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ACOUSTIC INVESTIGATION OF FISH BEHAVIOUR
APPROPOS AVOIDANCE REACTION

by

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ABSTRACT

Three methods are introduced for the detection of avoidance reaction. These depend on the resolution of single fish echoes, which are analyzed, respectively, for in situ target strength, echo length, and trace length. The search for significant variations with depth of statistical extracts of such measurements may be expected to determine the presence of avoidance reaction if the usual stimulus-reaction hypothesis is upheld. The use of historical or simulated data may allow absolute determination of fish behaviour through definition of the orientation distribution. The theoretical basis of the several methods is given and future applications are promised.

INTRODUCTION

Acoustic assessment of fish abundance requires knowledge of fish behaviour. This is evident from the simplest considerations of echo counting and echo integration, two widely used methods of estimating fish density (Forbes and Nakken 1972). Each depends upon knowledge of certain fish-related quantities which are needed to interpret the observations. These interpretative quantities, the mean acoustic sampling volume and mean backscattering cross section, are intimately connected with the backscattering cross section of individual fish (Foote 1979, 1980a). Since this is generally a sensitive function of fish orientation and since any practicable acoustic survey will involve a very large number of independent observations, it is the distributional characteristics of orientation which are decisive in determining the several averages. Fish behaviour, as an acoustic concept, is defined through the orientation distribution, i.e., the probability distribution of individual fish orientations (Foote 1980c).

A dramatic example of the possible effect of fish behaviour on abundance estimates has been provided by some recent observations on herring (Olsen 1979). These show a strong avoidance reaction in the form of rapid diving during passage of the survey vessel. Both echo counting and echo integration must be influenced by such a phenomenon. In the first case, the generally weaker echo strength due to adoption of extreme orientation will result in a lower echo signal-to-noise ratio, which will reduce the probability of single fish detection, thence mean sampling volume. In the case of echo integration, the weaker echo strength will manifest itself directly in a reduced measurement of energy. If the standard methods of estimating fish density are to be used, then proper compensation has to be made through the sampling volume and mean backscattering cross section.

The present motivation for studying fish behaviour: to elicit information about the orientation distribution, is clear. This has been the object of a fair number of investigations, in fact, but mainly in connection with problems of schooling and migration. In the first case, the relative orientation of fish in the plane of schooling has been examined. In the second, the absolute azimuthal or compass bearing has been used to determine navigation ability. Such information is unfortunately uninteresting for the ordinary surveying of fish populations by directional echo sounders. For this, the acoustically significant aspect is the so-called tilt or tilt angle, which measures the angle of fish body axis with respect to the horizontal. To the author's knowledge, the bulk of published experimental data on this subject is contained principally in just four works: Olsen (1971), Beltestad (1974), Carscadden and Miller (1980), and Sameoto (1981). Each of these has been accomplished photographically and is thus impugned or conditioned by the unknown influence of camera on object of the observation.

One advantage of an acoustic determination of fish behaviour is thus apparent. If performed remotely and at sufficiently high frequency, for example, in the ultrasonic range where fish are deaf (Chapman 1964, Popper and Fay 1973), the act of observation cannot influence the observed fish. If performed additionally under usual surveying conditions, the determination can be made for the precise conditions of ultimate application.

To this end, three new acoustic schemes for determining fish behaviour are introduced. When used singly or in combination the methods can determine relative or even absolute changes in the orientation distribution, if not specify the orientation distribution itself. The methods are thus ideally suited to the detection of avoidance reaction, which only requires observation of a relative change in orientation distribution. The paper addresses this particular application, but also describes the fuller use of the several methods in absolute determinations of the orientation distribution.

THEORY FOR FORMATION OF FISH ECHOES

The several methods are based on analyses of resolved echoes from individual fish, which are presumed to be representative of the surveyed aggregation as a whole. Systematic variations of the echo waveform with changing orientation are necessary for successful uses of the methods. Very low frequencies are thus excluded from consideration, but this is no real limitation as the envisaged studies are to be performed on commercially important fish at ultrasonic frequencies. To show that there is interesting or non-trivial information contained in fish echoes at such frequencies, elementary scattering theory is applied to derive an explicit expression for the backscattered pressure field from single fish as observed.

