Single-target echo detections of jellyfish

Andrew S. Brierley, Bjørn Eric Axelsen, David C. Boyer, Christopher P. Lynam, Carol A. Didcock, Helen J. Boyer, Conrad A. J. Sparks, Jennifer E. Purcell, and Mark J. Gibbons

Acoustic target-strength (TS) measurements are presented for tethered and free-swimming individual Chrysaora hysoscella (Scyphozoa) and Aequorea aequorea (Hydrozoa) medusae in Namibian waters. Tethered individual C. hysoscella (17–54 cm total umbrella diameter) and A. aequorea (19–28 cm total umbrella diameter) were ensonified at 38 kHz using a portable echosounder. Mean TS values for individual medusae at this frequency ranged from −67.3 to −52.8 dB for C. hysoscella and from −65.4 to −50.1 dB for A. aequorea. There was a positive relationship between medusa diameter and TS for both species. TS of individual medusae varied cyclically over time by about 15 dB, probably because of the periodic contraction of the medusae whilst swimming. C. hysoscella was parasitized by hyperid amphipods (maximum infestation >1800 parasites per medusa). A fluid-cylinder scattering model was used to determine the expected backscatter from the parasites, and it suggested that even at the highest observed level of infestation the jellyfish itself remained the major contributor to total backscatter at 38 kHz. Single-target echoes from targets identified by trawling as medusae were obtained from vessel-mounted echosounders at 18, 38, 120, and 200 kHz. Triangulation between echosounder beams to identify targets detected simultaneously at all four frequencies increased confidence that echoes were in fact from single targets. The 38-kHz TS values from free-swimming medusae corresponded with values obtained from tethered animals at the same frequency, providing strong evidence that the TS estimates were robust. TS values at all four frequencies (Chrysaora hysoscella mean umbrella diameter 41 cm, TS at 18 kHz = −60.0 dB, 38 kHz = −65.5 dB, 120 kHz = −68.0 dB, and 200 kHz = −70.5 dB. Aequorea aequorea mean inner-umbrella diameter 6.5 cm, TS at 18 kHz = −66.0 dB, 38 kHz = −66.5 dB, 120 kHz = −71.5 dB, and 200 kHz = −73 dB) were consistent with previously published data. Given these robust TS estimates, the possibility may now exist for multi-frequency identification and evaluation of these jellyfish species in some circumstances, and for the use of acoustic-survey techniques to estimate jellyfish abundance.

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Introduction

Jellyfish abundance appears to have increased in recent years in several pelagic ecosystems worldwide (e.g. Brodeur et al., 1999; 2002; Mills, 2001; Parsons and Lalli, 2003). It has been suggested that these increases are in some cases symptoms of “regime shifts” that have followed either climate change or increased commercial exploitation of pelagic finfish species, or both. Whatever the cause of jellyfish population blooms, it is desirable to be able to evaluate jellyfish population sizes quantitatively in order to monitor population changes over time. Jellyfish are important consumers of zooplankton and ichthyoplankton, and may detrimentally affect fish populations (Purcell and Arai,
Knowledge of jellyfish distribution and abundance is therefore of economic as well as ecological importance. Netting surveys have been used successfully in some locations to provide semi-quantitative estimates of jellyfish abundance (Brodeur et al., 1999; Purcell, 2003). In other locations, however, netting surveys have proved less informative either because the traditional plankton nets available have been too small to sample very large medusae (Fearon et al., 1991), or because the medusae occurred in such large numbers that they clogged and burst the nets (Brierley et al., 2001). Acoustic-survey techniques are used to evaluate the numerical abundance and biomass of many pelagic fish species and some crustacean zooplankton. Tank measurements have shown that jellyfish can also be detected acoustically (Monger et al., 1998) despite their lack of hard structures (such as shells or exoskeletons) or gas inclusions (such as swimbladders or vacuoles). Acoustic surveys at sea have detected jellyfish (Purcell et al., 2000; Brierley et al., 2001), but the quantitative nature of these observations has been questioned. Because of the physical structure and composition of jellyfish, echoes from them are widely presumed to be weak, and it is commonly thought that echoes from jellyfish are likely to be masked by the contribution that non-gelatinous zooplankton make to total water column backscatter. In order for jellyfish to be evaluated quantitatively in the field using acoustic techniques, accurate target strength (TS, the factor relating echo intensity to animal size) data are required. Here, we present TS estimates for medusae of two jellyfish species common in the Namibian Benguela ecosystem determined by single-target detections of tethered and free-swimming animals. TS estimates derived from data arising from echo detections of single animals are less likely to be biased, and therefore to be more accurate than TS estimates determined using water column, echo-integration techniques. This is because echoes from identified single targets are less likely to be contaminated with echo energy backscattered from the “background” zooplankton community.

