Determination of Composition and Vertical Structure of Fish Communities Using in situ Measurements of Acoustic Target Strength

M. Barange, I. Hampton, S.C. Pillar and M.A. Soule

Sea Fisheries Research Institute, Private Bag X2, 8012 Rogge Bay, Republic of South Africa

Barange, M., I. Hampton, S.C. Pillar, and M.A. Soule. 1994. Determination of composition and vertical structure of fish communities using in situ measurements of acoustic target strength. Can. J. Fish. Aquat. Sci. 51: 99–109.

A split-beam echo-sounder was used to estimate in situ acoustic target strengths (TS) of fish from a number of different fish communities on the South African continental shelf. The TS and size distributions (obtained by aimed trawling) were used to describe the size structure and vertical distribution of these communities. TS distributions obtained from several monospecific populations of juvenile Cape hake (*Merluccius capensis*), the dominant species present, were self-consistent, and there was good correspondence between modes in the TS and length distributions of juvenile hake, adult round herring (*Etrumeus whiteheadi*), anchovy (*Engraulis capensis*) recruits, pelagic goby (*Sufflogobius bibarbatus*), horse mackerel (*Trachurus trachurus capensis*), and ribbon fish (*Lepidopus caudatus*). Average TS values for all these species, both per individual and normalized by weight, are presented and compared with published values. The use of TS information in studies of the small-scale community structure and dynamics of fish populations is discussed. It is concluded that the method can be effective on low-density, multispecific assemblages such as those in our study, avoiding many of the pitfalls of conventional net sampling.

Un échosondeur à faisceau partagé a été utilisé pour estimer in situ les intensités de cible acoustique (TS) des poissons dans un certain nombre de différentes communautés sur le plateau continental de l'Afrique du Sud. Les distributions des TS et des tailles (obtenues par chalutage contrôlé) ont servi à décrire la structure des tailles et la distribution verticale de ces communautés. Les distributions des TS obtenues à partir de plusieurs populations monospécifiques de juvéniles de merlu du Cap (*Merluccius capensis*), la principale espèce présente, étaient cohérentes, et on observait une bonne correspondance entre les modes des distributions des TS et des longueurs chez les merlus juvéniles, les shadines adultes (*Etrumeus whiteheadi*), les recrues d'anchois du Cap (*Engraulis capensis*), le gobie pélagique (*Sufflogobius bibarbatus*), le chinchard du Cap (*Trachurus trachurus capensis*) et le sabre argenté (*Lepidopus caudatus*). Les valeurs moyennes des TS pour toutes ces espèces, aussi bien pour les individus qu'après normalisation par poids, sont présentées et comparées aux données publiées. Nous analysons l'utilisation de l'information sur les TS dans les études sur la structure à petite échelle des communautés et la dynamique des populations de poissons. Nous en concluons que la méthode peut être efficace pour des assemblages plurispécifiques à faible densité comme ceux de notre étude, et qu'elle permet d'éviter les écueils de l'échantillonnage classique au filet.

Received April 1, 1993
Accepted July 19, 1993
(JB868)

Reçu le 1 avril 1993
Accepté le 29 juillet 1993

Echo-integration has become a widespread acoustic technique to estimate the size of commercially important fish stocks (e.g. Karp 1990; MacLennan and Simmonds 1992). Accuracy, however, depends on the precision of target strength (TS) estimates used in converting measurements of acoustic scattering intensity to estimates of fish biomass. During the last two decades, much effort has been focused on refining techniques to improve the accuracy of TS estimates, resulting in the development of dual-beam and split-beam transducers (Ehrenberg 1983) to determine the position of single targets in the beam and thereby obtain direct in situ TS estimates from the strength of the echo and knowledge of the transducer directivity. These new improvements provide a better appraisal of spatial and temporal variability than does net sampling, in which deficiencies in sampling fish communities representatively are well recognized (e.g., Walsh 1991; Engås and Soldal 1992; MacLennan 1992). As such, they offer new perspectives into the study of the small-scale structure of fish communities (e.g., Burczynski and Johnson 1986; Rudstam et al. 1987; Jacobson et al. 1990; Boudreau 1992).

TS is related to fish size (e.g., MacLennan and Simmonds 1992) and can be strongly affected by behaviour and physiological state (e.g., Blaxter and Batty 1990; Dawson and Karp 1990; MacLennan et al. 1990; Ona 1990a). Consequently, it is a highly variable parameter that, together with the fact that TS studies have been restricted largely to commercially important species, has limited the use of TS information to studies on monospecific populations (e.g., Traynor and Williamson 1983; Williamson and Traynor 1984; Foote et al. 1986; Foote and Traynor 1988). Nevertheless, it has been proposed that it is possible to interpret TS differences in terms of differences in fish size (Dickie et al. 1983), suggesting that ecological studies of multispecific assemblages could benefit from the analysis of echo returns (e.g., Lindem 1983; Forbes 1985; Burczynski and Johnson 1986; MacLennan and Forbes 1987; Rudstam et al. 1987; Jacobson et al. 1990). If so, techniques of determining TS accurately (Thiebaux et al. 1991) would have the potential to address questions involving the behaviour and microstructure of fish at the population and community level. The need for such an approach has become increasingly clear, as there is growing evidence that fish communities are not randomly organized but are highly structured assemblages (e.g., Jackson et al. 1992) consisting of populations interacting at several scales (Crowder 1990).

In the present paper, we use TS information from a split-beam echo-sounder to analyze size, relative composition, abundance, and vertical structure of fish assemblages. We examine the hypothesis that, in simple communities under conditions of low species diversity, well segregated by size, the distribution of TS reflects the size composition of the community. If there are few overlapping echoes, the method will also provide an estimate of the relative abundance of each species, based on the target counts. The application of such developments to the study of small-scale fish community structure and behaviour at the individual and population levels is discussed.

Material and Methods

Sampling Strategy

Data were collected onboard F.R.S. *Africana* during February 1992 in nearshore waters (80–110 m depth) off the west coast of South Africa. The region between 29°S and 32°S was chosen because it is a known recruitment area for monospecific, nonshoaling populations of juvenile shallow-water Cape hake (*Merluccius capensis*) suitable for the study. Such conditions were required to ensure an adequate number of nonoverlapping echoes for in situ TS determination. In order to ensure a suitable spread of fish throughout the water column, data were collected only at night, when juvenile hake rise off the bottom (Pillar and Barange 1993).

Areas of study were selected according to the acoustic properties of fish communities, as recorded in echo-charts obtained daily at dawn. Sampling procedure was as follows. Temperature and salinity profiles were first obtained with a Neil Brown Mark III CTD. Fish sampling followed, using an aimed Engels 308 midwater trawl fitted with an 8-mm-mesh codend liner. The net was trawled at approximately 3 kn for 15–30 min. Several trawls were conducted at different depths over fixed transects to cover the entire water column. The transects were generally parallel to the isobaths and typically between 1 and 2 nautical miles long. While trawling, TS data were collected from the depth interval sampled by the net. Relative fish abundance was estimated from the ratio between the number of single identified targets and the number of acoustic transmissions ("pings"). Although it was originally intended to estimate abundance by echo-integration, this was prevented by failure of the echo-integrator during the cruise. Generally, four or five midwater trawls and TS experiments were carried out per night on each selected fish community. On occasion, TS data were collected from the entire water column independently of the depth intervals sampled by the net. In addition, bottom trawls were occasionally conducted to establish the composition of the nonmigrant population when considered necessary.

