

Controlled and *in situ* target strengths of the jumbo squid *Dosidicus gigas* and identification of potential acoustic scattering sources

Kelly J. Benoit-Bird^{a)}

College of Oceanic and Atmospheric Sciences, Oregon State University, 104 COAS Administration Building, Corvallis, Oregon 97331

William F. Gilly^{b)}

Hopkins Marine Station, Department of Biological Sciences, Stanford University, Oceanview Boulevard, Pacific Grove, California 93950

Whitlow W. L. Au^{c)}

Hawaii Institute of Marine Biology, University of Hawaii, P.O. Box 1106, Kailua, Hawaii 96734

Bruce Mate^{d)}

Hatfield Marine Science Center, Oregon State University, 2030 SE Marine Science Drive, Newport, Oregon 97365

(Received 26 April 2007; revised 3 December 2007; accepted 12 December 2007)

This study presents the first target strength measurements of *Dosidicus gigas*, a large squid that is a key predator, a significant prey, and the target of an important fishery. Target strength of live, tethered squid was related to mantle length with values standardized to the length squared of -62.0 , -67.4 , -67.9 , and -67.6 dB at 38, 70, 120, and 200 kHz, respectively. There were relatively small differences in target strength between dorsal and anterior aspects and none between live and freshly dead squid. Potential scattering mechanisms in squid have been long debated. Here, the reproductive organs had little effect on squid target strength. These data support the hypothesis that the pen may be an important source of squid acoustic scattering. The beak, eyes, and arms, probably via the sucker rings, also play a role in acoustic scattering though their effects were small and frequency specific. An unexpected source of scattering was the cranium of the squid which provided a target strength nearly as high as that of the entire squid though the mechanism remains unclear. Our *in situ* measurements of the target strength of free-swimming squid support the use of the values presented here in *D. gigas* assessment studies.

© 2008 Acoustical Society of America. [DOI: 10.1121/1.2832327]

PACS number(s): 43.30.Sf, 43.30.Ft, 43.20.Fn [KF]

Pages: 1318–1328

I. INTRODUCTION

Dosidicus gigas, the jumbo or Humboldt squid, ranges in adult size from 35 cm to about 2.5 m in total length and can weigh up to 50 kg, making it the largest of the nektonic squids. Individual squid grow extremely rapidly, reaching these sizes in only 1 to 2 years. They are found in the productive and relatively shallow waters of the Eastern Pacific from 125–140°W, 40°N to 45°S. They typically inhabit from surface waters to depths of about 500 m, with pronounced diel vertical migrations bringing them shallower at night (Gilly *et al.*, 2006) but Remotely Operated Vehicle (ROV) sightings have been made deeper than 1000 m (B. Robison, private communication). *D. gigas* is an active migratory predator, feeding primarily on myctophids and other fish, crustaceans, and squid (Markaida and Sosa-Nishizaki, 2003). As adults, they are a food resource for large fish in-

cluding tuna and swordfish, and marine mammals such as sperm whales and pilot whales. *D. gigas* has been shown to be a keystone species, transferring energy between planktivorous fish and the largest pelagic predators (Shchetinnikov, 1988).

Dosidicus gigas is probably the most abundant nektonic squid in the Eastern Pacific (Nigmatullin *et al.*, 2001), and it currently supports the world's largest cephalopod fishery, with landings of 800 000 tonnes in 2004 (FAO data at <ftp://ftp.fao.org/fi/stat/summary/a1e.pdf>) Approximately 15% of this catch comes from the Guaymas Basin in the Gulf of California, Mexico (Markaida and Sosa-Nishizaki, 2001), although annual landings can be quite variable (Nevarez-Martinez *et al.*, 2006).

Total standing biomass of *D. gigas* across its large range is unknown, but annual production in the Gulf of California has been estimated to be 210,000 tons/y (Sanchez-Juarez, 1991). This figure undoubtedly is an underestimate of the current situation, given the fact that commercial fishing has reached half of this figure, and consumption by resident sperm whales alone may be comparable (D. Gendron, private communication).

^{a)}Corresponding author. Electronic mail: kbenoit@coas.oregonstate.edu

^{b)}Electronic mail: lignje@stanford.edu

^{c)}Electronic mail: wau@hawaii.edu

^{d)}Electronic mail: bruce.mate@oregonstate.edu

Despite the economic importance of the *Dosidicus* fishery and the inherent difficulties in managing a highly variable population affected by strong environmental fluctuations, extensive migrations, and interactions with other fisheries (Morales-Bojorquez *et al.*, 2001), data on behavior, natural history, and biomass of the species remain limited. These factors are critical components to successful management of any fishery.

Assessment of biomass in squid fisheries has relied on commercial landing data, trawls, and quantitative hand-fishing (jigging) surveys, each of which has limitations (Boyle and Rodhouse, 2005). Although acoustic methods have been widely used in the assessment of fish stocks (Misuñd, 1997), application of acoustics to study the biology of squid has received much less attention, probably because of the belief that squid are particularly weak scatterers (Fristrup and Harbison, 2002). Nonetheless, acoustic methods have been successfully employed to observe spawning aggregations (Jefferts *et al.*, 1987; Lipinski and Prowse, 2002), to assess recruitment by quantifying benthic egg beds (Foote *et al.*, 2006), and to characterize acoustic features of different groups of squid for possible future efforts (see, for example, Boyle and Rodhouse, 2005; Goss *et al.*, 2001).

The first step for quantitative acoustic assessment of any marine species is measurement of its target strength distribution, and no such data exist for *D. gigas*. Our goals in this study were: (1) to obtain controlled measurements of the target strength of a wide size range of live *D. gigas* at four frequencies, (2) identify possible sources of scattering in *D. gigas*, and (3) to confirm the validity of target strength measurements *in situ* with free swimming squid.

II. METHODS

Research was conducted between 16 and 24 March 2007 from the 25 m R/V Pacific Storm in Guaymas Basin in the Gulf of California, Mexico. Individual squid were captured with weighted, luminescent jigs generally between dusk and 0100 local time. One squid (the smallest studied) was captured at the surface using a dip net. Squid were typically maintained in individual, covered tanks with a continuous input of fresh seawater overnight before their acoustic properties were measured during daylight hours.

A. Acoustic system

Acoustic characteristics of the squid were measured using a four-frequency, split-beam echosounder system (Simrad EK60s). The 38 kHz echosounder used a 1024 μ s pulse, the 70 kHz echosounder used a 512 μ s long pulse, while the 120 and 200 kHz echosounders used a 256 μ s pulse. The 38 kHz system had a 12° conical split beam while each of the higher frequencies had a 7° conical split beam. The transducers were affixed over the side of the vessel on a rigid pole mount so that they were 1 m beneath the water's surface. The system was calibrated using an indirect procedure incorporating a 38.1-mm-diam tungsten carbide reference sphere as prescribed by Foote *et al.* (1987). In addition, the target strength of the sphere was also measured attached to the mounting line that normally held the squid (described in the

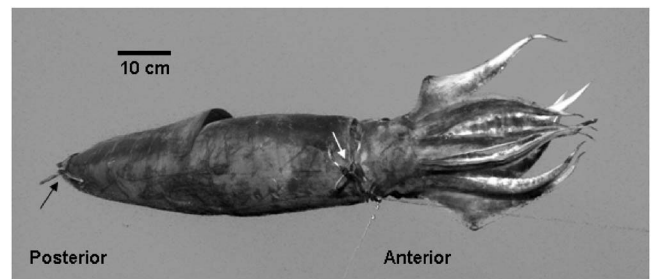


FIG. 1. A mounted squid underwater. A single loop of Tygon® tubing tied to a horizontal length of monofilament is visible at the posterior of the animal at the left of the photo and two loops tied together and then to the monofilament is visible at the anterior of the mantle, near the squid's head in the center of the photo.

following) to rule out any possible interference of the mounting arrangement. All the mounting lines were also placed in the water without the sphere or a squid to measure any potential backscatter from the experimental setup.