For the sake of simplicity, physostomes and physoclists are first examined. Their swimbladder is assumed to be the dominant scattering organ. Since this may account for 90 per cent of the echo energy (Foote 1980b), such fish are described entirely in terms of the swimbladder, which, moreover, is assumed to be an ideal pressure-release surface. This is a reasonable approximation in the light of morphology and measurements of fish tissue (Haslett 1962, Love 1978). The mathematical consequence is that the scattering is described by the solution of a Dirichlet problem. Direct application of the Kirchhoff diffraction integral (Born and Wolf 1970) thus specifies the scattered pressure field, before reception, through the equation

$$p_{sc} = -\frac{1}{4\pi} \oint_S G \frac{\partial p}{\partial n} ds, \quad (1)$$

where $p = p_{inc} + p_{sc}$, p_{inc} is the incident pressure field, G is the free-space Green's function connecting observation point and surface element dS on the swimbladder surface S , and $\partial/\partial n = \hat{n} \cdot \nabla$ describes the derivative operator performed along the outward normal \hat{n} to S . For plane-wave ensonification,

$$p_{inc} = A \exp(i\mathbf{k} \cdot \mathbf{r}) \quad , \quad (2)$$

where A is the constant amplitude, \mathbf{k} is the wavevector, and \mathbf{r} is the observation point. In the backscattering direction $-\mathbf{k}$ and farfield of S ,

$$p_{bsc} \sim A \frac{e^{i\mathbf{k}r}}{r} F \quad , \quad (3)$$

where F is the backscattering amplitude,

$$F = -\frac{1}{4\pi} \oint_S \frac{\partial p}{\partial n} e^{-i\mathbf{k} \cdot \mathbf{r}'} dS' \quad . \quad (4)$$

The gradient $\partial p/\partial n$ is given here by solution of Eq. (1) with respect to the backscattering direction. For some purposes this may be approximated by the gradient $\partial p_{inc}/\partial n$, which is called a Kirchhoff boundary condition.

Equation (4) describes the monochromatic backscattering amplitude in water, before reception. If the influence of transient ensonification and reception by an intrinsically broadband receiver are included, the received pressure field as observed will be

$$p_{rec} = FT^{-1}(SFH) \quad , \quad (5)$$

where S is the spectrum of the incident signal, H is the frequency response function of the receiver, and $FT^{-1}(\cdot)$ denotes Fourier transformation of the argument from the frequency to time domain.

The derived expression is approximate because of the use of the swimbladder as a pressure-release surface to represent physostomes and physoclists. This is unnecessary, of course, for the entire fish could define the boundary surface, although with other constraints on the pressure field and its gradient than those of the Dirichlet problem. In the more general case,

non-swimbladder-bearing fish are included. Defensible and useful simplifications are nearly always possible, however. For example, the elasmobranch liver might define the scattering surface on which an impedance boundary condition is satisfied (Bone and Roberts 1969).

For the present, Eq. (4) is adequate, for it shows that scattering as a temporal process is highly dependent on fish size, shape, and orientation, as long as the wavenumber k is not too small. In the scattering regime of interest, $ka \gg 0(1)$, i.e., the characteristic wavenumber-to-size product is at least of the order of unity. The scattering will thus be complicated. According to Eq. (5), systematic variations in the waveform may survive the signal transformation implicit in the filtering operation.

ACOUSTIC METHODS

Detection of avoidance reaction depends on its magnitude varying with the size of the perceived stimulus, which is nearly a truism in behavioural work (Satersdal 1969, Saila 1969). Given the resolution of single fish echoes, determination of the presence of avoidance reaction is simple. Three methods are enumerated here. They are classified according to the discriminating quantity.

1. In situ target strength

A regular change in target strength with increasing depth may be expected. This will not necessarily be simply monotonic, but will probably indicate a clear trend. For 20-30 cm herring observed with a 38 kHz echo sounder the expected effect is a steady increase in mean target strength with increasing depth, if avoidance reaction is marked. In the absence of a reaction, the individual fish target strength should remain constant in the mean. Should some fish undergo avoidance reaction while others remain undisturbed, this may manifest itself more strongly in the second moment of the observed distribution of target strengths than in the mean, which will also be affected. The first two cases described here are depicted qualitatively in Fig. 1.