Materials and methods

In September 2001, data were collected during and in association with a 7-day cruise on the RV “Dr Fridtjof Nansen” that sailed from and returned to Walvis Bay, Namibia. Two approaches were taken to obtain echo detections of single jellyfish. In the first, single medusae were tethered beneath a small boat and ensonified at 38 kHz using a SIMRAD EY500 portable echosounder. In the second, single-target echo detections from free-swimming medusae were identified from data collected simultaneously at 18, 38, 120, and 200 kHz using SIMRAD EK500 echosounders on board the research vessel. The research vessel’s echosounders were calibrated using standard targets at the end of the cruise.

Tethered medusae

Individual Chrysaora hysoscella and Aequorea aequorea were obtained by dipnetting from a small boat in the vicinity of Walvis Bay, Namibia. Great care was taken to keep the net-caught medusae immersed in water at all times prior to acoustic measurements because we did not want to risk air bubbles, which are very strong acoustic targets, becoming attached to the jellyfish and contaminating the biological target. Medusae were transferred from the dipnet to a large plastic bucket in the water before the bucket was lifted into the small boat. A total of four C. hysoscella and seven A. aequorea were collected.

One by one, each medusa, still immersed in water, was attached by a loop of monofilament line passed dorsoventrally through its centre to a second length of monofilament line that was fixed at one end to the side of the small boat. A 38.1-mm diameter tungsten-carbide, calibration sphere was attached to the free end of the line, and the line, calibration sphere, and medusa were deployed over the side of the boat. The calibration sphere served to keep the line vertical in the water, to pull the medusa beneath the transducer, and to provide a standard reference against which all echoes could be calibrated. With the line in place, the medusa was approximately 8 m below the transducer face, well beyond the near-field boundary which is at approximately 1.5 m for the ES38-12 transducer. The calibration sphere was a further 8 m below the medusa.

Echoes were recorded from each medusa for a period of about 20 min (ping interval ca. 0.3 s). After this time, the medusa was recovered and the total umbrella diameter was measured to the nearest 0.5 cm. The diameter of the thick central disk of the tethered A. aequorea was also measured in order to determine a relationship between inner- and outer-umbrella diameters. This was necessary so that comparisons between the sizes of whole, dipnetted, and damaged trawl-caught A. aequorea could be made (see “Free-swimming medusae” section below).

Single-target echo detections from each medusa as determined by the EY500 single-target echo-detection algorithm were filtered to retain only those echoes that were from targets less than 3° off the central axis of the transducer. We were confident that these detections were in fact from medusa single targets because the detections came from the depth at which we knew the single medusa was suspended on the line. All medusa single-target TS (target strength) values were calibration-corrected with reference to the difference between the observed TS from the calibration sphere and that expected from the sphere under the prevailing hydrographic conditions, as determined by a CTD cast prior to the acoustic observations. The mean corrected TS for each medusa was computed as the mean (in the linear domain) compensated TS for these calibration-corrected echoes.

C. hysoscella is often parasitized by the amphipod Hyperia medusarum off Namibia (Buecher et al., 2001). All amphipod parasites infesting the tethered C. hysoscella were collected after the acoustic measurements on the tethered individual had been made. Total lengths of the amphipods were measured to the nearest 0.1 mm under...
Doubts have been raised as to the reliability of the EK500 continuous acoustic record corresponding to the section of extracted at all four frequencies from that portion of the total catch, calibrated single-target echo detections were in situ this shortcoming, Demer the true TS for a single organism. In an effort to overcome an erroneously identified individual would be higher than target echo. If that were the case, then the TS reported for more closely located targets as originating from a single-target would have exhibited had it been detected on axis, were then further filtered to select those that were also detected at 200 kHz. The 200-kHz transducer was a single-beam transducer and was unable to determine the angular location of single targets. We knew the position of the 200-kHz transducer relative to the other frequency transducers, however, and were able to use target angular-position data provided by the split-beam transducers to determine where in the 200-kHz beam the target would have been. We were then able to use this position information along with knowledge of the beam pattern of the 200-kHz transducer to manually compensate the 200-kHz data to provide equivalent on-axis TS estimates (SIMRAD, 1996). Histograms of single-target echo intensities for targets detected at all four frequencies were constructed, as were histograms of medusa diameter for each trawl.