B. Mounting of live squid

An individual squid was removed from its holding tank and placed ventral side down for attachment of the mounting hardware. During this time (<5 min total) the gills were continuously irrigated with flowing seawater. The squid did not struggle, and no anesthesia was necessary. Two locations on either side of the midline of the dorsal mantle surface near the anterior edge, and one location through the posterior tip of the gladius, were pierced with a stainless-steel cannula (6 mm o.d.; Floy Tag, Seattle WA), allowing a small length of 6 mm diameter Tygon tubing to be passed through each hole. A plastic cable tie was passed through the tubing and then cinched to form a loop, with the soft tubing acting as a “bushing” to minimize tissue damage (Fig. 1).

For dorsal-aspect measurements, the loops through the squid were then attached to two loops tied approximately the length of squid's mantle apart near the center of a 7.5 m horizontal length of monofilament. The squid, attached to the monofilament mounting line, was then gently lifted onto a cloth stretcher and lowered into the water. Great care was taken to avoid the introduction of air into the squid's mantle during the mounting procedure. The mantle was continuously flushed with gently running seawater while on deck and then held compressed by the stretcher until the squid was released in the water by removing the stretcher. The squid was then observed just below the surface to ensure that it was actively swimming in the proper orientation, that no lines were tangled, and that no air was observed leaving the mantle or around the animal's appendages. The animals were all observed to be vigorously alive and their attempts to swim away from the mounting rig resulted in strong mantle compressions and jetting, likely removing any potential residual air. After observation of the squid near the surface, the horizontal mounting line was lowered to a depth of between 6 and 16 m, depending on currents and other sea conditions. In all cases, the depth was at least twice what was necessary for the entire target to be within the 3 dB beamwidth of the narrowest transducer and in the far field of all transducers

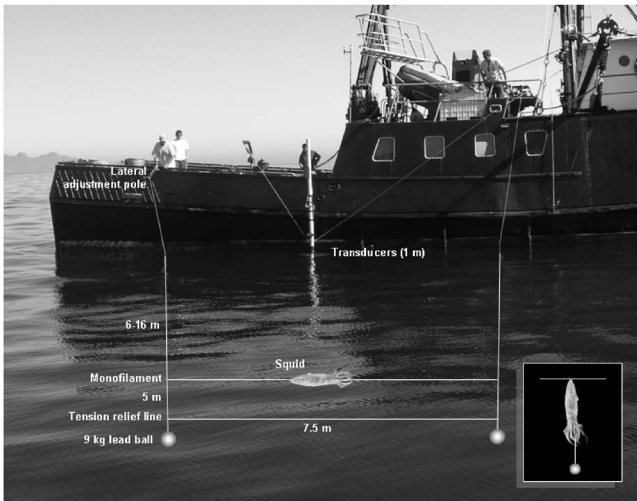


FIG. 2. The squid was mounted to a horizontal piece of monofilament stretched apart by two vertical lines lowered by lead balls. The transducers were mounted 1 m below the water's surface on a rigid pole over the side. Lateral aspect setup is shown in the main figure. Changes for posterior aspect (head down) measurements are shown in the inset on the lower right on the same scale.

when considering the cross-sectional area of the scattering surface perpendicular to the incident signal at the wavelengths used.

As indicated in Fig. 2, the horizontal mounting line was held taut between two vertical nylon lines spaced 10 m apart. Each vertical line was weighted with a 9 kg lead ball 5 m below the attachment point of the mounting line. An additional 7.5 m length of polypropylene line connected the lead weights and provided strain relief. The inboard/outboard position of the lines was adjusted with poles affixed across the rail of the vessel. Dorsal-aspect measurements were taken from a total of 14 squid that were alive both upon entry into the water and after removal from the water postexperiment. Measurements were also made from one animal that had recently expired. Only live animals were used for the acoustic measurements presented in the figures and equations.

After measuring the dorsal aspect of the squid, a subset of the animals were measured from the posterior aspect by suspending the squid in a head-down vertical orientation. In this case, the posterior attachment loop was retained, but the anterior loops were detached from the mounting line, and the corresponding end of that line was disconnected from its vertical line, and the end was directly attached to a 5 m length of monofilament leading to a 5 kg lead ball.

Upon completion of all measurements, we measured dorsal mantle length (DML), length from the tip of the mantle to the end of the outstretched arms (not tentacles), maximum mantle width, and total mass. After these measurements were completed, the squid was euthanized by rapid decapitation, and sex and maturity stage (Lipinski and Underhill, 1995) were visually determined. Effects of maturity and gender on target strength were assessed with a multivariate analysis of variance (ANOVA).

C. Acoustic scattering source assessments

Measurements were made in an attempt to determine the important individual sources of the acoustic scattering from

squid. In several cases, following the whole-animal measurements, the dorsal aspects of the head and body were measured separately. Each portion was suspended from the mounting line in a manner similar to that described earlier. Care was taken to avoid the introduction of air into the body parts since it could dramatically impact acoustic measurements. The dense, cartilaginous posterior of the gladius (the conus) was removed and the body was remeasured. The beak, followed by the eyes, arms, and all soft tissue were successively removed from the head with measurements repeated at each step so that ultimately, only the cartilaginous cranium (braincase) remained.

D. Acoustic measurements

Acoustic measurements were either made while the boat was anchored in at least 30 m of water or drifting in calm seas. The position of the squid was adjusted so that it was maintained within 2° of the center of each of the four transducers as identified in real time via the split beam target identification that is part of the Simrad recording software. A minimum of 100 measurements of target strength were made from each squid in each position. Most often, at least 500 measurements were made. Analysis of target strength was only made for echoes that were within 2.5° of the center of the beam along both axes and were at the known depth of the squid. The average target strength and standard deviation (both calculated from linearized data) were determined for each squid. The target strengths of scattering from different parts of the squid were compared using t-tests based on target strengths from individual echoes of the same squid rather than from mean values.

For all measurements, targets were extracted using SonarData's ECHOVIEW program. The single target detection criteria were based on the transmitted pulse length, measurements of target strength of the calibration sphere in the squid mounting setup, and through empirical minimization of the standard deviation of the target strength of individual tethered squid when their depth relative to the transducer's was known and surrounding acoustic clutter was at a minimum. The target strength threshold was set to -55 dB. A "pulse length determination level," the value in decibels below peak value considered when determining the pulse length, or envelope, of a single-target detection, of 12 dB was used. "Normalized pulse lengths," the measured pulse length divided by transmitted pulse length, were required to be between 0.8 and 2.0. The "maximum beam compensation" for correcting for transducer directivity was set to 12 dB. To confirm all sources of scattering within the measured pulse length were from a single target, all samples within this pulse envelope must have had a standard deviation in angular position of less than 3° in both the along and athwart ship directions of the beam. We confirmed that these settings permitted the integrated pulse envelope to enclose the entire body of the squid by observing the standard deviation of the target strength measurements; when the pulse envelope was too short to encompass the entire squid the variation in estimated target strength was extremely high.