Target number	....	1
Ping number	....	12
Range	....	77.6 m
Peak Amplitude	....	144 units
Target Strength	....	-56.15 dB
Athwartships Angle	....	-0.14 deg
Alongships Angle	....	-1.56 deg

RANGE	AMPLIT	ATHWART.	ALONG.
773	26	-47	38
774	23	-6	-12
775	43	-1	-12
776	79	-2	-14
777	111	-3	-14
778	131	-3	-14
779	139	-1	-13
780	142	0	-14
781	144	1	-13
782	135	4	-4
783	96	9	7
784	67	27	14
785	45	13	10
786	31	3	5
787	25	2	11

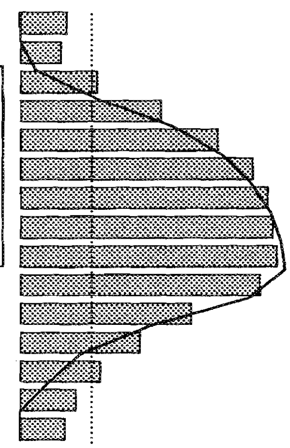

FIG. 1. ES400 parallel output data from a depth layer, 77.3–78.7 m, containing one well-defined fish echo. Threshold set at 40 units. Superimposed line denotes shape of the echo of a calibration sphere, normalized in amplitude to fish echo. Box indicates region of phase lock. Phase readings in columns are in electrical units (1 unit = 0.13°).

All fish collected in the trawls were measured to the nearest centimetre and classified to species level to produce size frequencies of the communities under study. Acoustic data were analyzed as decribed in the following section.

Acoustic Measurements

TS data were obtained from a Simrad ES400 (38-kHz) echo-sounder, using a Simrad ES-38 split-beam transducer (directivity index 29 dB, nominal beamwidth 8.0° between half-power points) fired by a Simrad EK400 transmitter using a 1.0-ms pulse. A month after the cruise the system was calibrated to within an estimated 0.5 dB with a 60-mm copper sphere according to procedures set out in Foote et al. (1987). Pertinent parameters measured were the combined source level and voltage response and the half-power points of the beam. The latter were obtained by moving the transducer relative to the sphere and plotting sphere amplitude against angular bearing.

Target amplitude, range, and bearing, both alongships and athwartships, were sampled from the parallel port of the ES400 at 0.133-ms intervals (corresponding to depth intervals of 0.1 m) by an IBM-compatible AT computer. The range, peak amplitude, and bearings of an echo were stored if (a) the peak fell within the depth range of interest and exceeded a threshold set marginally above the noise level

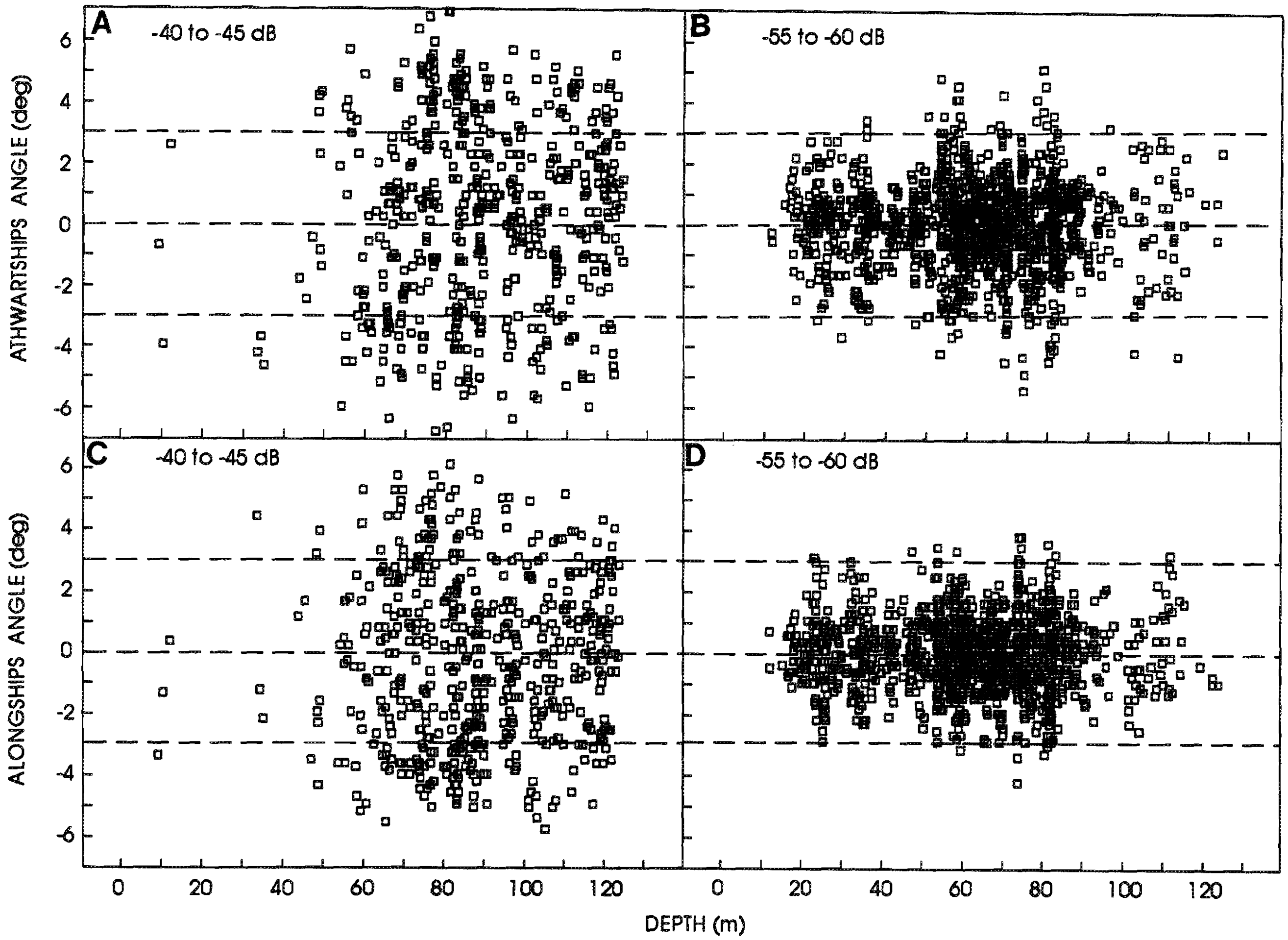

Fig. 2. Scatterplot showing position in the beam of all single targets isolated during the cruise. (A and B) Targets between −40 and −45 dB; (C and D) targets between −55 and −60 dB.

and (b) the sample-to-sample variation in bearing in both directions was less than 3 units (0.4°) for at least six successive samples. These conditions are similar to those imposed by Dengbol and Lewy (1990) and Brede et al. (1990) in isolating single fish echoes from ES400 data. We found them to be appropriate for recognizing single sphere echoes, both in a test tank and at sea.

In the processing phase, potential single fish echoes were screened further according to shape, being rejected if the envelope did not show a reasonably monotonic variation about a single peak. An example of an echo satisfying all the above criteria is given in Fig. 1. In this case the threshold was set at 40 bits.

For each accepted echo, the angular bearing was used to compensate the peak recorded amplitude according to the position of the target in the beam, enabling TS to be estimated directly. Data for the compensation were obtained by fitting the amplitude and bearing of sphere echoes in different parts of the beam (obtained during the calibration) to Ona's (1990b) empirical beam function expression for the same type of transducer. The resultant expression, which was used in compensating all accepted echoes in the experiment, was

$$(1)\quad B(\alpha,\beta) = 2^{-\left\{\left[(\alpha-\Delta\alpha)/0.5\alpha_1\right]^2+\left[(\beta-\Delta\beta)/0.5\beta_1\right]^2\right\}^{1.1}}$$

where α and β are the bearings in the alongships and athwartships directions, respectively, α_1 and β_1 the half-power beamwidth in these two directions, and $\Delta\alpha$ and $\Delta\beta$ the angular offsets in the phase detectors, measured during calibration.

For part of the study, a multichannel digital echo-integrator (Anonymous 1986) was also available and was used to estimate volume back-scattering strengths in 5-m channels throughout the water column. The integrator was coupled to the EK400 receiver and calibrated by sphere at the same time as the ES400.

