kHz, a pulse repetition rate of 150 pings/min and sound beam width of 36° were first recorded on the Data Recorder (TEAC R-200), and then analyzed by a FFT Analyzer (ONO SOKKI CF-920). An Oscilloscope (KIKUSUI COM-7101A) was used for monitoring the signals during measurements. The target strength values, PDFs and averaged target strengths, then were computed from analyzed data (echo energy) by personal computer (NEC PC-9801 Vm2). The results then printed out or plotted by printer (NEC PC-PR201) and plotter (EPSON HI-80), respectively. The complete data acquistion and processing system and the directivity pattern of the 50 kHz transducer are shown in Fig. 3 and Fig. 4, respectively.

Results and Discussion

1. *Swimming speed of squid*

The results of these squid swimming speed observations obtained from sequences of 150 data (video images) mainly ranged from 0.12 to 0.40 m/s and an average of 0.28m/s. Surume ika are negatively buoyant and apparently use their fins primarily for control. During normal cruising they maintains their body at an angle such that the thrust from their jet is balanced between pushing the body fins-forward through the water and countering gravity. At speeds from 0.20 to 0.30 m/s, most squid used their fins at near the jet frequency. As swimming speed increased, the strength and frequency of mantle contractions increased and the use of the fins usually decreased. In this case, squid increased both jet frequency and

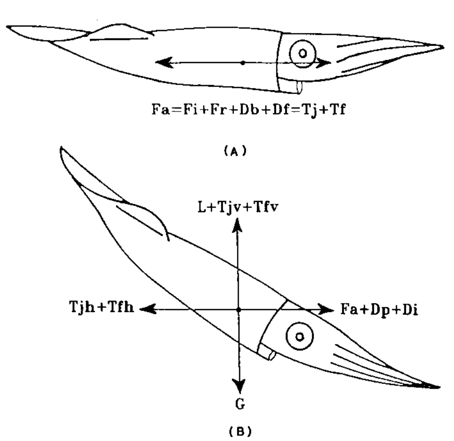

Fig. 5. An analytical approach of hydrodynamic lift of squid.

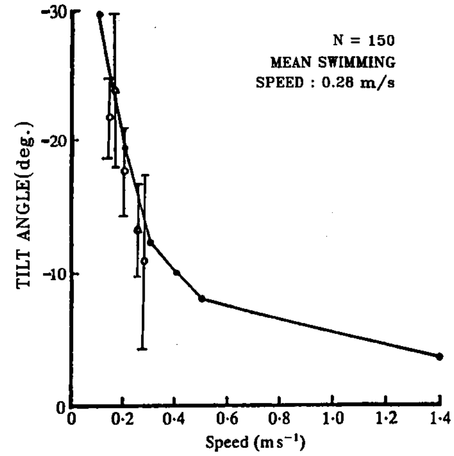

Fig. 6. The dependence of tilt angle θ on swimming speed.

jet pressure with increased swimming speed. At the highest speed of 0.40 m/s, squid frequently tucked their fins under and against the mantle, probably to minimize drag. Under these conditions, the jet alone control the tilt angle and the forward momentum.

To explain why the above swimming movement occured, an analytical approach of hyodrodynamic lift of squid to compensate for the negative buoyancy during enforced horizontal swimming may be suitable as reported by JOHNSON *et al.*[12] and O'DOR[16]. However, it is beyond the scope of this study to review this force acting on swimming squid; consequently, only a summary in schematic form is given here as shown in Fig. 5, a modification of O'DOR's figure.

Fig. 5(A) is a summary of the forces acting on a theoretical, neutrally buoyant squid moving with its body axis parallel to the flow. Jet (T_j) and fin (T_f) thrust act against the axial force (F_a) (the sum of body (D_b) and fin (D_f) drag and inertial (F_i) and refilling (F_r) forces).