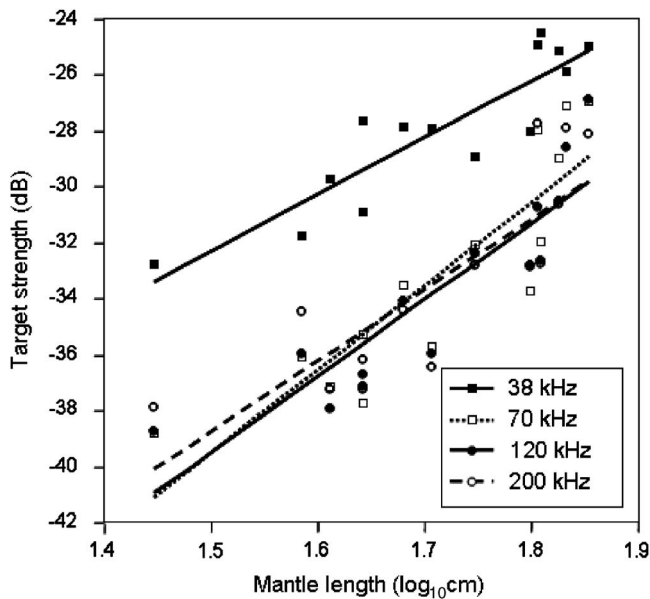


FIG. 3. Dorsal aspect target strength as a function of the log of squid mantle length for each of the four frequencies measured. Standard deviations of the means of all measurements at each frequency for each squid are too small to be shown. Linear regressions through the mean values for each squid are shown. There was no significant difference between the 70, 120, and 200 kHz target strength measurements.

E. *In situ* measurements

In situ measurements of targets that were highly likely to be squid were also made. One night, fishing (jigging) was conducted by two persons while the vessel was at anchor in approximately 30 m of water. Over 15 min, 20 squid were captured and DML measured for each. Targets that met the criteria to be analyzed individually during that time period on the echosounders were extracted and the results compared with those made under controlled circumstances. Results were also compared with *in situ* measurements made while many (15–20) small commercial fishing boats surrounded our vessel and two to three fishermen per boat continuously landed *D. gigas*. Unfortunately, no length measurements were made during this second *in situ* experiment.

III. RESULTS

A. Controlled measurements

The empty squid-holding setup was almost undetectable at all frequencies, and the target strength of the sphere measured in the same arrangement compared well with standard calibration measurements in terms of both the mean and the distribution. This provides convincing evidence that the measurements of squid target strength described in the following are not affected by the hardware setup.

Dorsal-aspect target strength measurements were obtained from 14 live squid ranging in mantle length from 28.0 to 71.5 cm (41.5 to 118.0 cm total length). The average difference in mantle length between successively larger animals was approximately 3.6 cm, and in no case was greater than 10 cm. Mean values of target strength from the dorsal aspect target of each of the 14 live squid are shown in Fig. 3. The standard deviations of the target strength measurements for

each individual squid were extremely small (0.005–0.00008 calculated on the linearized data and converted to decibels) and are not shown. An ANOVA with post-hoc tests corrected using the Bonferroni method for multiple comparisons showed that standard deviation was significantly affected by frequency with each frequency having a higher standard deviation in target strength than the frequencies above it. Increasingly larger squid also had significantly higher standard deviations in target strength at a given frequency.

The relationships between mantle length and target strength can be described by the equations:

$$TS_{38 \text{ kHz}} = 20.4 \log_{10}(\text{DML}) - 62.8, \quad R^2 = 0.81, \quad (1)$$

$$TS_{70 \text{ kHz}} = 29.9 \log_{10}(\text{DML}) - 84.4, \quad R^2 = 0.77, \quad (2)$$

$$TS_{120 \text{ kHz}} = 27.3 \log_{10}(\text{DML}) - 80.5, \quad R^2 = 0.80, \quad (3)$$

$$TS_{200 \text{ kHz}} = 25.4 \log_{10}(\text{DML}) - 76.8, \quad R^2 = 0.69, \quad (4)$$

where TS is the target strength at the frequency noted in the subscript, DML is dorsal mantle length in centimeters, and R^2 is a unit-less descriptor of the goodness of fit of the linear regressions illustrated in Fig. 3 and can be interpreted as the amount of variability in target strength that can be explained by variability in DML. F-tests showed that the slope of each regression was significantly different from zero ($p < 0.05$). If we force the slope of the line to equal 20, expecting the relationship to be related to the cross-sectional area of the squid (McClatchie *et al.*, 2003), the relationships can be described as

$$TS_{38 \text{ kHz}} = 20 \log_{10}(\text{DML}) - 62.0, \quad \Delta R^2 = -0.01, \quad (5)$$

$$TS_{70 \text{ kHz}} = 20 \log_{10}(\text{DML}) - 67.4, \quad \Delta R^2 = -0.09, \quad (6)$$

$$TS_{120 \text{ kHz}} = 20 \log_{10}(\text{DML}) - 67.9, \quad \Delta R^2 = -0.06, \quad (7)$$

$$TS_{200 \text{ kHz}} = 20 \log_{10}(\text{DML}) - 67.6, \quad \Delta R^2 = -0.03. \quad (8)$$

Although this results in a small but significant ($p < 0.05$) decrease in the goodness of fit (ΔR^2) for all frequencies except 38 kHz, these standardized values can be more readily compared to those from the literature.

Of the squid measured, nine were female and five were male, eight were sexually immature, and six were mature. The effect of gender and maturity were assessed on target strength after the effect of length was removed by subtracting $20 \log_{10}(\text{DML})$ from each target strength value. Individual measurements of target strength, rather than the mean, were used in the statistical analysis. There was no significant effect of gender or sexual maturity on the target strengths at any frequency ($p < 0.05$ for each comparison).

The dorsal-aspect target strength values of a single freshly deceased squid were compared to the measurements of the two live squid closest in length (1.5 cm larger and 3.0 cm smaller) using t-tests. Target strength of the dead squid was not statistically significantly different from that of the live squid at any frequency ($p < 0.05$ for each comparison).

TABLE I. Summary of comparisons between various target strength measurements in decibels. N represents the number of measurements. ns is shown for comparisons that did not show a significant difference at the $p < 0.05$ level.

| | Posterior vs dorsal | Body vs dorsal | Body - Pen vs body | Head vs dorsal | Head vs body | Head vs head - Beak | Head vs head - Beak - eyes | Head vs head - Beak - eyes - arms | Head vs cranium | Cranium vs dorsal |
|---------|---------------------|----------------|--------------------|----------------|--------------|---------------------|----------------------------|-----------------------------------|-----------------|-------------------|
| N | 5 | 5 | 4 | 5 | 4 | 4 | 4 | 2 | 4 | 4 |
| 38 kHz | 0.9 | -1.3 | -0.5 | ns | 1.1 | -2.2 | -2.1 | -6.0 | -5.7 | -6.0 |
| 70 kHz | -3.0 | -1.5 | -2.6 | -1.0 | -3.1 | ns | ns | ns | -1.5 | -2.2 |
| 120 kHz | -3.1 | ns | -4.9 | -1.1 | ns | ns | -5.0 | -4.9 | ns | ns |
| 200 kHz | -1.8 | ns | ns | ns | ns | ns | ns | ns | ns | ns |

Posterior end-on measurements of the target strengths of five live squid ranging from 41 to 68 cm in mantle length were measured. Target strengths were compared to the dorsal aspect target strength of the same individuals. The results are shown in the first column of Table I. The posterior-aspect target strength measurements were significantly different at all frequencies with slightly higher target strengths from the posterior aspect relative to the dorsal aspect at 38 kHz and lower target strengths from the posterior aspect for all other frequencies measured. Although standard deviations of posterior-aspect target strength at individual frequencies were small, they were significantly larger than those of dorsal aspect measurements.

After the measurements were made on the live squid, some were sacrificed and immediately had various parts of their bodies measured. A summary of the statistical comparisons of various target-strength measurements is shown in Table I. Any measurement type in the header that is preceded by a minus sign means that this body part was removed from the other body part after a measurement had been made, and a comparison measurement was then repeated. In the body of Table I, a negative value for the observed change in target strength means that the target strength corresponding to the upper row of the header was lower than that corresponding to the lower row, and a positive sign means the opposite. Indicated values represent the mean difference (calculated on linearized data) in target strength for all squid. Any values that were not statistically significant at the $p < 0.05$ level are indicated “ns.”