Patterns in the distribution of target bearing with depth for different signal strengths were examined for evidence of bias arising from the application of a threshold (equivalent to an echo level of −66 dB) in the target-recognition software. Comparable results are presented in Fig. 2 for strong (−40 to −45 dB) and weak (−55 to −60 dB) targets. Strong targets were detected relatively evenly within the examined sector of the beam (7° on either side of the axis). In contrast, comparatively few weak targets were detected more than 3° off-axis, indicating a bias against weak targets on the edge of the beam. To minimize this effect, only targets located less than 3° off-axis were considered. Within this sector, no obvious patterns indicative of bias against weaker targets with increasing depth were evident, suggesting that the targets were equally detectable throughout the depth range considered.

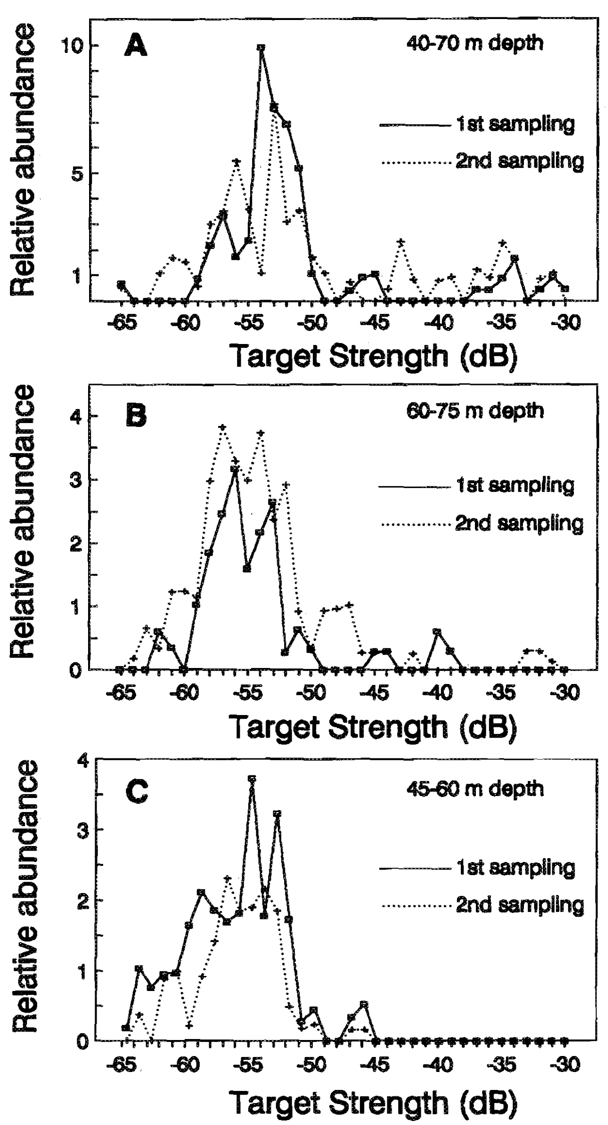

FIG. 3. Comparison between pairs of TS frequency distributions collected over similar transects. Time lapses between samples were (A) 90 min and (B and C) 24 h.

Finally, relative indices of abundance were calculated for each experiment according to the expression

$$(2)\quad I = \frac{k}{N}\sum_{i=1}^{n}\frac{1}{D_i^2}$$

where n is the number of targets fulfilling the selection criteria, N the number of pings transmitted in the experiment, D_i the depth of the ith target, and k a scaling factor. The depth factor is necessary to account for the increasing sampling volume with depth (e.g., Dengbol and Lewy 1990). The expression assumes that any bias in single target selection is independent of depth, i.e., that densities were sufficiently low for the probability of echo overlap to be negligible, even at maximum range. Echo-chart recordings support this assumption for juvenile hake, showing widely separated individual targets, even close to the bottom (e.g., see Fig. 8). Also, echo-integrator and TS data from the hake targets between 80 and 100 m depth (see Fig. 4C), which were exceptionally dense, suggest that even in this case, the probability of more than one fish occupying the pulse volume at that depth was less than 1%.

Results

To establish the consistency of the TS distributions obtained, paired experiments were carried out over similar areas at spaced time intervals. The objective was twofold: (a) to assess the consistency of the method in reflecting the fish population under study (i.e., if the same population is sampled repetitively the TS distributions should be similar) and (b) to examine the change in TS distributions associated with short-term temporal changes in community composition and behaviour.

The paired experiments (Fig. 3) were in good overall agreement with each other, suggesting that the TS distributions reflected the composition of each community accurately. In the first experimental example (Fig. 3A), targets were recorded between 40 and 70 m depth for approximately 5 min and then recorded again over the same depth range for a similar time period 90 min later. In the remaining examples (Fig. 3C and 3D), paired samplings were separated by 24 h. It is important to note that these pairs are not considered to be replicate samples from the same population because of small-scale temporal and spatial variability in the relative abundance of the dominant species in the community. Slight differences probably reflect changes in the dorsal aspect of fish (e.g., MacLennan and Simmonds 1992), or small differences in the size distribution of the targets insonified. Of a total of seven comparative experiments carried out in similar manner, only one resulted in a substantial difference between paired TS distributions.

Our next objective was to investigate whether monospecific, unimodal communities result in unimodal distributions of TS, which was motivated by observations of bimodalities in TS frequency distributions obtained from unimodal populations of walleye pollock (*Theragra chalcogramma*) (Traynor and Williamson 1983) and Pacific whiting (*Merluccius productus*) (Williamson and Traynor 1984). Data for all these experiments were obtained from a comparison between TS distributions and the length and species composition of midwater trawl catches made concurrently from the same depths. The results of two of these experiments are presented in Fig. 4, showing size and TS frequency distributions of largely monospecific populations of juvenile hake, one at 20–40 m depth (Fig. 4A and 4B) and the other between 80 and 100 m depth (Fig. 4C and 4D). Modes in total length of 14 and 15 cm corresponded to TS peaks at −51 and −48 dB, respectively. The weaker, less abundant targets in Fig. 4A perhaps originate from a population of small pelagic gobies (*Sufflogobius bibarbatus*) which were also present in the water column (Fig. 4B). A few stronger targets are evident in Fig. 4C, probably reflecting the horse mackerel (*Trachurus trachurus capensis*) (27–34 cm total length), which were also in the trawl collections, but less abundant than hake. Two more examples of near-monospecific catches are presented in Fig. 5. In the first illustration (Fig. 5A and 5B), a population of juvenile hake of 15-cm mode was associated with a TS peak centred at approximately −50 dB. Small gobies and larger horse mackerel were also present in the catches, contributing to the broader TS spectrum. The second example (Fig. 5C and 5D) shows the size distribution of ribbon fish (*Lepidopus caudatus*)