Free-swimming medusae

Throughout the first six days of the cruise, a series of pelagic trawls were undertaken to catch jellyfish. Fishing activities essentially followed those described for a previous investigation of jellyfish in Namibian waters from the RV “Dr Fridtjof Nansen” (Brierley et al., 2001; Buecher et al., 2001) and so the details are not repeated here. A typical trawl lasted for around 5 min. Species composition, and size and mass distributions of species, were determined for all trawls. Chrysaora hysoscella were recovered intact from the trawl in most cases but the fragile outer umbrella of Aequorea aequorea was usually missing.

The research vessel’s EK500 echosounders were run continuously throughout the cruise and multi-frequency acoustic data were available in association with each trawl. The transducers (split-beam 18, 38, and 120 kHz, and single-beam 200 kHz) were located close together on a drop keel and had overlapping sampling volumes. For those trawls where medusae contributed >99.5% by mass to the total catch, calibrated single-target echo detections were extracted at all four frequencies from that portion of the continuous acoustic record corresponding to the section of the water column (time and depth) sampled by the net. Doubts have been raised as to the reliability of the EK500 single-target detection algorithm (Soule et al., 1995), and it has been suggested that in some instances the algorithm may incorrectly identify echoes originating from two or more closely located targets as originating from a single-target echo. If that were the case, then the TS reported for an erroneously identified individual would be higher than the true TS for a single organism. In an effort to overcome this shortcoming, Demer et al. (1999) proposed a multi-frequency technique to improve in situ single-target identification. Their technique uses information on the relative positions of multiple transducers and the reported angular positions of single targets, degrees off the central axis of the transducer athwart and along ship, to determine, using geometry, if a single target identified in one echosounder beam was also detected at the corresponding position in another beam. The rationale behind the technique is that if multiple independent frequencies all identify an echo from the same location as originating from a single target, then the probability that the target is in fact a single target is high. We used Matlab to search through all single-target detections from the split-beam transducers (18, 38, and 120 kHz) corresponding to each trawl where medusa catches were >99.5% by mass, and to collate those that matched between frequencies on time, depth, and angular position. The compensated TS values, compensated by the EK500 software to provide the TS that the target would have exhibited had it been detected on axis, were then further filtered to select those that were also detected at 200 kHz. The 200-kHz transducer was a single-beam transducer and was unable to determine the angular location of single targets. We knew the position of the 200-kHz transducer relative to the other frequency transducers, however, and were able to use target angular-position data provided by the split-beam transducers to determine where in the 200-kHz beam the target would have been. We were then able to use this position information along with knowledge of the beam pattern of the 200-kHz transducer to manually compensate the 200-kHz data to provide equivalent on-axis TS estimates (SIMRAD, 1996). Histograms of single-target echo intensities for targets detected at all four frequencies were constructed, as were histograms of medusa diameter for each trawl.

Linking TS with medusa size

Finally, we sought to associate distributions of medusae size with distributions of TS. Our TS data were sparse (small sample sizes) and modes in the TS distributions were not always obvious. We used a Bayesian Maximum-Entropy (MaxEnt) technique that works well with sparse data (Sivia, 1996; Brierley et al., 2003) to fit an optimal number of normal distributions to the observed TS—frequency and diameter—frequency distributions for each species, and to identify modes in distributions. The “optimal” number of normal distributions was determined in the conventional, objective Bayesian manner by considering the evidence for the posterior probability distribution. In the case of the TS data, we fit Gaussians to the distributions of TS at all four frequencies, seeking the best distributions that would fit, in four dimensions, the equivalent observations at 18, 38, 120, and 200 kHz simultaneously.

Results

Tethered medusae

Echoes from the standard target and the suspended medusae were clearly visible on the echogram once the monofilament line had stabilized beneath the transducer. They were recorded from 11 individual medusae (seven A. aequorea and four C. hysoscella). One A. aequorea became disconnected from the line on recovery and we were unable to
measure its size. For the six A. aequorea measured, the relative sizes of the inner and outer umbrella were described by the relationship:

\[ \text{outer diameter} = (0.95 \times \text{inner diameter}) + 14.0 [r^2 = 0.69]. \]  

The 38-kHz TS of single medusa of both species varied cyclically by about 15 dB (Figure 1). There was, however, a significant (at 10%) positive relationship between umbrella diameter and the observed mean TS for C. hysoscella (ANOVA, n = 4, F = 12.96, p = 0.069; Figure 2a). The relationship between log medusa outer diameter and mean TS at 38 kHz for A. aequorea was also positive (Figure 2b) but was not significant. The relationship between log outer diameter and maximum TS at 38 kHz was, however, significant for A. aequorea at the 10% level (ANOVA, n = 6, F = 5.74, p = 0.075).