2. Echo length

Avoidance reaction, if sufficiently prompt, will result in the observation of fish in a more elongated aspect than otherwise. This will extend or stretch the echo waveform from that of a more ordinary aspect. The echo length or number of digitized amplitudes per fish echo, in the mean, will thus increase with increasing stimulus. Under those circumstances where avoidance reaction is present, the mean echo length may be expected to decrease with increasing depth. This is suggested in Fig. 2.

3. Trace length

The name connotes the length or number of registrations of the same fish, due to successive ensonifications, as it might be observed on an echogram or B-scan. It is used more generally here to describe the number of successive echo registrations from the same fish, whether visible or not on a display, whose dynamic range is often quite limited compared to that of the primary receiving electronics. In the absence of avoidance reaction, deeper lying fish will be observed longer in the mean because of the greater beam size at depth. Since the beam diameter increases linearly with depth, the average trace length should be normalized by the depth to remove the geometrical influence. Avoidance reaction can then be assessed by observing deviations from constancy. By the principle of increasing reaction with increasing stimulus, the mean trace length, after normalization, should be shorter with stronger stimulus, hence at shallower depth. This is indicated in Fig. 3.

CRITIQUE

Each of the three methods may allow detection of avoidance reaction, if present. The structure or manner of investigating stimuli- or depth-dependent behavioural effects is very convenient for statistical testing. This is obvious from a glance at Fig. 4, which summarizes comparisons of the several statistical quantities both with and without avoidance reaction. Both parametric and non-parametric tests are immediately applicable. In the case of separate uses of the methods, the distributional characteristics can be quantified when determining the appropriate mean. Ad hoc parametric tests can then be developed from these, if not conforming to well-known statistics. The collection or arrangement of data by depth interval will allow application of powerful non-parametric tests to observed depth-dependent trends in the data. The treatment of several methods jointly will allow similar, if more powerful tests to be used.

The statistics of the several quantities will, of course, govern the success of their applications. Such statistics can be deduced either theoretically or from prior measurement, and are worthy of study for assessing or anticipating the sensitivity of the methods. Although data are not presented here, some preliminary applications based on survey data on freshwater fishes, gathered by T. Lindem of the University of Oslo, have been successful in demonstrating the acoustic inconsequentiality of avoidance reaction during these surveys.

In addition to detecting avoidance reactions, the methods can, by reference to simulated or historical data, enable behaviour or changes in behaviour to be determined in an absolute sense. This is achieved simply by relating observations to reference data spanning a range of orientation distributions. This will be the subject of a future paper.

Two tacit assumptions have been made throughout this work: first, that there are no depth-dependent sizing effects in the vertical distribution of fish, and second, that the observed fish are species-homogeneous or, at least, of known species composition. If one or both of the assumptions is violated, then the methods must be revised to represent the more complicated conditions of observation. For example, the tests based on observations of in situ target strengths and echo lengths may be adapted by simple scaling to meet the circumstance of depth-dependent sizing effects of a single species, if known. The same tests, without revision, in similar situations can be used to infer sizing effects, if the behaviour can be assumed to be constant, i.e., undisturbed by the stimulus of passing survey vessel.

This last remark raises the matter of the connection between stimulus and reaction. For aggregating fish such as gadoids, the assumption of greater stimulus-greater or faster reaction appears quite reasonable. For schooling fish such as herring and some other pelagic species, the fact of schooling may prompt a change in behaviour analogous to the quantum-jump of physics. If this is the case, an avoidance reaction would propagate rapidly through a school and possibly cause the most distant fish in it to react as the one nearest the causative stimulus. Of course, in this case the schooling density will be high and the proposed methods will carry no force anyway as the demand of resolution of single fish echoes will be violated. It appears plausible, therefore, that when the three methods can be used, avoidance reactions can be sought on the basis of depth-dependent effects.