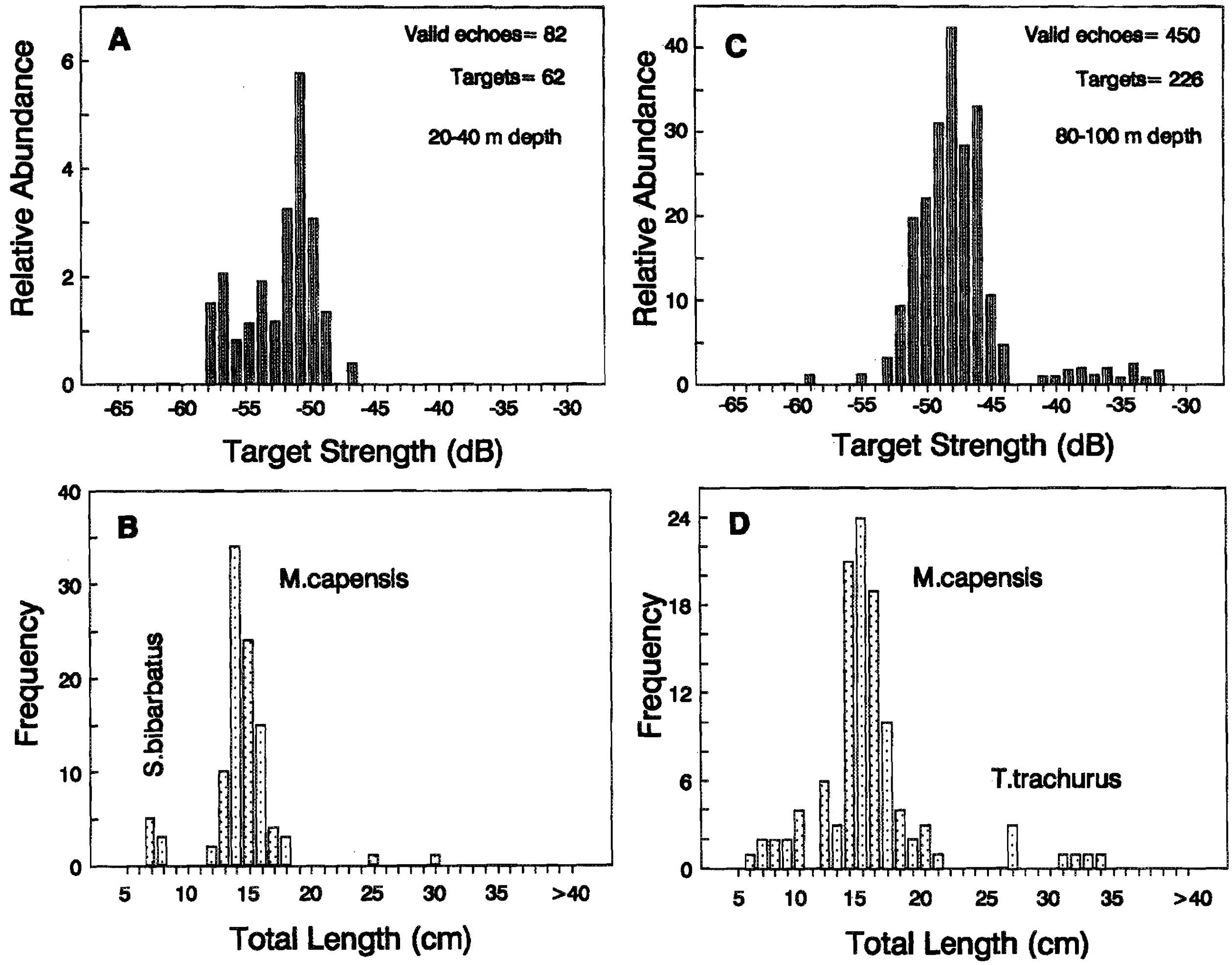

FIG. 4. Comparison between (A and C) TS distributions and (B and D) size distributions obtained from net catches collected from two deep monospecific communities of juvenile hake.

between 112 and 120 m depth, and the TS distribution for the fish population between these depths. In the four essentially unimodal populations displayed in Fig. 4 and 5, single peak modes in TS values were observed, which was the general trend in other monospecific populations of juvenile hake encountered during the study.

Two examples illustrating the acoustic discrimination of multispecific assemblages are presented in Fig. 6 and 7. The size frequencies were constructed from pooled midwater trawl collections, taken at four depth strata of the water column, which reflected the size distribution of the midwater community. TS distributions were obtained from depth strata similar to those sampled by the net and were combined taking into account the volume insonified at each depth. The first example (Fig. 6) shows a community of small gobies, juvenile hake, horse mackerel, and Cape gurnard (*Chelidonichthys capensis*). The last two species, which overlapped in size, gave a broad distribution of TS values greater than −42 dB. The modal length of the juvenile hake (15 cm) corresponded to a TS mode centred between −46 and −53 dB. This corresponds to a fivefold range in backscattering cross section, compared with about a twofold range in fish cross-sectional area and about a threefold range in their mass. The broader distributions of TS values compared with fish size are to be expected because of variation in aspect and the statistical nature of back-scattering intensities from individual fish (e.g., Clay and Heist 1984; Denbigh et al. 1991). In the next illustration (Fig. 7), even though horse mackerel and gurnard were less abundant than in the previous example, they were still identifiable in the TS distribution. A second peak in the TS distribution, centred at −47 dB, probably arose from a population of round herring (*Etrumeus whiteheadi*) of lengths ranging between 19 and 23 cm (Fig. 7). The main peak in the TS distribution arises from the large proportion of juvenile hake in the assemblage.

Figure 8 shows an echo-chart representing a multispecies fish community that is dominated by a dense layer of anchovy (*Engraulis capensis*) recruits in the upper 20–30 m, with single targets of larger fish, at lower densities, throughout the water column. TS values could be obtained from the dense layer of anchovies by the split-beam system, but the relative abundance index is negatively biased because only a few single echoes could be isolated from the layer. However, valid TS and relative abundance estimates were obtained for the larger, nonshoaling individuals and are presented in Fig. 9 as a three-dimensional structure. The figure was derived by producing TS distributions at 10-m depth intervals throughout the water column. The water column is dominated by a single peak at −49 dB in the upper 30 m,

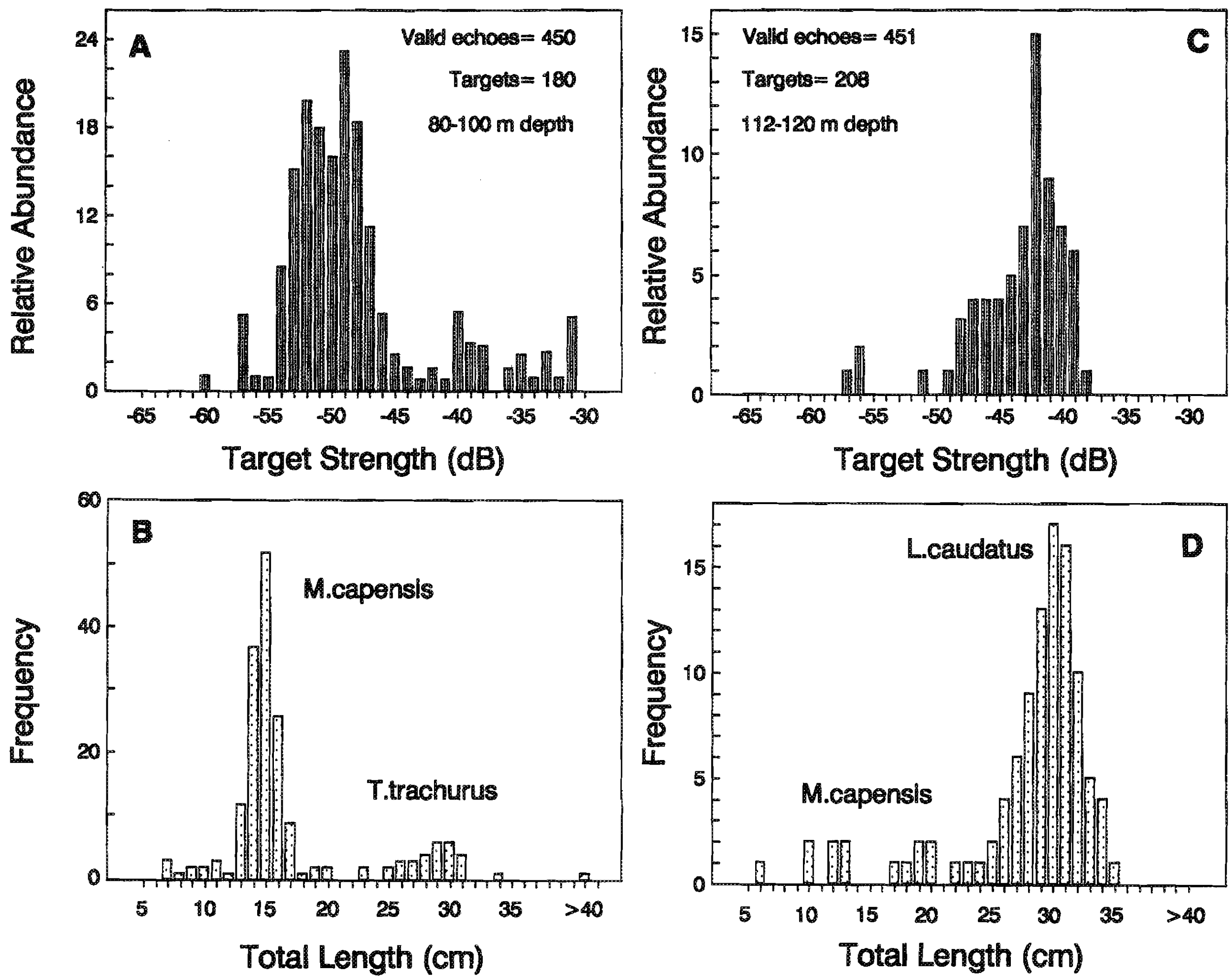

FIG. 5. Comparison between (A and C) TS distributions and (B and D) size distributions obtained from net catches collected from largely monospecific communities of (A and B) juvenile hake and (C and D) ribbon fish.