B. *In situ* measurements

During 15 min of fishing effort by two individuals on 23 March 2007, 20 squid were captured and their dorsal mantle lengths measured. These squid ranged in mantle length from 38.5 to 53.5 cm with a mean mantle length of 46.4 cm. A histogram of the captured squid sizes is shown in Fig. 4. During this same 15 min, a total of 40 718 individual targets fitting the criteria for individual detection [e.g., only one target per acoustic reverberation volume in for each pulse (Sawada *et al.*, 1993)] were detected by the 12°, 38 kHz system and 66 136 were detected by each of the higher frequency, 7° systems. These values correspond to an average detection rate of 45 squid/s at 38 kHz and 74 squid/s at the higher frequencies. The narrower beams had higher detection

rates because they had more than one target in each resolvable volume of water less often than the wider beam of the 38 kHz echosounder.

The mean target strength at each frequency for individually identified targets is shown in Fig. 5. The target strength distribution for single targets at each individual frequency was unimodal. While the standard deviations of the *in situ* target strength measures were substantially larger than those from the controlled experiment, they were still too small to be represented in the graph (< 0.7 in \log_{10} space for all cases, representing a 95% confidence limit of ± 1.4 dB). Also shown in the graph are the target strengths predicted by the unforced regressions developed from the controlled measurement experiment for the mean mantle length measured from the 20 captured squid. The differences between the predicted measurements and the actual measurements were small, with the largest difference a 1.3 dB greater than expected target strength at 38 kHz.

Earlier the evening of 23 March 2007, our stationary research vessel was surrounded by approximately 15–20 small squid fishing boats, each with two to three fisherman continuously landing jumbo squid. Squid were also visible at

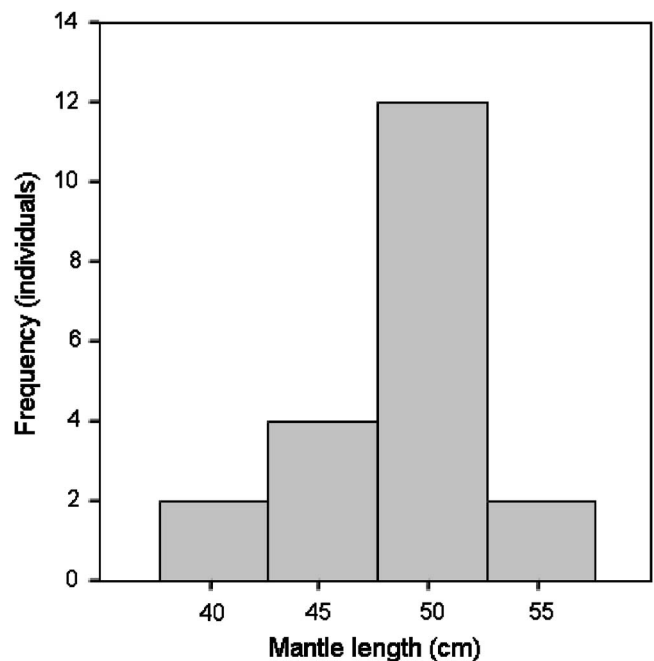


FIG. 4. Histogram of squid mantle lengths for the 20 squid captured during 15 min of *in situ* acoustic measurements.

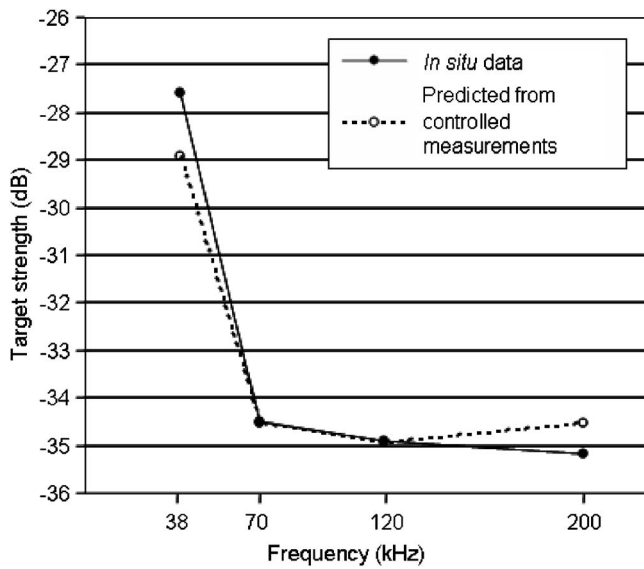


FIG. 5. Mean *in situ* measurements of target strength (closed circles) collected between 23:45 and 00:00 local time on 23 March 2007. Fishing efforts during this same time period resulted in the capture of 20 squid with a mean length of 46.4 cm. Using the unforced regressions for target strength vs length from the controlled measurements, a predicted target strength for each frequency was calculated for this size squid, shown by the open circles.

the surface in high densities. Mean *in situ* measurements of target strength during three, 15 min intervals are shown in Fig. 6. In all measurements, the distribution of target strength was unimodal with a 95% confidence interval of less than ± 2 dB, suggesting a single size class of a uniform target (e.g. one species). Using the unforced regression relationships from the controlled measurement experiment [Eqs. (1)–(4)], the approximate mean squid mantle length that these measurements would equate to are 35, 45, and 55 cm for 2100–2115, 2130–2145, and 2200–2215 h local time, re-

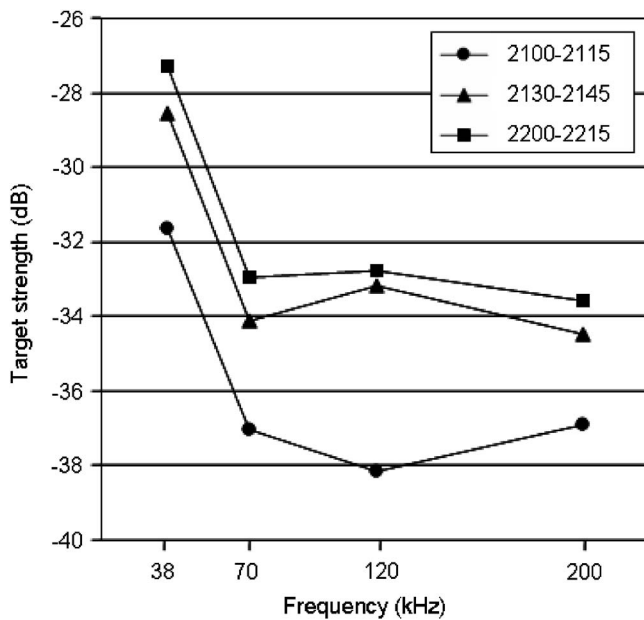


FIG. 6. Mean *in situ* measurements of target strength during three, 15 min intervals on 23 March 2007. During this time, the research vessel was surrounded by approximately 15–20 small squid fishing boats, each with two to three fisherman continuously landing jumbo squid.