Amphipod parasites (Hyperia medusarum) were collected from three of the four C. hysoscella, with large medusae generally having more and larger parasites than small medusae (see Table 1). Mean amphipod lengths are given in Table 1 and distributions of length are given in Figure 3. Amphipod TS was predicted on the basis of length using a fluid-cylinder model (Stanton, 1989) parameterized with sound speed and density contrast \( Z_{1.04} \), sound velocity \( Z_{1504} \) ms\(^{-1}\) and diameter of cylinder = length/6 (Trevorrow and Tanaka, 1997). Modelled variation in amphipod TS with length is shown graphically in Figure 4. For the most heavily parasitized C. hysoscella, the modelled backscatter from the amphipods was less than half the observed TS (Table 1). For the other C. hysoscella individuals, backscatter from the amphipod community was more than an order of magnitude less than the total backscatter. The corrected TS—size relationship for C. hysoscella (Figure 2a) was roughly similar to the uncorrected relationship, but statistical analysis was not attempted because of the low sample size since parasites were only sampled from three medusae.

Free-swimming medusae

From the total of 72 trawls fished during the cruise, catches in 23 contained more than 99.5% jellyfish by mass and contained few or no fish viz. less than 0.26% by mass. Of these, 15 were dominated by A. aequorea and eight by C. hysoscella. Echograms corresponding to A. aequorea-dominated and C. hysoscella-dominated trawls, respectively, are shown in Figure 5. For the 23 jellyfish-dominated trawls combined, a total of 3489 single-target echo detections were made at 38 kHz. As filtering was undertaken to match detections between an increasing number of echosounder frequencies, an increasing number of single targets were rejected: 235 targets matched for 38 and 120 kHz combined, and 79 matched for 38, 120, and 18 kHz combined. Of these 79 targets, 46 were also detected at 200 kHz, giving 23 simultaneous single-target detections at all four frequencies for each species of jellyfish. Thus, it seems that only as few as 1.3% of detections at 38 kHz reported as “single targets” were actually single according to our multi-frequency triangulation criteria (cf Ona et al., 1999). Histograms of the distribution of the compensated TS values at all four frequencies are given by species for the targets common at all frequencies in Figure 6a, b, along with histograms of medusa diameter.

![Figure 1. Chrysaora hysoscella. Example of the cyclical variation in TS of an individual medusa over time.](https://academic.oup.com/icesjms/article-abstract/61/3/383/671936)
Bayesian inferences of diameter and TS distributions

The most probable Bayesian Maximum-Entropy inferences of the size distributions for sampled populations of both jellyfish species are shown in Figure 7. Both size distributions are essentially unimodal, with peaks at 41 cm for *C. hysoscella* and 6.5 cm for *A. aequorea*. Examples of these inferred TS distributions are shown in Figure 8. The most probable TS distributions for *C. hysoscella* were unimodal and centred on TS = −60.0 dB at 18 kHz, TS = −65.5 dB at 38 kHz, TS = −68.0 dB at 120 kHz, and TS = −70.5 dB at 200 kHz. The TS distributions for *A. aequorea*, however, were markedly bimodal, with peaks at −66.0 and −52.5 dB at 18 kHz, −66.5 and −53.5 dB at 38 kHz, −71.5 and −55.5 dB at 120 kHz, and −73.0 and −58.5 dB at 200 kHz.

Discussion

The data from the tethered medusae show clearly that *A. aequorea* and *C. hysoscella* can be detected acoustically at 38 kHz. The data also suggest that for both species, the TS at 38 kHz increases with umbrella diameter. The TS for individual jellyfish of both species varied cyclically by as much as 15 dB (see Figure 1). Mutlu (1996) reported a similar variation for individual *Aurelia aurita* in cages and attributed the variation to the regular contraction and dilation of the umbrella as the medusae swim. Spectral analysis of the TS time-series data presented here in Figure 1, which is typical of the observations we made for all suspended medusae, suggests that TS reaches a maximum value about every 15 s. This periodicity is very similar to that reported by Mutlu (1996). We were unable to observe the tethered medusae because the water clarity was very poor, but observations of near-surface medusae from the deck of the RV “Dr Fridtjof Nansen” revealed that both *C. hysoscella* and *A. aequorea* exhibited umbrella contractions at approximately this rate. Modelling studies suggest that umbrella contractions will lead to large variations in TS of individual medusae (Monger et al., 1998; J. Horne pers. commun., June 2002).