which is close to that of juvenile hake (peaks in Fig. 4–7). Abundances, however, decrease sharply with depth until 60 m, between which depth and the bottom targets of similar and higher strength than those near the surface were again abundant. Strong targets were recorded close to the seabed, suggesting that larger fish were present at that depth. The size distribution of the fish community was derived from midwater and bottom trawl catches and grouped into subsurface (0–40 m depth), midwater (50–80 m depth), and bottom trawls (Fig. 10). The subsurface catches were dominated by anchovy recruits of 5–10 cm, although their abundance could not be compared with the second peak of juvenile hake (10–17 cm), as the mesh was too coarse to retain the small anchovy efficiently. All other catches were dominated by young hake, larger individuals being less abundant in midwater than on the bottom. Horse mackerel, gurnard, and St Joseph sharks (*Callorhynchus capensis*) dominate the larger size class of fish, presumably accounting for the higher TS values close to the bottom in Fig. 9.

Discussion

The results presented suggest that the composition and abundance of certain low-density fish communities can be estimated by means of a split-beam echo-sounder. Considering the close agreement we obtained between the modes in the size and TS distributions, it seems that split-beam echo-sounders have the potential to resolve the vertical distribution of certain multispecies fish assemblages. Accordance between size and TS modes has been observed before, using both indirect (Robinson 1982; Halldórson and Reynisson 1983; Lindem 1983) and direct methods (Forbes 1985; MacLennan and Forbes 1987; Rudstam et al. 1987), but the use of TS analysis for studying community ecology has been hampered by large variation in TS and the difficulty in discriminating objectively among species of scatterer. The physiological condition of the animal, notably the state of the swim bladder, is a major source of variation in TS (Ona 1990a). Also, TS depends strongly on the orientation of the target relative to the acoustic beam, which in turn is dictated by the behaviour of fish (e.g., Nakken and Olsen 1977; Buerkle 1987; MacLennan et al. 1990). For example, Nakken and Olsen (1977) have shown that the maximum TS of cod at 38 kHz can change by up to 6 dB with a change in tilt angle of about 13°. It is therefore advisable to regard TS as a stochastic parameter and carefully assess the adequacy of the community under study to be resolved through TS methodology in terms of species diversity and fish abundance. Our results suggest that reliable target identification by aimed net trawling can greatly facilitate studies of fish communities through analysis of TS distributions.

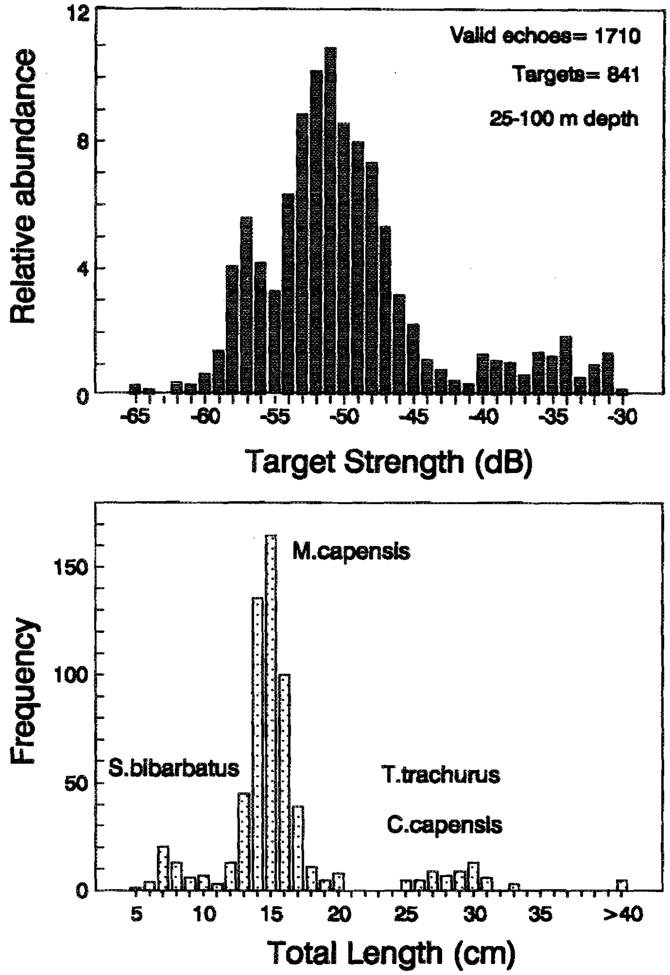

FIG. 6. Comparison between the TS distribution and size distribution derived from net catches of a multispecific community between 25 and 100 m depth.

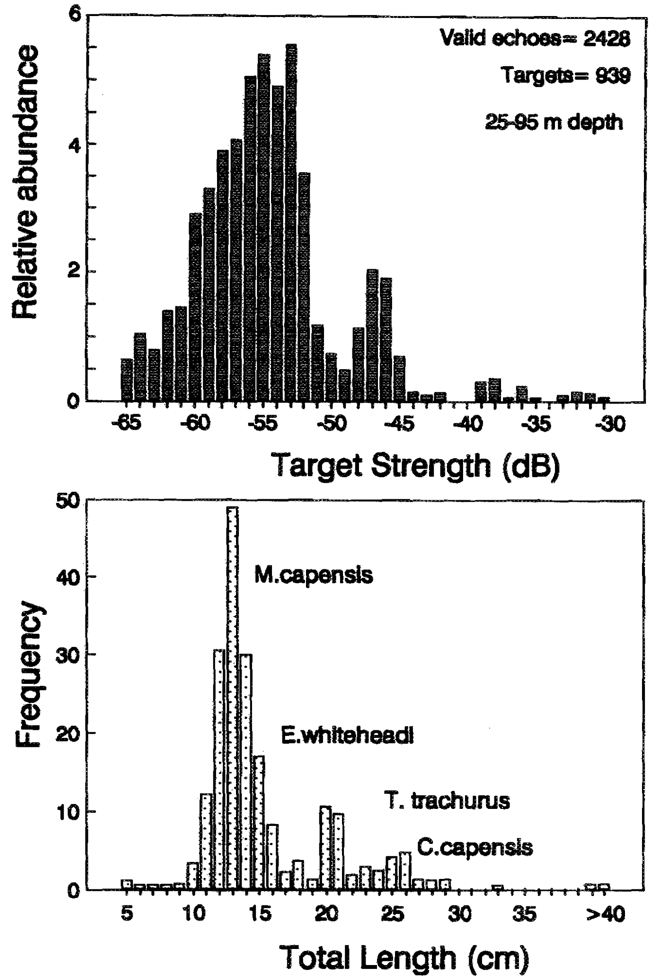

FIG. 7. Comparison between the TS distribution and size distribution derived from net catches of a multispecific community between 30 and 95 m depth.

The advantages of acoustic versus conventional net sampling are threefold: (a) it can achieve a much higher spatial and temporal resolution than net sampling, (b) it is free of the central problems associated with net sampling for community analysis (i.e., net avoidance and selectivity), and it offers a means of quantifying the migratory behaviour of some species from the bottom to midwater, particularly if coupled with echo-integration techniques. One limitation of the present TS analysis is the restriction concerning the degree of fish density to which it can be applied. The densities of the species analyzed here were generally low and comparable between species. With highly aggregated populations, however, the echoes could overlap to such an extent that very few single targets would be detected. There would also be doubt as to whether the TS values of isolated single fish were representative of the aggregated part of the population. We are currently developing new systems aimed at isolating single targets at higher densities than is possible with the system described here to alleviate these problems. A further limitation in the present data is that all acoustic data were obtained from populations that were more than 1–2 m above the seabed, therefore excluding populations that live in close contact with the bottom during the night. Results from over 100 bottom trawls taken around the clock at a fixed station during 11 cruises in the Benguela ecosystem suggest that approximately 20% of the *Merluccius capensis* biomass remains close to the bottom at night (Sea Fisheries Research Institute, unpublished data). Most of this biomass would not have been adequately sampled acoustically.