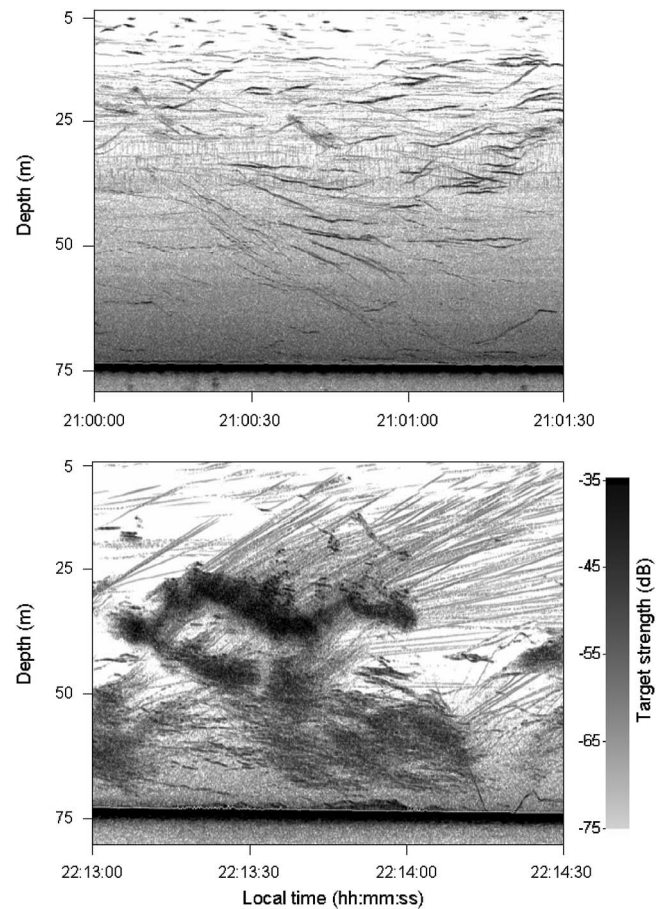


FIG. 7. Two echograms collected from the stationary vessel at 120 kHz for two, 1.5 min intervals on 23 March 2007. The bottom depth was approximately 74 m. Data are expressed with a range compensation function of $40 \log r + 2\alpha r$ to show target strength values for individual targets.

spectively. The distribution of target strength measurements of single targets at each individual frequency was unimodal at all time intervals. However, from 2100 to 2215 h the detection rate of individual targets increased by approximately tenfold from 34 to 361 targets/s on the 7° transducers despite the boat being stationary and no changes in the mean target depth. Echograms of target strength from the beginning (2100 h) of the sampling time when target detection rate was moderate and the end (2213 h) of the sampling time when the detection rate was very high are shown in Fig. 7. It is difficult to determine the number of individual squid detected during these time periods, as opposed to the number of single targets because of our stationary position. Animals likely moved into and out of the beam many times during the observation period. In addition, the conical shape of the transducers' beams means that substantially more area is covered at 75 m (32-m-diam circle for the 38 kHz sensor and 18 m diameter for the higher frequencies) than at 5 m (2.1–1.2 m diameter, respectively) further complicating quantitative assessment from this small sample set.

IV. DISCUSSION

We present controlled measurements of individual *Dosidicus gigas* covering nearly the full size range of the species as sampled by commercial fisheries, as well as *in situ*

TABLE II. Published standardized dorsal aspect target strengths as a function of the square of mantle length compared with the results of the standardized dorsal aspect target strengths obtained in this study.

| Source | Condition | Frequency (kHz) | Slope | Intercept | Min ML (cm) | Max ML (cm) | Species |
|-----------------------------|----------------|-----------------|-------|-----------|-------------|-------------|----------------------------|
| This study | Live | 38 | 20 | -62.0 | 28.0 | 71.5 | <i>Dosidicus gigas</i> |
| Benoit-Bird and Au, 2001 | Anesthetized | 200 | 20 | -62.1 | 1.2 | 4.2 | Various mesopelagic spp. |
| Lee <i>et al.</i> , 1991 | Dead | 200 | 20 | -65.7 | 4.4 | 16.0 | <i>Loligo edulis</i> |
| This study | Live | 70 | 20 | -67.4 | 28.0 | 71.5 | <i>Dosidicus gigas</i> |
| This study | Live | 200 | 20 | -67.6 | 28.0 | 71.5 | <i>Dosidicus gigas</i> |
| This study | Live | 120 | 20 | -67.9 | 28.0 | 71.5 | <i>Dosidicus gigas</i> |
| Kawabata, 2005 | Live | 38 | 20 | -73.1 | 18.0 | 28.4 | <i>Todarodes pacificus</i> |
| Kang <i>et al.</i> , 2005 | Anesthetized | 120 | 20 | -73.5 | 21.0 | 27.0 | <i>Todarodes pacificus</i> |
| Kawabata, 2001 | Live | 38 | 20 | -73.7 | 20.0 | 28.0 | <i>Todarodes pacificus</i> |
| Kang <i>et al.</i> , 2005 | Anesthetized | 38 | 20 | -75.4 | 21.0 | 27.0 | <i>Todarodes pacificus</i> |
| Sawada <i>et al.</i> , 2006 | <i>in situ</i> | 70 | 20 | -81.9 | 18.0 | 37.0 | <i>Gonatopsis borealis</i> |

measurements of free-swimming individuals along with a simultaneously obtained estimate of size.

A. Controlled measurements

Controlled measurements of *D. gigas* dorsal aspect target strength show a strong, positive linear relationship with the log of squid dorsal mantle length. Target strength increases slightly more rapidly with squid length at 70, 120, and 200 kHz than at 38 kHz. Target strength at 38 kHz was also significantly higher by about 5.5 dB than the target strength at the higher frequencies measured. The reasons for this difference are not apparent. Measurements of a standard sphere do not suggest any instrumental or analysis artifacts and the similarity of the response in free-swimming squid *in situ* eliminates potential artifacts from squid capture, mounting, or air entrapment. The target strengths at 70, 120, and 200 kHz were not significantly different from each other.

Relatively few measurements of squid target strength have been made at multiple frequencies. Arnaya *et al.* (1989a) found that two species of squid that they measured after thawing dead specimens had a 5–10 dB higher target strength at 200 kHz relative to 50 kHz. Similarly, Kang *et al.* (2005) found a 0.7–2.5 dB higher target strength at 120 kHz relative to 38 kHz for live specimens of one species also measured by Arnaya *et al.* (1989a). While the squid measured in these two studies were much smaller than the *D. gigas* measured here, there was some overlap in mantle length. As shown in Fig. 3, the patterns in relative target strength we observed were maintained when considering only these animals of smaller body size suggesting that the frequency response of target strength is species specific, not size specific.

Target strength can be normalized by forcing the slope of the regression to 20, representing a relationship with the square of squid mantle length. The intercepts of these relationships [Eqs. (5)–(8)] can then be compared with normalized target strength measurements from other studies, regardless of animal size. Table II provides such a standardized comparison of dorsal-aspect target strengths from studies in the literature that showed (1) a relationship between target strength and mantle length, and (2) a slope of 20° or enough data to refit the curve with a 20° slope. Because most squid in the present study were substantially larger than those in

previous work, only our smaller individuals overlapped with the largest squid measured in other studies, if at all. Despite this, our standardized target strengths were similar to those measured for very small individuals: various mesopelagic species (Benoit-Bird and Au, 2001) and *Loligo edulis* (Lee *et al.*, 1991). Standardized target strengths for *Todarodes pacificus* were 5–10 dB lower than data reported here (Kang *et al.*, 2005; Kawabata, 2001, 2005), and *Gonatopsis borealis* standardized target strengths were 15–20 dB lower (Sawada *et al.*, 2006).

Comparisons of target strength for species with very different size distributions are more difficult when the slope of the relationship between body size and target strength is not simply related to the square of length. To compare our results with those from published studies of squid dorsal-aspect target strength, the target strength of a 28 cm dorsal mantle length squid was calculated using the equations from each of the studies as well as Eqs. (1)–(4) from this study (Table III). For most of the published studies, 28 cm was at or very slightly above the high end of the size distribution measured. For this study, it was the smallest animal measured. This minimized extrapolation to allow the best comparison of data. The target strengths measured here were relatively low when compared with these studies. The target strength values are, however, very similar to the predicted target strengths from those studies that measured target strength *in situ*. All of the curves generated from animals that had been previously preserved (usually frozen followed by thawing for the measurements) had substantially higher predicted target strengths than those obtained from live animals either tethered or *in situ*.