As shown in Fig. 5(B), real squid use a combination of thrust (T) and lift (L) produced by cross-flow to counter their buoyant weight (G) during horizontal swimming. The positive tilt angle required to produce lift also produces added pressure drag (D_p) and induced drag (D_j). T_{jv} and T_{fv} are the vertical components of jet and fin thrust, respectively. T_{jh} and T_{fh} are the horizontal components of jet and fin thrust, F_j is the inertial force related to acceleration or deceleration of the squid and the water it contains, F_r is the force required to accelerate water entering the mantle during refilling to the speed of the squid. It is important to note here that the negative forces act in the direction of motion, and the positive forces act in the direction of water current.

If we compared these results with the field data reported by SHEVTSOV[17] (results of tagging of the surume ika *Todarodes pacificus* in the Kuril-Hokkaido region), it is clear that both values of average speed are very close, i.e., up to 0.30 m/s or 0.9 ML/s, where ML is the dorsal mantle length (in m). So, the average speed of surume ika of 0.28 m/s is considered reasonable for the present study of the effect of swimming on dorsal aspect target strength of squid.

The relationship between the swimming speed U(m/s) and tilt angle θ (degrees) is shown in Fig. 6. From this Figure it is clear that the average tilt angle typically decreases from about $-30°$ when hovering to near $-3°$ at high speeds. For the present study in which the normal squid speeds were not higher than 0.40 m/s, the average tilt angle was not more than -10 degrees. The variation of the tilt angle of squid is very important in that the target strength on it. This will be discussed in the next section of this paper.

2. *Effect of swimming movement on target strength*

As described in the previous section, because of many difficulties in carrying out target strength experiments on free swimming squid in the sea, only target strength measurements of moving dead squid are performed and the results then reanalyzed taking into account the free swimming movement as observed previously, especially the relationship between swimming speed and body tilt angle, body volume or body shape.

The PDF of the target strengths was calculated to be between 19 and 300 pings depending on the moving speeds of the squid in the sound beam. For different moving speeds, the target strength PDFs are shown in Fig. 7 for squid of 23.0 cm as an example. As seen in this Figure, there is high variability of the PDF from one speed to another and dependence of the mean target strength on the swimming speed. Compared to the PDF for non-swimming squid (swimming speed of 0.0 m/s), the PDF for moving squid has a large range of target strengths. A squid exhibiting "slow moving behaviour" (swimming speed of 0.12 m/s) has a narrow range of target strengths and is somewhat like the steel sphere or squid of 0.0 m/s swimming speed. An "active behaviour" squid (swimming speed of 0.28 m/s) has a broader PDF, and a "wild behaviour" squid (swimming speed of 0.40 m/s) has the largest range of PDF. Thus, target strength from the same squid can have a wide range of values as the squid moves or swims. These results are also supported by the results of backscattering cross-sections of live fish as described by HUANG and CLAY[3].

Since there is great variation of the PDF of the target strengths one needs the average of many measurements to determine the mean target strength. We need to know the mean target strength because it this quantity that relates the integral echo squared measurements to the number of squid per cubic meter in acoustic surveys.

As shown in Fig. 7, the mean target strengths of 23.0 cm squid vary as swimming speed changes, but there are not linear relationships between the swimming speed and mean target strength values. The mean target strengths are -46.80 dB, -48.20 dB, -45.20 dB and -47.20 dB for a swimming speed of 0.0, 0.12, 0.28, and 0.40 m/s, respectively. Thus in applying the results of these laboratory measurements to field measurements of target strength, there are two points to consider. The first is the relationship between the swimming speed and the body volume/shape. The second is the relationship between the swimming speed and the body tilt angle.