On the hake recruitment grounds studied here, there were very few other groundfish species, most of which remained close to the bottom during the night. Juvenile hake, however, made nocturnal vertical migrations towards the surface. Approximately 10% by number of the juvenile hake population illustrated in Fig. 9 (assumed to be those targets between −46 and −55 dB) were deeper than 80 m during the study, while 65% were shallower than 25 m. Nocturnal movement of juvenile hake towards the surface has been observed by Pillar and Barange (1993), who related this movement to foraging behaviour. The communities under study seem to be highly structured assemblages whose aggregating and migratory behaviour is likely to be dictated by physical mechanisms and/or biological interactions. Further progress in the identification and quantification of such structures would improve our present capacity to understand the functioning of the communities of which they form a part.

The actual TS values obtained for the different species are of interest. Table 1 summarizes the average TS and size for several species examined during experiments where tar-

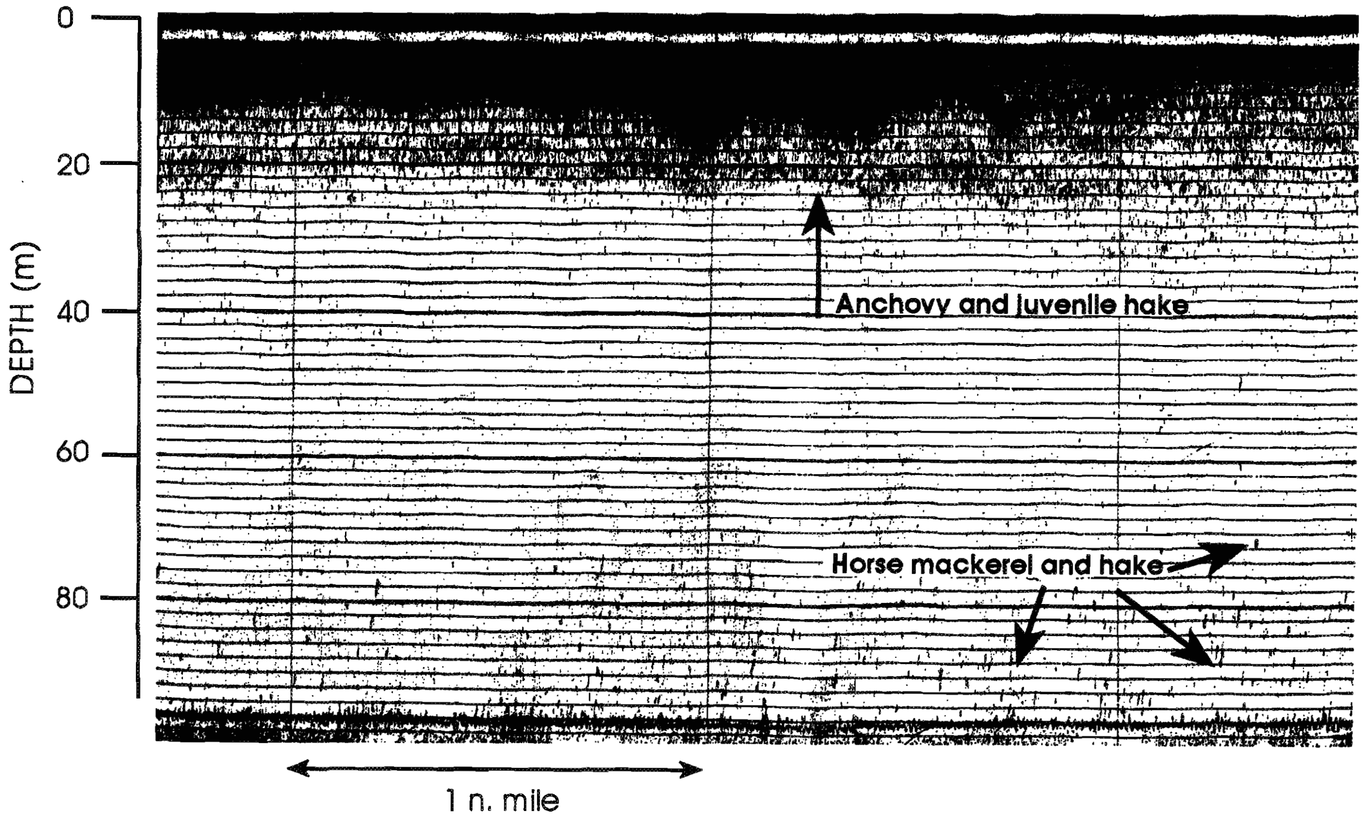

FIG. 8. Echo-chart obtained during collection of the TS and catch data presented in Fig. 9 and 10.

TABLE 1. Average size (total length) from net samples and average TS (derived from mean scattering cross sections) of *Merluccius capensis*, *Engraulis capensis*, *Etrumeus whiteheadi*, *Sufflogobius bibarbatus*, *Trachurus trachurus capensis*, and *Lepidopus caudatus* obtained during this study. Weight-normalized TS also presented.

Species	Total length (cm)	TS (dB)	Weight-normalized TS ($dB \cdot kg^{-1}$)
Merluccius capensis	11.86	−50.98	−32.07
	12.23	−53.34	−34.84
	13.95	−52.36	−35.62
	14.69	−49.03	−32.98
	14.69	−51.14	−35.09
	15.13	−49.65	−34.00
	15.16	−52.66	−37.04
	15.38	−49.34	−33.91
	15.60	−48.68	−33.44
Engraulis capensis	7.50	−57.84	−31.58
	7.34	−57.73	−31.16
Etrumeus whiteheadi	20.66	−46.61	−34.20
	20.71	−47.37	−34.99
Sufflogobius bibarbatus	9.42	−55.73	−36.89
	8.08	−56.88	−35.98
	6.50	−56.35	−32.53
Trachurus trachurus capensis	28.10	−39.52	−32.17
	27.50	−36.67	−29.04
Lepidopus caudatus	28.98	−42.44	—

get identification was considered to be reliable. Averages of mass-normalized TS, calculated according to the expression

(3) $\overline{TS}(dB \cdot kg^{-1}) = \overline{TS} + 10 \cdot \log_{10} (\overline{W})$

where $\overline{W}$ is the average individual mass (kilograms), are presented to facilitate comparison between the species in our study and other published values for similar species elsewhere.