Infestation of *C. hysoscella* by *Hyperia medusarum* appeared to increase, both in the number and size of parasites, with increasing medusa size. The number of amphipods recovered from dipnetted individuals was about an order of magnitude higher than the numbers observed from trawl-caught medusae (Buecher et al., 2001). This suggests either that parasites are shed from the medusae...
during trawling or that the medusae in the eutrophic waters of Walvis Bay had higher infestation rates than those in the open ocean (medusae in Walvis Bay showed some deterioration of the oral arms, which we did not see in the samples collected offshore). As a consequence of the positive relationship between medusa size and the level of parasitism, backscatter from the parasites also increased with increasing medusa size. However, even at the very highest of infestation rates, the backscatter from the medusa itself remained dominant (Table 1).

The intensities of the single-target echoes at 38 kHz, as identified by between-beam triangulation, from individual free-swimming *A. aequorea* and *C. hysoscella* were of a magnitude similar to those obtained from the tethered individuals. This provides strong support for our application of the multi-frequency method of Demer et al. (1999) for single-target identification. Inspection of Figures 6a and 7a reveals a unimodal distribution of *C. hysoscella* medusae umbrella diameter centred on 41 cm. The most probable inference of TS distributions were also unimodal (see the

![Figure 3](https://academic.oup.com/icesjms/article-abstract/61/3/383/671936)

*Figure 3. Hyperia medusarum. Histograms of amphipod lengths on medusae: the numbers refer to medusae in Table 1.*

![Figure 4](https://academic.oup.com/icesjms/article-abstract/61/3/383/671936)

*Figure 4. Hyperia medusarum. Modelled variation of amphipod TS at 38 kHz with length.*
Figure 5. Some examples of raw echograms corresponding to trawls in which the catch was dominated by *Aequorea aequorea* (left panels) and *Chrysaora hysoscella* (right panels). The echograms are 18 kHz (top), 38 kHz (second from top), 120 kHz (third from top), and 200 kHz (bottom). The colour scale is in 3-dB increments from $-80$ to $-44$ dB. The vertical lines on the echograms are 0.25-nmi increments; the horizontal lines are 50 m apart. The horizontal boxes on the echograms indicate the region of the water column sampled by the net.
example in Figure 8a). The size–TS relationship at 38 kHz (TS = −65.5 dB) falls about 6 dB below the relationships between size and mean TS for tethered *C. hysoscella* shown in Figure 2a. We should expect the mean TS of free-swimming medusae to be less than the mean TS for tethered animals because the tethered animals would all have been orientated dorsal surface upwards. Free-swimming medusae, by contrast, could have been in any orientation and some echoes will, without doubt, come from side-aspect and ventral-aspect ensonifications. The mean TS at 38 kHz determined by Brierley *et al.* (2001) for *C. hysoscella* from data collected in 1999 is plotted over data from the present analysis in Figure 2a. The 1999 mean is substantially higher (−46.6 dB) than the present values and this is perhaps indicative of the 1999 acoustic data being contaminated by an echo contribution from non-jellyfish targets that were not sampled by the trawl net. The inferred peak in single-target TS at 120 kHz for *C. hysoscella* was −68 dB (see Figure 8a). Previous echo-integration work on *C. hysoscella* has suggested that the TS of this species is stronger by 3.5 dB at 38 kHz than at 120 kHz (Brierley *et al.*, 2001), and the present data, where the difference between frequencies is 2.5 dB, are in good agreement with that suggestion. Brierley *et al.* (2001) were not able to present a robust TS estimate for *C. hysoscella* at 18 kHz because the relationship they obtained using the comparison method between net catch and the integrated-echo intensity at that frequency was not statistically significant. Present observations suggest that TS at 18 kHz for *C. hysoscella* is probably 8 dB higher than at 38 kHz. Present observations also suggest that the modal TS at 200 kHz for *C. hysoscella* of the size we encountered is −70.5 dB.