It is to be noted that the methods introduced here are hardly exhaustive in their application of acoustics to the problem of determining avoidance reaction or, more generally, behaviour. Consideration of the various systematics implied in the several equations above suggests other tests for elucidating behaviour and changes in behaviour. One particularly promising method, which is only mentioned here, is based on a statistical analysis of the coefficients in a regression of true rms amplitude on peak amplitude in single fish echoes. Such a method may be expected to be helpful when the length group of observed fish is not very narrow. This and other methods are being developed as the present ones are being applied.

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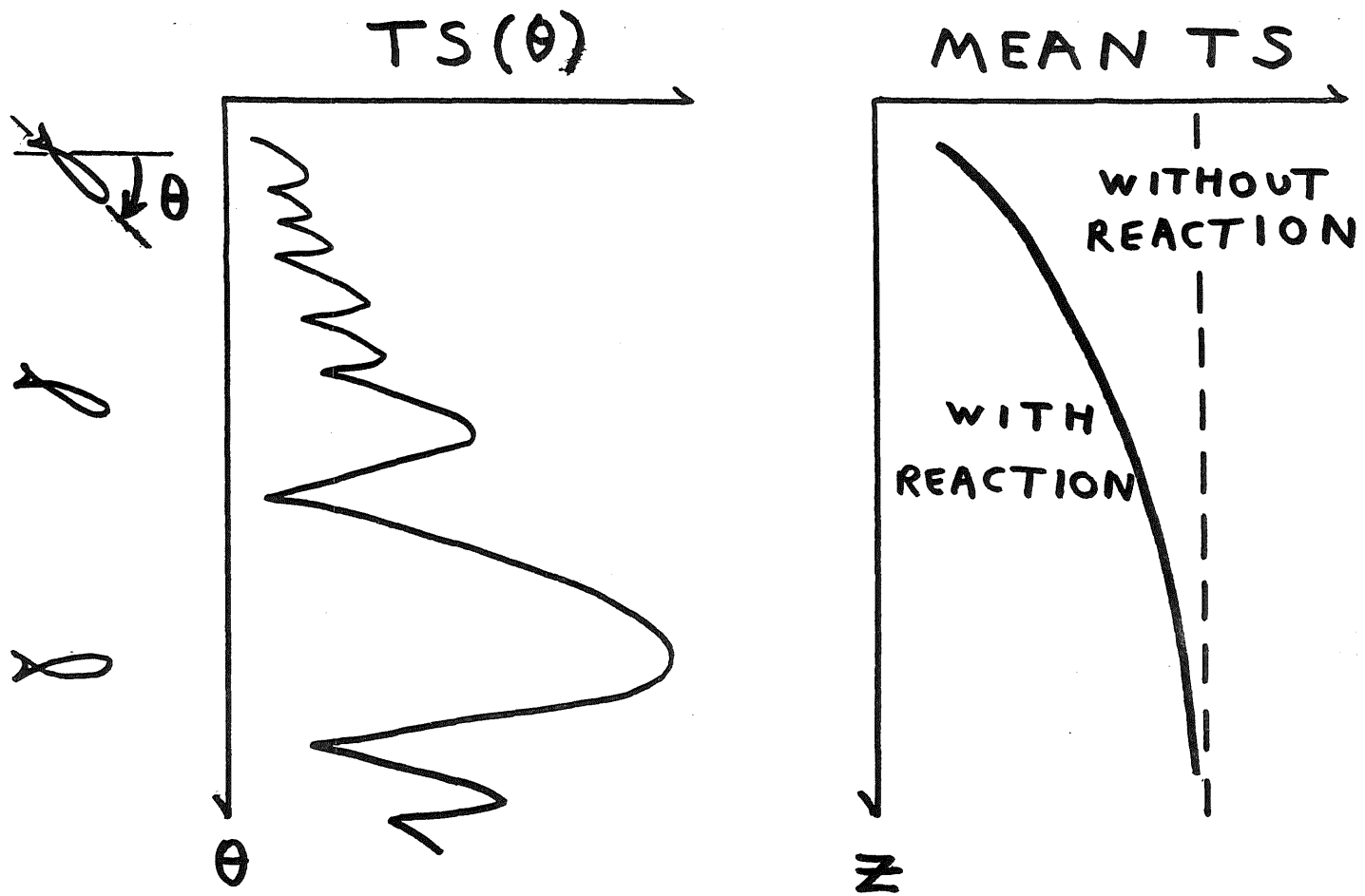


Fig. 1. Example of qualitative variation with depth z of mean in situ target strength TS.