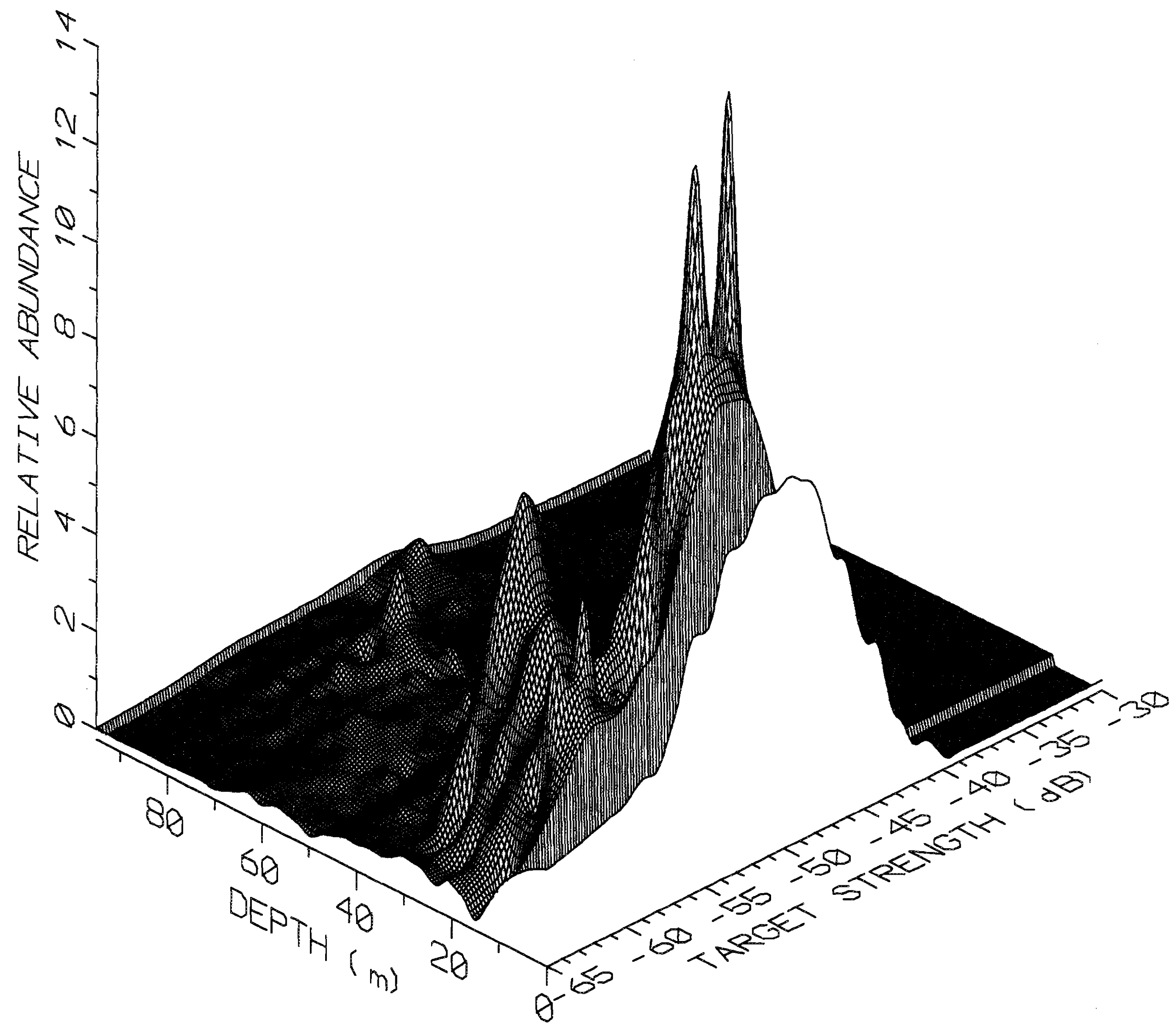

FIG. 9. Three-dimensional image showing the relationship between TS, abundance, and depth for the targets in Fig. 7. Note that no data were collected from the upper 10 m of the water column or within 3 m of the bottom (see text for explanation).

The round herring TS values agree closely with values expected from Foote's (1987) general clupeoid expression, which gives a value of −45.6 dB for a fish of 20.7 cm. Agreement is even closer with predictions from Halldórson and Reynisson's (1983) 38-kHz expression for Icelandic herring (*Clupea harengus*) which gives a value of −46.9 dB for a 20.7-cm fish. The anchovy values differ by about 3.4 dB from those predicted by Foote's clupeoid expression (−54.4 dB for a 7.5-cm fish) and by about 1.3 dB from those predicted by Halldórsson and Reynisson's expression for herring (−56.5 dB). We note, however, that since both expressions were derived from measurements on much larger fish (typically 20 cm), the discrepancies could be at least partially due to the extrapolation to smaller sizes. Average TS per unit of weight for *Merluccius capensis* varies between −32.7 and −37.0 dB·kg^{-1}, which agrees relatively well with values reported for the gadoids blue whiting (*Micromesistius poutassou*) (−33 to −33.5 dB·kg^{-1}, Robinson 1982) and Pacific whiting (−35 to −36 dB·kg^{-1}, Williamson and Traynor 1984), although it is lower than expected for other gadoids of similar size (−28.1 dB·kg^{-1} for a 15-cm fish, Foote 1987).

The only published values for horse mackerel TS at 38 kHz that we are aware of are a measurement by Nakken and Olsen (1977) on a single tethered 33-cm specimen (species not reported, but probably *Trachurus trachurus*) and several measurements of 32- to 39-cm specimens of *Trachurus murphyi* by Torres et al. (1984). The former reported a value of −34.0 dB and the latter measurements ranging between −35 and −37 dB, which are broadly consistent with our values for somewhat smaller specimens (Table 1). Our results for horse mackerel are also in general agreement with more comprehensive results obtained subsequently from a horse mackerel survey on the Cape south coast (−31.9 to −33.2 dB·kg^{-1}, Barange and Hampton 1993). We are not aware of any published TS values for any of the other species listed in Table 1.

There could be a number of explanations for the com-

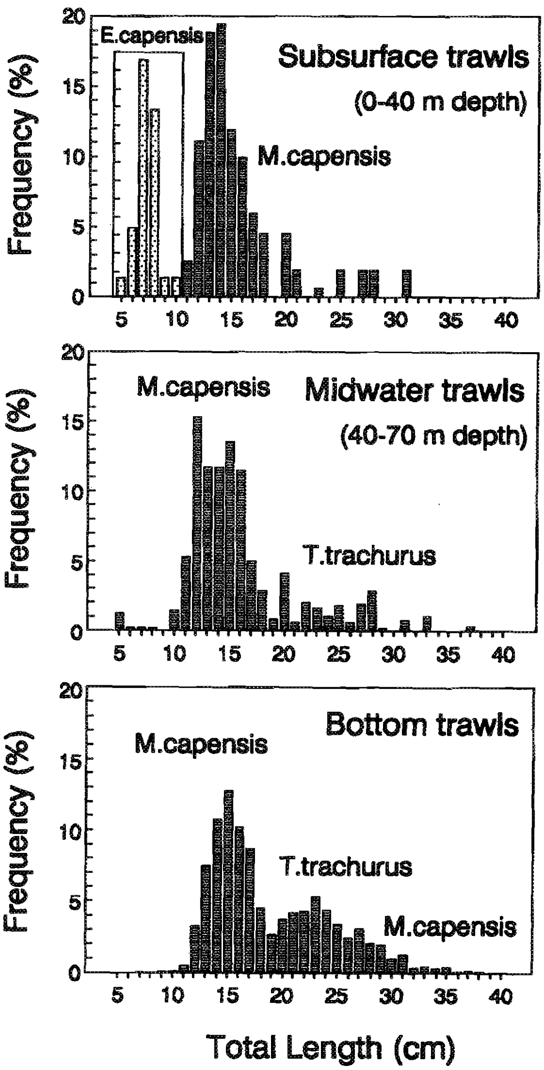

FIG. 10. Size frequency distributions obtained from trawling at several depth intervals during the collection of TS data presented in Fig. 9. Relative abundance of anchovy not comparable with the other species because of differences in catchability.

paratively low TS values recorded for the juvenile hake. Since hake are physoclists, the extensive vertical migrations that juveniles are known to perform (Pillar and Barange 1993) suggest that either they have a relatively small swim bladder or that it is severely compressed, e.g., by feeding. The latter possibility seems particularly real, as a large proportion of the juvenile hake caught off the bottom had full stomachs (Pillar and Barange 1993). We note that Ona (1990a) has found a reduction of up to 90% in swimbladder volume for cod with full stomachs, which would clearly result in a substantial reduction in TS. Careful studies on the relationship between TS, activity, and physiological state are needed. Fortunately, the suitability of juvenile hake for in situ TS studies makes such an investigation feasible.

We conclude that split-beam acoustic techniques can be used effectively to estimate the size structure, numerical abundance, and vertical distribution of low-density fish assemblages, offering a number of advantages over trawl net collections, not the least of which is the capacity for real-time examination of spatial variability.