As was described in Fig. 1 of the previous section, when squid are swimming quickly (by jet-propulsion), the jet cycle of squid begins with hyperinflation, in which the external diameter of the mantle increases by approximately 10% compared with the relaxed state and the volume of the internal cavity rises by about 22%. In contraction, the external diameter is reduced by some 30%, the internal cavity's

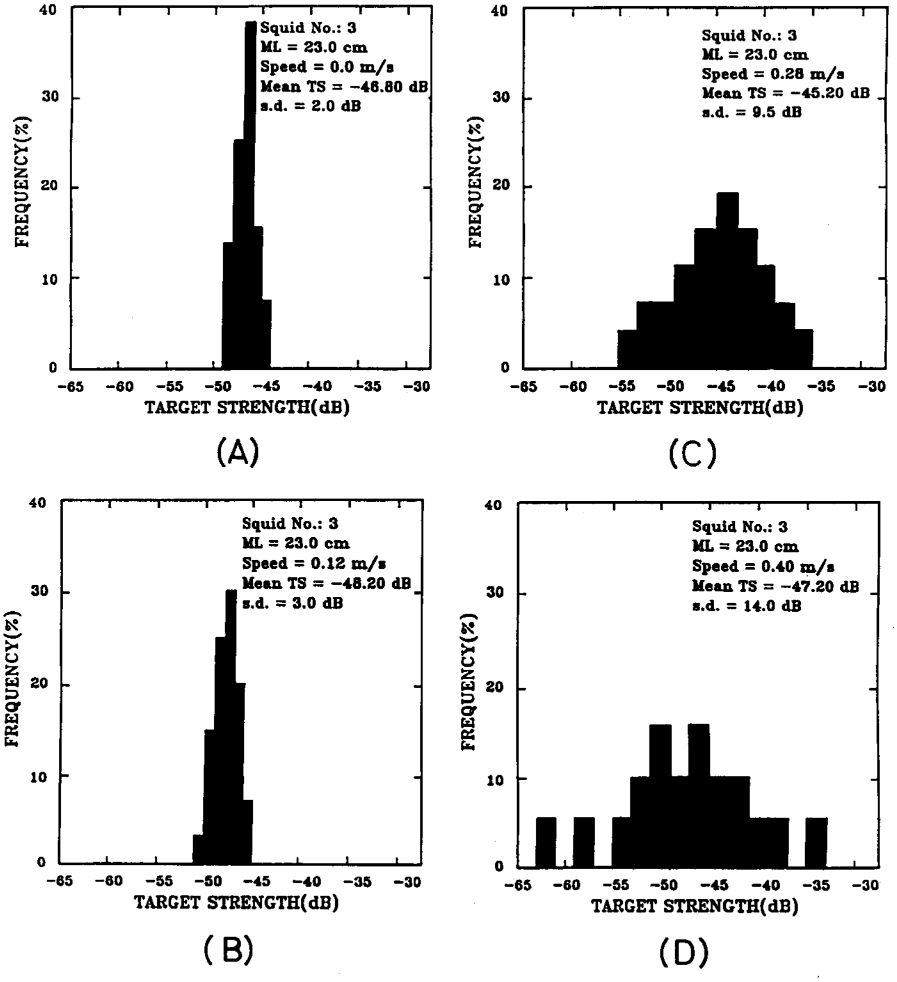

Fig. 7. Probability density functions of squid target strength at different swimming speeds. (A) 0.0 m/s, (B) 0.12 m/s, (C) 0.28 m/s, and (D) 0.40 m/s.

volume drops by roughly 40%. When a squid is swimming slowly, its mantle contracts, without hyperinflating, to about 90% of its relaxed diameter. The simple schematic diagram of those two different swimming mechanisms is shown in Fig. 8. The theoretical approach to determine the effect of body shape or thickness on target strength will be reported in the next paper[18].

As shown in Fig. 6, the body tilt angle of squid depends on swimming speed. As swimming speed increases, tilt angle generally decreases. Therefore we cannot predict the swimming speed at which the body has a zero or positive tilt angle because squid are negatively-buoyant marine organism generally having a negative tilt angle in active swimming. A squid must swim all its life if it is to avoid sinking, and therefore swimming speed has an important role as expressed in the simple Equation (5) above.