The size frequency distribution of *Aequorea aequorea* in the trawl samples from which the *in situ* single-target TS
detections were obtained for that species is essentially unimodal (Figures 6b and 7b). The TS histograms for this species were however bimodal. From the data for tethered individuals, and noting that in Equation (1) the modal diameter in the trawled samples equates to a log outer diameter of 1.30, an A. aequorea of central-disc diameter 6.5 cm might be expected to have a TS of about −64 dB at 38 kHz (see Figure 2b). The 38-kHz TS histogram has a mode at −66.5 dB. Following the same argument given for the expected difference between mean TS for tethered and in situ animals in relation to C. hysoscella, it is reasonable to infer that the TS mode of −66.5 dB at 38 kHz does correspond to the 6.5-cm inner-umbrella diameter A. aequorea size class. This TS–diameter pairing is plotted on Figure 2b and falls very close to the lower points on the relationship between mean TS and the diameter obtained from the tethered organisms. Brierley et al. (2001) reported TS values at 18 and 120 kHz for A. aequorea of about 2 dB less than the TS at 38 kHz. Figure 8b shows modal TS values at −66.0 dB for A. aequorea at 18 kHz and −71.5 dB at 120 kHz, and we suggest that these peaks correspond to the modal A. aequorea size class. Our data also suggest a TS of −73.0 dB at 200 kHz for A aequorea. Previous acoustic observations of A. aequorea (>Alvares Columbo et al., 2003) and the morphologically similar congeneric species, that may even be the same species, A. victoria (Monger et al., 1988), have suggested a mean TS of −64.15 dB at 200 kHz, size of jellyfish not reported, and of −67.3 dB for an individual with a radius of 18.2 mm. These values lie within the tail of the most probable Gaussian distribution of TS reconstructed using the MaxEnt technique from our present study, and our data are therefore not inconsistent with previous findings.

Assuming that the diameter–TS correspondences we propose for A. aequorea are correct, we have then to explain the remaining mode in the TS histograms. Although we were careful to include only data from trawls where catches were not contaminated by fish, it is possible that fish were present in the water column but managed to evade the net. We suggest, therefore, that the unallocated peaks in TS shown in Figure 8b, peaks that are all higher than the TS peaks for A. aequorea, are due to fish that we did not catch with the net.

Figure 7. Bayesian-Maximum-Entropy inferences of medusae-diameter distributions for Chrysaora hysoscella (a) and Aequorea aequorea (b). The error bars are one standard deviation derived by sampling 20 times from the posterior distribution.

Figure 8. Examples of Bayesian MaxEnt inferences on the distribution of TS of Chrysaora hysoscella (a) and Aequorea aequorea (b). These examples show 18 kHz in the z plane. Contour lines show 5, 10, 15 ..., 95 percentiles of the total distribution.
In conclusion, our observations of single-target TS values for both *C. hysoscella* and *A. aequorea* obtained from tethered and *in situ* individuals are fairly consistent. This is particularly so for *A. aequorea*, and for this species, the TS values determined here are also very similar to those determined previously from aggregations of medusae (Brierley et al., 2001). The present observations for *C. hysoscella* are internally consistent between methods but result in estimates of TS that are somewhat lower than those reported previously. *A. aequorea* tends to occur further offshore and in higher numerical densities than *C. hysoscella*. Offshore waters tend to contain lower concentrations of crustacean zooplankton (Boyer et al., in prep.), and TS estimates from the comparison method for jellyfish in this region (*A. aequorea*) are less likely to be biased by echo contributions from zooplankton that were not sampled by the jellyfish trawls. Conversely, in inshore waters, a high concentration of unsampled zooplankton would raise the total integrated-echo intensity, and misallocation of this echo contribution to low numerical densities of jellyfish (*C. hysoscella*) would serve to bias the TS for the jellyfish upwards; hence the difference between TS for *C. hysoscella* reported here compared with the value reported in the 1999 study (Brierley et al., 2001).

The present study has resulted in knowledge of multi-frequency TS for two common medusae in the Benguela ecosystem. This knowledge may improve our capability to identify jellyfish in fishery acoustic-survey data. This in turn may lead to greater accuracy in the assessment of pelagic fish stocks in regions where jellyfish are very abundant, may reduce the number of instances when pelagic trawls are damaged following inadvertent capture of large tonnages of jellyfish medusae, and may enable routine acoustic-survey data to be analysed to extract information on the distribution and abundance of jellyfish. This in turn may lead to an improved knowledge of seasonal variation in the distribution and abundance of a group that is of major ecological importance in the Benguela ecosystem.

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