Many measurements of squid target strength in the literature have been made on dead animals. A squid we measured shortly after its death (with no evidence of rigor) did not have significantly different dorsal-aspect target strengths than similarly sized live animals, suggesting that target strength does not change immediately following death, however it may change as a result of preservation or with greater time delay. This result also suggests that the target strength values we obtained were not a result of the behavior of the squid or any alteration of their angle due to swimming against our mounting setup.

The posterior-aspect target strength of five squid was

TABLE III. Target strengths of a 28 cm mantle length squid calculated from the published equations describing the target strength length relationship from various species as well as predicted and actual measurements from this study.

| Source | Condition | Frequency (kHz) | Slope | Intercept | Min ML (cm) | Max ML (cm) | Species | Predicted TS 28 cm ML (dB) | Actual TS 28 cm ML (dB) |
|-------------------------------|----------------|-----------------|-------|-----------|-------------|-------------|------------------------------|----------------------------|-------------------------|
| Arnaya <i>et al.</i> , 1989a | Dead/preserved | 200 | 24.7 | -64.8 | 18.0 | 30.0 | <i>Ommastrephes bartrami</i> | -29.0 | |
| Kaiiwara <i>et al.</i> , 1990 | Dead/preserved | ? | 19.0 | -56.8 | ? | ? | <i>Ommastrephes bartrami</i> | -29.3 | |
| Arnaya <i>et al.</i> , 1989a | Dead/preserved | 200 | 42.0 | -91.5 | 15.0 | 35.0 | <i>Todarodes pacificus</i> | -30.7 | |
| Arnaya <i>et al.</i> , 1989a | Dead/preserved | 50 | 23.4 | -65.0 | 18.0 | 30.0 | <i>Ommastrephes bartrami</i> | -31.2 | |
| Arnaya <i>et al.</i> , 1989a | Dead/preserved | 50 | 47.5 | -101.9 | 15.0 | 35.0 | <i>Todarodes pacificus</i> | -33.2 | |
| This study | Live | 38 | 20.4 | -62.8 | 28.0 | 71.5 | <i>Dosidicus gigas</i> | -33.3 | -32.8 |
| Kawabata, 1999 | <i>in situ</i> | 38 | 40.9 | -94.2 | 18.0 | 24.0 | <i>Todarodes pacificus</i> | -35.0 | |
| Lee <i>et al.</i> , 1992 | <i>in situ</i> | 420 | 33.7 | -88.5 | 3.0 | 17.0 | <i>Loligo edulis</i> | -39.7 | |
| This study | Live | 120 | 25.4 | -76.8 | 28.0 | 71.5 | <i>Dosidicus gigas</i> | -40.0 | -38.9 |
| This study | Live | 200 | 27.3 | -80.5 | 28.0 | 71.5 | <i>Dosidicus gigas</i> | -41.0 | -38.7 |
| This study | Live | 70 | 29.9 | -84.4 | 28.0 | 71.5 | <i>Dosidicus gigas</i> | -41.1 | -37.9 |

measured. Standard deviations of these measurements were small but considerably larger than those for the corresponding measurements of dorsal-aspect target strength. Animals in the anterior aspect measurements had relatively more freedom of movement than animals being measured from the dorsal aspect. We suspect this led to the more variable target strengths, both because the animals presented more angles to the signal but also because they were harder to keep centered in the beam. A small but significant increase in target strength relative to the dorsal aspect of the same individuals was found at 38 kHz. The scattering mechanism for an increase in target strength at 38 kHz is unclear.

We found a 2–3 dB decrease in posterior-aspect target strength relative to dorsal aspect at 70, 120, and 200 kHz. This compares well with changes of 3–5 dB between dorsal and tail-on measurements at 200 kHz found by Lee *et al.* (1991) in *Loligo edulis*. However, they found that the difference in target strength increased with increasing body size. Their study encompassed a total span in mantle length span of about 12 cm. Despite covering a mantle length range of more than 43 cm, we saw no body-size effect on the differences in target strength as a function of orientation.

B. Potential sources of scattering

Many sources of scattering in squid have been proposed including the flesh itself, chitinous pen (gladius) and beak, thickened suckers on the arms (Goss *et al.*, 2001), internal organs especially the liver and reproductive organs (Iida *et al.*, 1996; Tang and Sato, 2006), outstretched fins (Lee *et al.*, 1991), and even their wake (Selivanovsky and Ezersky, 1996). The fins can be ruled out for the results of the current study because the target strengths of a freshly dead squid were not different from those of live animals of the same size and its fins were not outstretched. The wake can be similarly ruled out. Although the liver and reproductive organs have been shown to be the most important contributors to acoustics scattering in squid at much higher frequencies (Iida *et al.*, 1996; Tang and Sato, 2006), our data do not suggest this. Despite extreme differences in gonadal size between mature and immature individuals of similar body size, and between males and females, we found no significant differences in

normalized target strength as a function of gender or sexual maturity, suggesting that the gonads are of limited importance in determining target strength. The effects of the liver could not be investigated in this study.

In order to elucidate the potential contributors to scattering in squid empirically, we measured the target strengths of various parts of several squid immediately after they were studied alive and then sacrificed. Our results suggest that it is indeed the inanimate parts of the squid, not behavior, that causes the backscattering. The results show that both the body and the head strongly contributed to the scattering at all frequencies. At 38 and 70 kHz, the body had a target about 1 dB less than the entire squid, while at 120 and 200 kHz, the target strength of the body was not different from that of the entire squid. Similarly, the head had a target strength 1 dB less than the entire squid at 70 and 120 kHz while the target strengths of the head versus the entire squid at the other frequencies were not different. These results show that the scattering strength of the entire squid is not a simple linear summation of individual parts but does indicate the parts of the animal that could contribute to the backscattering process.

In order to maintain the integrity of the body, only an easily accessible and distinctive part of the pen, the cartilaginous conus, was removed. This had a significant effect on the backscatter at all except the highest frequency suggesting that this dense structure may indeed be an important source of scattering. *Dosidicus* also has a highly muscularized body so the difference in the acoustic impedance of the muscle and seawater may also be an important source of backscatter. The density difference between muscle and seawater is at least 5% and there is a significant difference in sound speed between the muscle and seawater (Arnaya and Sano, 1990).

Many parts of the head showed some effects on scattering. We removed parts of the head successively—beak first, followed by eyes, then arms so we cannot look at the effects of each of these parts on the strength of the reflection but we can examine their potential contribution to the backscattering process. The beak appeared to affect scattering only weakly and only at 38 kHz. The additional removal of the arms had



FIG. 8. Lateral (left) and anterior (right) view of the cranium, or braincase, of the largest squid we measured (71.5 cm mantle length, 118 cm total length).

a stronger effect, also only at 38 kHz. The arms have numerous sucker-cups, each of which has a chitinous ring of teeth, instead of simply being thickened flesh like those of *Loligo* and *Martialia* (Goss *et al.*, 2001). These hardened suckers could thus be an even stronger source of scattering than originally proposed by Goss *et al.* (2001). Removal of the large eyes of the squid had the strongest effect of any removal but only at 120 kHz. Removal of the eyes had no effect on the target strength at any of the other frequencies studied.

Finally, we measured the target strength of only the cranium, or braincase, of *D. gigas*. The braincase is made of very dense cartilage and feels much like stiff plastic (Fig. 8). It contains the statocysts, organs that form the vestibular system. These small dense structures contain statolith crystals made primarily of the aragonite crystal form of calcium carbonate. The target strength of the cranium was 6 dB less than the target strength of the entire squid at 38 kHz. This relative reduction in target strength decreased with frequency to only about 2 dB at 70 kHz and then to 0 dB at higher frequencies. The cranium appears to be the single most important source of acoustic scattering in the head of *D. gigas*. It is remarkable that a single part of the body of this fleshy animal can nearly equal the backscattering strength of the entire animal.