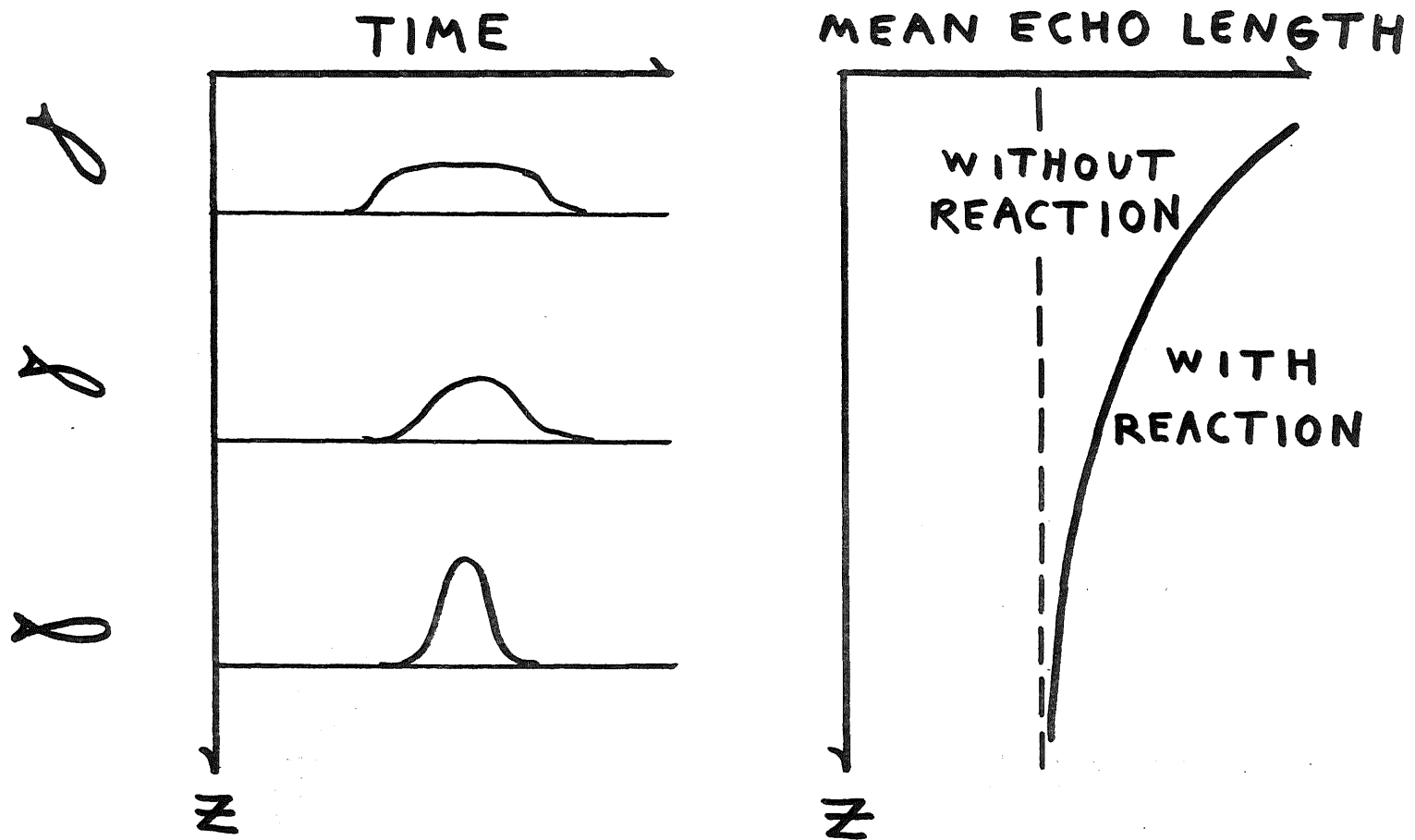


Fig. 2. Example of qualitative variation with depth z of mean echo length.