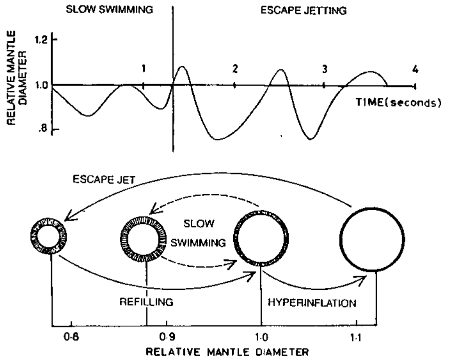

Fig. 8. The relationship between the fast and slow swimming speeds and body shape of squid (the external diameter of mantle).

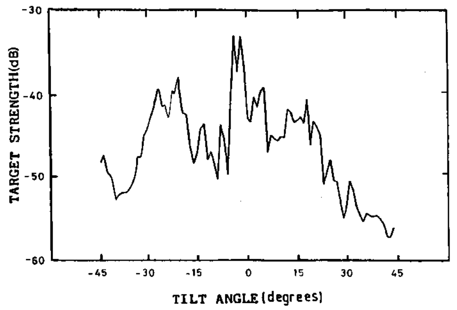

Fig. 9. Target strength function of 23.0 cm squid at 50 kHz.

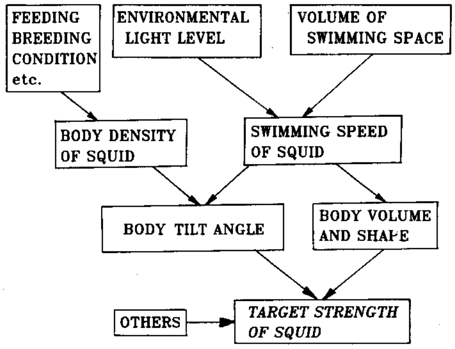

Fig. 10. Factors affecting the body tilt angle and body volume/shape of free-swimming squid, and subsequent change in target strength.

In order to test the significance of the tilt angle in explaining observed target strength variations, we must know the target strength function of squid. An example of this squid target strength function is shown in linear form in Fig. 9 for squid of 23.0 cm dorsal mantle length at 50 kHz. As shown in this Figure, the target strength function is less satisfactory. It does not exhibit a clear maximum near the dorsal aspect but is very directive. It is possible that the result may be affected by the very low target strength of squid compared with bladder fish[4,7,9]. Thus, the large differences noted in the tilt angle distributions should cause relatively large changes in the echo energy, according to the target strength function as shown in Fig. 9.

This possible effect of squid behaviour, especially swimming movement or speed on target strength, is summarized in Fig. 10. It is clear that the target strength of squid of the same species and size changes with body tilt angle, body volume and shape, and other nonbiological factors. A negative tilt angle (head down) produces lower target strength. It is possible that the lower target strength of squid recorded at night is also caused by behavioural changes, due to the environmental light level. At lower light levels, squid tend to swim more slowly, and at higher light levels, they no longer school, although they are still swimming slowly on their own (personal observation). Thus given a lower target strength, a larger body tilt angle can be expected for these squid.

Conclusions

Evidence for the effect of the swimming movement on squid target strength is scant and conflicting. Squid swim mainly by a jet-propulsion system, and there are significantly different propulsion mechanisms used for fast swimming and slow swimming. When the squid are swimming quickly, the external diameter of the mantle and the cavity's volume change by about 30% and 40%, respectively. However, when they are swimming slowly, the mantle diameter and volume changes are not more than 10%.

The body tilt angle of squid also depends on swimming speed. As swimming speed increases, tilt angle generally decreases. The average tilt angle typically decreases from about $-30°$ when hovering to near $-3°$ at high speeds. For the present study in which the average swimming speed was 0.28 m/s and the normal speeds were not higher than 0.40 m/s, the average tilt angles was not more than $-10°$.

We conclude that, contrary to bladder fish[4,6,9], swimming movement significantly effects squid target strength. Thus, in applying the results of these laboratory measurements to field measurements of squid target strength, there are two points to consider. The first is the relationship between the swimming speed and the body volume/shape ; and the second is the relationship between the swimming speed and the tilt angle. The large differences noted in tilt angle distributions should cause ralatively large changes in the target strength, according to the target strength function with respect to tilt angle.

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