Our results suggest that it should not be surprising that the posterior-aspect target strengths were similar to those from the dorsal aspect. The pen, which seems to be a significant source of backscatter from the dorsal aspect, will not contribute much to the acoustic reflection when the squid is ensouled from the posterior aspect since the cross section perpendicular to the incident signal in this orientation is relatively small. However, the cranium of the head, shown Fig. 8, has a shape that would present a relatively large target to an acoustic signal propagating along the longitudinal axis of the squid from any orientation. The backscatter with the squid from the posterior aspect was probably emanating from the head of the squid.

C. *In situ* measurements

In situ measurements of target strength made during 15 min of concerted fishing effort revealed that the target strengths were remarkably consistent both in amplitude and in frequency response to those predicted by the relationship of length to target strength obtained from animals in controlled conditions. This supports the validity of the tethered

measurements, suggesting that there were no artifacts such as air entrapment in the tethered squid or effects of the mounting rig. Arnaya *et al.* (1989b) found that the target strengths of free-swimming squid were lower than those obtained from the same species that were tethered. Lee *et al.* (1992) similarly found a 10 dB lower target strength *in situ* as opposed to tethered. However, in both cases, the animals in tethered measurements were dead, frozen, and thawed before measurement which may cause significant changes in the material properties of the squid. In addition, the species in these studies showed much more significant changes in target strength with orientation than we observed here. Thus, behavioral effects of swimming and orientation adjustments on the *in situ* target strengths in *D. gigas* may be significantly less than in other species. Our *in situ* results combined with the measurements of the length of the squid validate our measurements of tethered animals. These results suggest that it is appropriate to use our target strength curves for the estimation of squid mean sizes *in situ* from mean target strengths of single targets as well as for biomass estimates from volume scattering by squid of known length.

We can begin by applying these measurements to *in situ* measurements of single targets likely to be squid earlier the same night. During this time period of several hours, squid were visible actively feeding at the surface and appeared to be separated by no more than one to three body lengths, at least within the range of illumination provided by the vessel's deck lights. No other large targets were visible near the surface. Fishermen, two to three to a small boat, were each pulling up squid at a remarkable rate, often exceeding 1 squid per minute. With a typical body mass of 5–10 kg, the rate of squid captured per boat would be consistent with the reported figure of 1.0–1.2 ts in 2–4 h of fishing effort (Morales-Bojorquez *et al.*, 2001). This observation suggests that the density of squid in the immediate area of our stationary vessel was extremely high and the rate at which we were able to detect individual targets supports this. We measured the mean target strength of all large, individually detectable targets (see the above-mentioned single target detection) at each frequency in three, 15 min intervals over a period of 2.25 h. During this time, the rate of target detection increased by an order of magnitude, paralleling an apparent increase in fishing success for *D. gigas*, suggesting the majority of large targets were indeed *Dosidicus*. Measured target strengths also changed during this time. The mean target strengths in each 15 min interval showed the same frequency response seen in our controlled experiments (and our *in situ* measurements combined with squid length measurements), but mean target strength at each frequency increased in each successive 15 min interval. Though no independent measurements of squid length were obtained during any of these sampling intervals, the data strongly suggest that the targets were primarily *Dosidicus* so we can extrapolate from both our controlled experiment and verified *in situ* results to infer that squid size also increased during this time. The mean target strengths would equate to mean squid mantle lengths of approximately 25, 35, and 45 cm at 2100–2115, 2130–2145, and 2200–2215, respectively. These differences are not likely due to changes in behavior because of the limited ef-

fects on target strength we observed as a function of orientation. However, these differences were accompanied by changes in aggregation behavior of squid with dense, distinct groups observed only later in the night. Alternative explanations of the limited results include the mixture of other species. The individual target frequency response and the unimodal and narrow (e.g., small confidence interval) distribution of target strength do not suggest a large number of other targets. However, we cannot rule out that the differences in density over time could cause a target strength bias due to single target detection errors with increasing multiple echoes. Over the sampling period, there were also obvious changes in swimming tracks of individual squid (see examples in Fig. 7). This may prove to be the greatest strength of our ability to observe these squid *in situ*—the possibility of observing their behavior in the wild.

V. CONCLUSIONS

This study presents the first target strength measurements of *Dosidicus gigas*, a large squid that is an ecologically significant predator, a key prey resource, and the target of an economically important fishery. Our results show a strong relationship between squid length and target strength over a wide range of sizes encompassing all but the largest individuals of this species. Individual *Dosidicus* showed little variation in target strength at 70 kHz, 120, and 200 kHz but the target strength at 38 kHz was substantially higher, regardless of squid size (Fig. 5). We found little change in target strength when the squid was dorsal versus when it was tilted completely head down. We also found no difference between live and freshly dead squid.

The scattering mechanisms in squid have been long debated with many possibilities suggested. From our results, we can infer that the reproductive organs, or at least variability in their size and state, had little effect on squid target strength. We empirically tested several hypotheses and found that the body and the head are nearly equally important sources of scattering. Our results support the hypothesis that the pen may be an important source of acoustic scattering in squid. We can also support the hypothesis that the beak, eyes, and arms (probably via the sucker rings) play some role in acoustic scattering though their effects were relatively small and affected scattering only at one of four measured frequencies. We found an unexpected source of scattering in the cranium of the squid which provided a target strength nearly as high as that of the entire squid. Measurements of the material properties of this structure are not available so the mechanism of scattering remains unclear. However, the cranium does house the extremely dense statocysts, or balance organs, that should be further investigated.

Our *in situ* measurements of target strength paired with jigged squid samples support the use of the values presented here in squid stock assessment studies. The ease of detection of these squid and their relatively unique frequency response in target strength suggest acoustic studies of *D. gigas* are feasible. With the substantial target strengths measured, depending on density, it should be possible to detect individual squid to the full depth range of most high-frequency scien-

tific echosounders (up to 1000 m for the 38 kHz Simrad EK60) and to detect aggregations of squid to those depths as well. Based on the scattering mechanisms observed in this and other studies for squid, there is no reason to suspect a change in acoustic properties with this increased depth. Acoustics have been used as an effective sampling method for many fish species but only rarely for invertebrates, especially large, commercially exploited species. A fundamental requirement for application of acoustics to quantitative assessment is knowledge of the target strength distribution of the species in question. These results provide that information.

Even more understanding of the biology of these animals could come from *in situ* observations of squid in relatively shallow water where individual animals can be observed and potentially tracked. Individual target tracks are clearly visible in Fig. 7 with many different diving patterns observable. The results provide an enticing glimpse into the behavioral dynamics of individual squid and with further investigation, the possibility of understanding the behavior of populations of *D. gigas*.

ACKNOWLEDGMENTS

We thank Unai Markaida for determinations of sexual maturity stage. Ashley Booth, Abram Fleishman, Ladd Irvine, Dana Shulman, and Chad Waluk provided assistance in the field. Bonnie Anderson-Becktold, Cyndee Pekar, and Cesar Salinas and his students from CIBNOR provided logistical support. Bob Pedro, the captain of the R/V Pacific Storm, and Willi Schlecter, its engineer, provided invaluable assistance both in preparation for, and during the cruise. Funding was provided by donors to the Oregon State University Marine Mammal Institute. The R/V Pacific Storm was donated by Scot and Janet Hockema. This work was also supported by grants from the National Science Foundation (No. OCE 0526640) and the David and Lucile Packard Foundation to W.F.G.