References

ANONYMOUS. 1986. Research ship *Africana*. Spec. Rep. Sea Fish. Res. Inst. S. Afr. 3: 80 p.

BARANGE, M., AND I. HAMPTON. 1993. Influence of trawling on estimates of Cape Horse mackerel, *Trachurus trachurus capensis*, target strength. ICES J. Mar. Sci. (In press)

BLAXTER, J.H.S., AND R.S. BATTY. 1990. Swimbladder "behaviour" and target strength. Rapp. P.-v. Réun. Cons. int. Explor. Mer 189: 233–244.

BOUDREAU, P.R. 1992. Acoustic observations of patterns of aggregation in haddock (*Melanogrammus aeglefinus*) and their significance to production and catch. Can. J. Fish. Aquat. Sci. 49: 23–31.

BREDE, R., F.H. KRISTENSEN, H. SOLLI, AND E. ONA. 1990. Target tracking with a split-beam echosounder. Rapp. P.-v. Réun. Const. int. Explor. Mer 189: 254–263.

BUERKLE, U. 1987. Estimation of fish length from acoustic target strength. Can. J. Fish Aquat. Sci. 44: 1782–1785.

BURCZYNSKI, J.J., AND R.L. JOHNSON. 1986. Application of dual-beam acoustic survey techniques to limnetic populations of juvenile sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 43: 1776–1788.

CLAY, C.S., AND B.G. HEIST. 1984. Acoustic scattering by fish — acoustic models and a two-parameter fit. J. Acoust. Soc. Am. 75: 1077–1083.

CROWDER, L.B. 1990. Community ecology, p. 609–632. *In* C.B. Schreck and P.B. Moyle [ed.] Methods for fish biology. American Fisheries Society, Bethesda, Md.

DAWSON, J.J., AND W.A. KARP. 1990. *In situ* measures of target-strength variability of individual fish. Rapp. P.-v. Réun. Cons. int. Explor. Mer 189: 264–273.

DENBIGH, P.[N.], Q. SMITH, AND I. HAMPTON. 1991. Determination of fish number density by a statistical analysis of backscattered sound. J. Acoust. Soc. Am. 90: 457–469.

DENGBOL, P., AND P. LEWY. 1990. Interpretation of target-strength information from split-beam data. Rapp. P.-v. Réun. Cons. int. Explor. Mer 189: 274–282.

DICKIE, L.M., R.G. DOWD, AND P.R. BOUDREAU. 1983. An echo counting and logging system (ECOLOG) for demersal fish size distributions and densities. Can. J. Fish. Aquat. Sci. 40: 487–498.

EHRENBERG, J.E. 1983. A review of *in-situ* target strength estimation techniques. FAO Fish. Rep. 300: 85–90.

ENGÅS, A., AND A.V. SOLDAL. 1992. Diurnal variations in bottom trawl catch rates of cod and haddock and their influence on abundance indices. ICES. J. Mar. Sci. 49: 89–95.

FOOTE, K.G. 1987. Fish target strengths for use in echo integrator surveys. J. Acoust. Soc. Am. 82: 981–987.

FOOTE, K.G., A. AGLEN, AND O. NAKKEN. 1986. Measurement of fish target strength with a split-beam echo sounder. J. Acoust. Soc. Am. 80: 612–621.

FOOTE, K.G., H.P. KNUDSEN, G. VESTNES, D.N. MACLENNAN, AND E.J. SIMMONDS. 1987. Calibration of acoustic instruments for density estimation: a practical guide. Int. Counc. Explor. Sea Coop. Res. Rep. 144: 57 p.

FOOTE, K.G., AND J.J. TRAYNOR. 1988. Comparison of walleye pollock target strength estimates determined from *in situ* measurements and calculations based on swimbladder form. J. Acoust. Soc. Am. 83: 9–17.

FORBES, S.T. 1985. Progress in dual-beam target strength measurement on herring and blue whiting. Int. Counc. Explor. Sea CM 1985/B:22: 5 p. (Mimeo.)

HALLDÓRSSON, O., AND P. REYNISSON. 1983. Target strength measurement of herring and capelin in situ at Iceland. FAO Fish. Rep. 300: 78–84.

JACKSON, D.A., K.M. SOMERS, AND H.H. HARVEY. 1992. Null models and fish communities: evidence of nonrandom patterns. Am. Nat. 139: 930–951.

JACOBSON, P.T., C.S. CLAY, AND J.J. MAGNUSON. 1990. Size, distribution, and abundance of pelagic fish by deconvolution of single-beam acoustic data. Rapp. P.-v. Réun. Cons. int. Explor. Mer 189: 304–311.

KARP, W.A. [ED.] 1990. Developments in fisheries acoustics. A symposium held in Seattle 22–26 June 1987. Rapp. P.-v. Réun. Cons. int. Explor. Mer 189: 442 p.

LINDEM, T. 1983. Successes with conventional *in situ* determinations of fish target strength, p. 104–111. *In* O. Nakken and S.C. Venema [ed.] Symposium on fisheries acoustics. Selected Papers of the ICES/FAO Symposium on Fisheries Acoustics, Bergen, Norway, 21–24 June 1982. FAO Fish. Rep. 300.

MACLENNAN, D.N. [ED.] 1992. Fishing gear selectivity (Spec. Issue). Fish. Res. 13(3): 201–352.

MacLennan, D.N., and S.T. Forbes. 1987. Acoustic methods of fish stock estimation, p. 40–45. *In* R.S. Bailey and B.B. Parrish [ed.] Developments in fisheries research in Scotland. Fishing News Books, London.

MacLennan, D.N., A.E. Magurran, T.J. Pitcher, and C.E. Hollingworth. 1990. Behavioural determinants of fish target strength. Rapp. P.-v. Réun. Cons. int. Explor. Mer 189: 245–253.

MacLennan, D.N., and E.J. Simmonds. 1992. Fisheries acoustics. Fish and Fisheries Series 5. Chapman and Hall, New York, N.Y.

Nakken, O., and K. Olsen. 1977. Target strength measurements of fish. Rapp. P.-v. Réun. Cons. int. Explor. Mer 170: 52–69.

Ona, E. 1990a. Physiological factors causing natural variations in acoustic target strength of fish. J. Mar. Biol. Assoc. U.K. 70: 107–127.

Ona, E. 1990b. Optimal acoustic beam pattern corrections for split beam transducers. ICES C.M. 1990/B: 30.

Pillar, S.C., and M. Barange. 1993. Feeding selectivity of juvenile Cape hake, *Merluccius capensis* in the southern Benguela. S. Afr. J. Mar. Sci. 13: 255–268.

Robinson, B.J. 1982. An *in situ* technique to determine fish target strength, with results for blue whiting (*Micromesistius poutassou* (Risso)). J. Cons. int. Explor. Mer 40: 153–160.

Rudstam, L.G., C.S. Clay, and J.J. Magnuson. 1987. Density and size estimates of cisco (*Coregonus artedii*) using analysis of echo peak PDF from a single-transducer sonar. Can. J. Fish. Aquat. Sci. 44: 811–821.

Thiebaux, M.L., P.R. Boudreau, and L.M. Dickie. 1991. An analytical model of acoustic fish reflection for estimation of maximum dorsal aspect target strength. Can. J. Fish. Aquat. Sci. 48: 1772–1782.

Torres, A., O. Guzmán, and J. Castillo. 1984. La vejiga gaseosa como órgano resonante y su influencia en la intensidad sónica. Invest. Pesq. (Santiago) 31: 81–88.

Traynor, J.J., and N.J. Williamson. 1983. Target strength measurements of walleye pollock (*Theragra chalcogramma*) and a simulation study of the dual beam method. FAO Fish. Rep. 300: 112–124.

Walsh, S.J. 1991. Diel variation in availability and vulnerability of fish to a survey trawl. J. Appl. Ichthyol. 7: 147–159.

Williamson, N.J., and J.J. Traynor. 1984. *In situ* target-strength estimation of Pacific whiting (*Merluccius productus*) using dual-beam transducer. J. Cons. int. Explor. Mer 41: 285–292.