A. TRACE LENGTH L WITHOUT AVOIDANCE REACTION

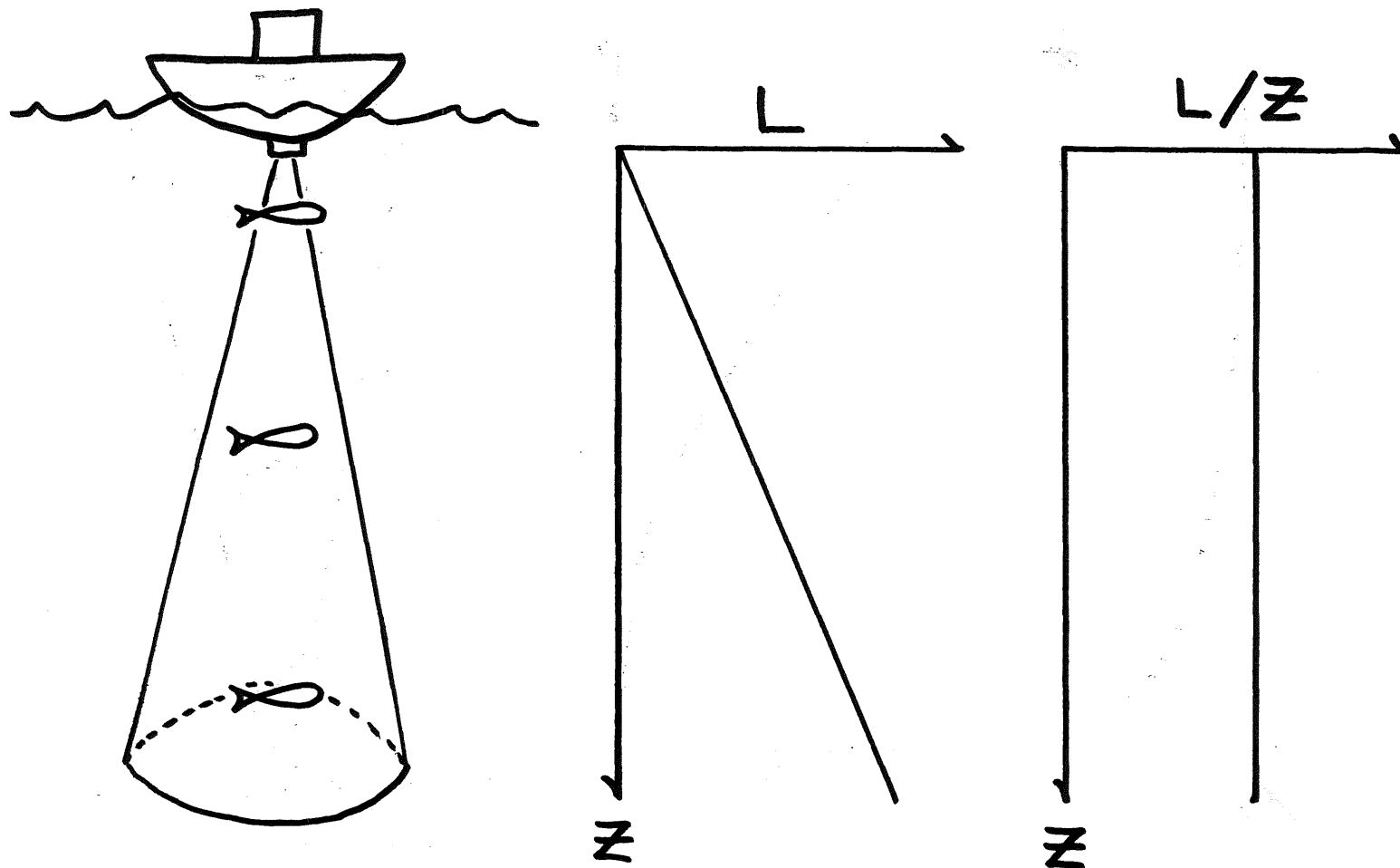


Fig. 3. Example of qualitative variation with depth z of mean trace length L and mean normalized trace length L/z , without (A) and with (B) avoidance reaction.