- Arnaya, I. N., and Sano, N. (1990). "Studies on acoustic target strength of squid V. Effect of swimming on target strength of squid." Bull. Fac. Fish. Hokkaido Univ. **41**, 18–31.
- Arnaya, I. N., Sano, N., and Iida, K. (1989a). "Studies on acoustic target strength of squid. II. Effect of behaviour on averaged dorsal aspect target strength," Bull. Fac. Fish. Hokkaido Univ. **40**, 83–99.
- Arnaya, I. N., Sano, N., and Iida, K. (1989b). "Studies on acoustic target strength of squid. III. Measurement of the mean target strength of small live squid," Bull. Fac. Fish. Hokkaido Univ. **40**, 100–115.
- Benoit-Bird, K. J., and Au, W. W. L. (2001). "Target strength measurements of animals from the Hawaiian mesopelagic boundary community," J. Acoust. Soc. Am. **110**, 812–819.
- Boyle, P., and Rodhouse, P. G. (2005). "Fishing methods and scientific sampling," in *Cephalopods: Ecology and fisheries*, edited by P. Boyle, and P. G. Rodhouse (Blackwell, London), pp. 259–276.
- Foote, K. G., Hanlon, R. T., Iampietro, P. J., and Kvitek, R. G. (2006). "Acoustic detection and quantification of benthic egg beds of the squid *Loligo opalescens* in Monterey Bay, California," J. Acoust. Soc. Am. **119**, 844–856.
- Foote, K. G., Vestnes, G., Maclennan, D. N., and Simmonds, E. J. (1987). "Calibration of acoustic instruments for fish density information: A practical guide," in International Council for the Exploration of the Sea Cooperative Research Report No. 144, Copenhagen, Denmark.
- Fristrup, K. M., and Harbison, G. R. (2002). "How do sperm whales catch squids?," Marine Mammal Sci. **18**, 42–54.
- Gilly, W. F., Markaida, U., Baxter, C. H., Block, B. A., Boustany, A.,

- Zeidberg, L., Reisenbichler, K., Robison, B., Bazzino, G., and Salinas, C. (2006). "Vertical and horizontal migrations by the jumbo squid *Dosidicus gigas* revealed by electronic tagging," *Mar. Ecol.: Prog. Ser.* **324**, 1–17.
- Goss, C., Middleton, D., and Rodhouse, P. G. (2001). "Investigations of squid stocks using acoustic survey methods," *Fish. Res.* **54**, 111–121.
- Iida, K., Mukai, T., and Hwang, D. (1996). "Relationship between acoustic backscattering strength and density of zooplankton in the sound scattering layer," *ICES J. Mar. Sci.* **53**, 507–512.
- Jefferts, K., Burczynski, J., and Percy, W. G. (1987). "Acoustical assessment of squid (*Loligo opalecens*) off the central Oregon coast," *Can. J. Fish. Aquat. Sci.* **44**, 1261–1267.
- Kang, D., Mukai, T., Iida, K., Hwang, D.J., and Myoung, J.G. (2005). "The influence of tilt angle on the acoustic target strength of the Japanese common squid," *ICES J. Mar. Sci.* **62**, 779–789.
- Kawabata, A. (1999). "Measurement of the target strength of the Japanese flying squid, *Todarodes pacificus* Steenstrup," *Bull. Tohoku Nat. Fish. Res. Inst.* **61**, 29–40.
- Kawabata, A. (2001). "Measurement of the target strength of live squid, *Todarodes pacificus* Steenstrup, in controlled body tilt angle," *Bull. Tohoku Natl. Fish. Res. Inst.* **64**, 61–67.
- Kawabata, A. (2005). "Target strength measurements of suspended live ommastrephid squid, *Todarodes pacificus*, and its application in density estimations," *Fish. Sci.* **71**, 63–72.
- Lee, K. T., Liao, C. H., Shih, W. H., and Chyn, S. S. (1992). "Application of dual-beam acoustic survey techniques to assess the size distribution of squid, *Loligo edulis*," *J. Fish. Soc. Taiwan* **19**, 25–34.
- Lee, K. T., Shih, W. H., Liao, C. H., and Wang, J. P. (1991). "Studies on the hydroacoustic scattering properties of individual squid, *Loligo edulis*," *J. Fish. Soc. Taiwan* **18**, 215–225.
- Lipinski, M. R., and Prowse, M. (2002). "Direct hydroacoustic observations of chokka squid *Loligo vulgaris reynaudii* spawning activity in deep water," *S. Afr. J. Mar. Sci.* **24**, 387–393.
- Lipinski, M. R., and Underhill, L. (1995). "Sexual maturation in squid: Quantum or continuum?," *S. Afr. J. Mar. Sci.* **15**, 207–223.
- Markaida, U., and Sosa-Nishizaki, O. (2001). "Reproductive biology of jumbo squid *Dosidicus gigas* in the Gulf of California, 1995–1997," *Fish. Res.* **54**, 63–82.
- Markaida, U., and Sosa-Nishizaki, O. (2003). "Food and feeding habits of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico," *J. Mar. Biol. Assoc. U.K.* **83**, 507–522.
- McClatchie, S., Macaulay, G., and Coombs, R. F. (2003). "A requiem for the use of 20logLength for acoustic target strength with special reference to deep-sea fishes," *ICES J. Mar. Sci.* **60**, 419–428.
- Misund, O. A. (1997). "Underwater acoustics in marine fisheries and fisheries research," *Rev. Fish Biol. Fish.* **7**, 1–34.
- Morales-Bojorquez, E., Cisneros-Mata, M. A., Nevarez-Martinez, M. O., and Hernandez-Herrera, A. (2001). "Review of the stock assessment and fishery biology of *Dosidicus gigas* in the Gulf of California, Mexico," *Fish. Res.* **54**, 83–94.
- Nevarez-Martinez, M. O., Mendez-Tenoria, F. J., Cervantes-Valle, C., Lopez-Martinez, J., and Anguiano-Carrasco, M. L. (2006). "Growth, mortality, recruitment, and yield of the jumbo squid (*Dosidicus gigas*) off Guaymas, Mexico," *Fish. Res.* **79**, 38–47.
- Nigmatullin, C. M., Nesis, K. N., and Arkhipkin, A. I. (2001). "A review of the biology of the jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae)," *Fish. Res.* **54**, 9–19.
- Sanchez-Juarez, E. (1991). "Preliminary estimate of the size of the adult population and spawning biomass of jumbo squid *Dosidicus gigas* in the Exclusive Economic zone of the Mexican Pacific," (Spanish Translation "Estimacion preliminar del tamano de la poblacion adulta e biomasa reproductora de calamar gigante *Dosidicus gigas* en la Zona Economica Exclusiva del Pacifico Mexicano, en diciembre de, 1990), Secretaria de Pesca, Instituto Nacional de la Pesca, Informe Tecnico, CRIP, El Sauzal. B.C., Mexico, pp. 1–13.
- Sawada, K., Furusawa, M., and Williamson, N. J. (1993). "Conditions for the precise measurement of fish target strength *in situ*," *Fish. Sci.* **20**, 15–21.
- Sawada, K., Takahashi, H., Abe, K., and Takao, Y. (2006). "In situ measurement of target strength, tilt angle, and swimming speed of Boreopacific gonate squid (*Gonatopsis borealis*)," *J. Acoust. Soc. Am.* **120**, 3107.
- Selivanovsky, D., and Ezersky, A. (1996). "Sound scattering by hydrodynamic wakes of sea animals," *ICES J. Mar. Sci.* **53**, 377–381.
- Shchetinnikov, A. S. (1988). "Feeding and food relations of abundant squids in southeastern part of the Pacific Ocean," *Autoreferat Dissertatsii na Soiskani Uchenoj Stepeni Kandidata Biologicheskikh* (Nauka, Moscow).
- Tang, Y., and Sato, M. (2006). "Acoustical imaging of nonbladdered animals using underwater acoustic camera," *J. Acoust. Soc. Am.* **120**, 3058.