B. TRACE LENGTH L WITH AVOIDANCE REACTION

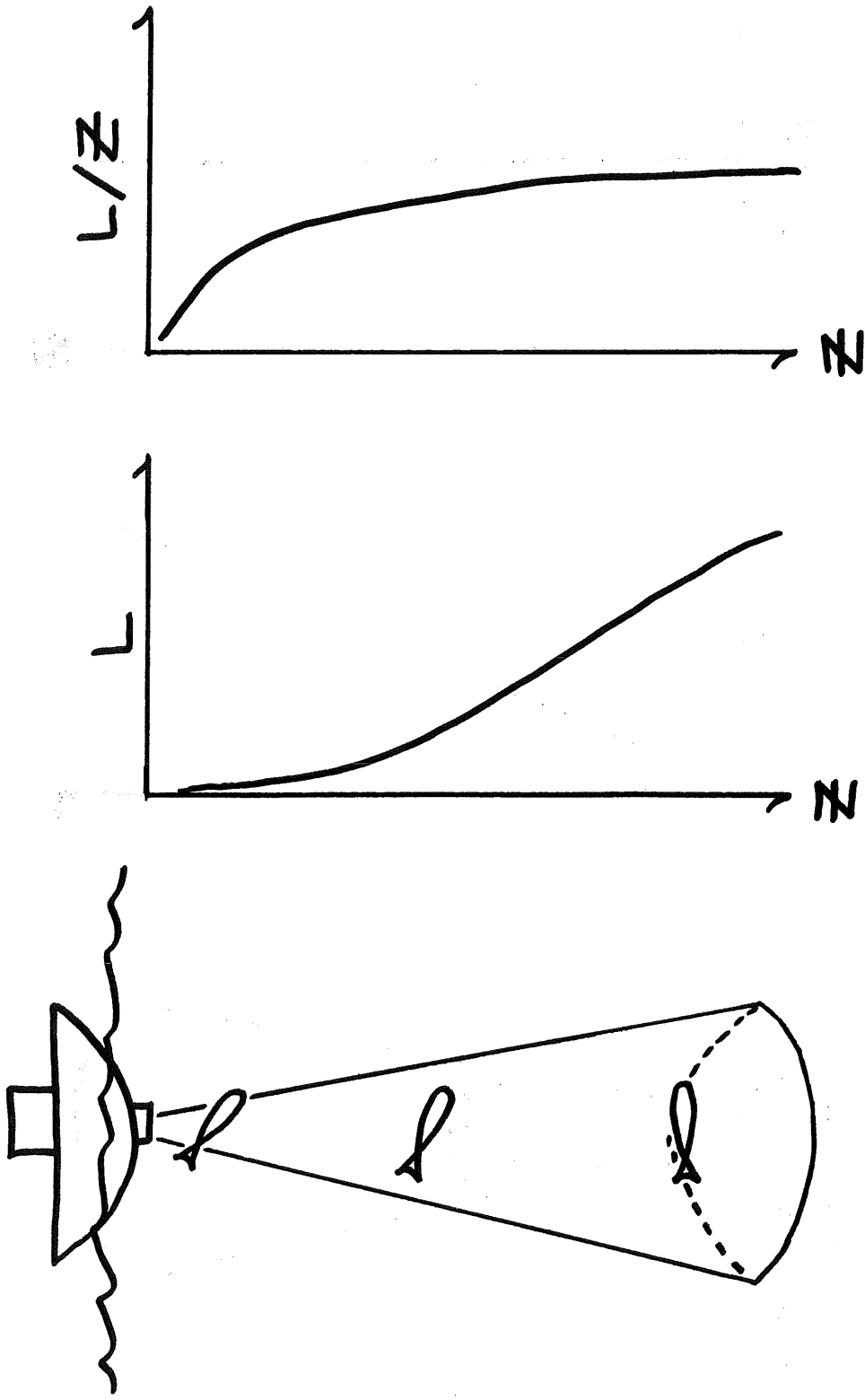


Fig. 3. (Cont.)

LEGEND { ——— WITH REACTION
 - - - - WITHOUT REACTION

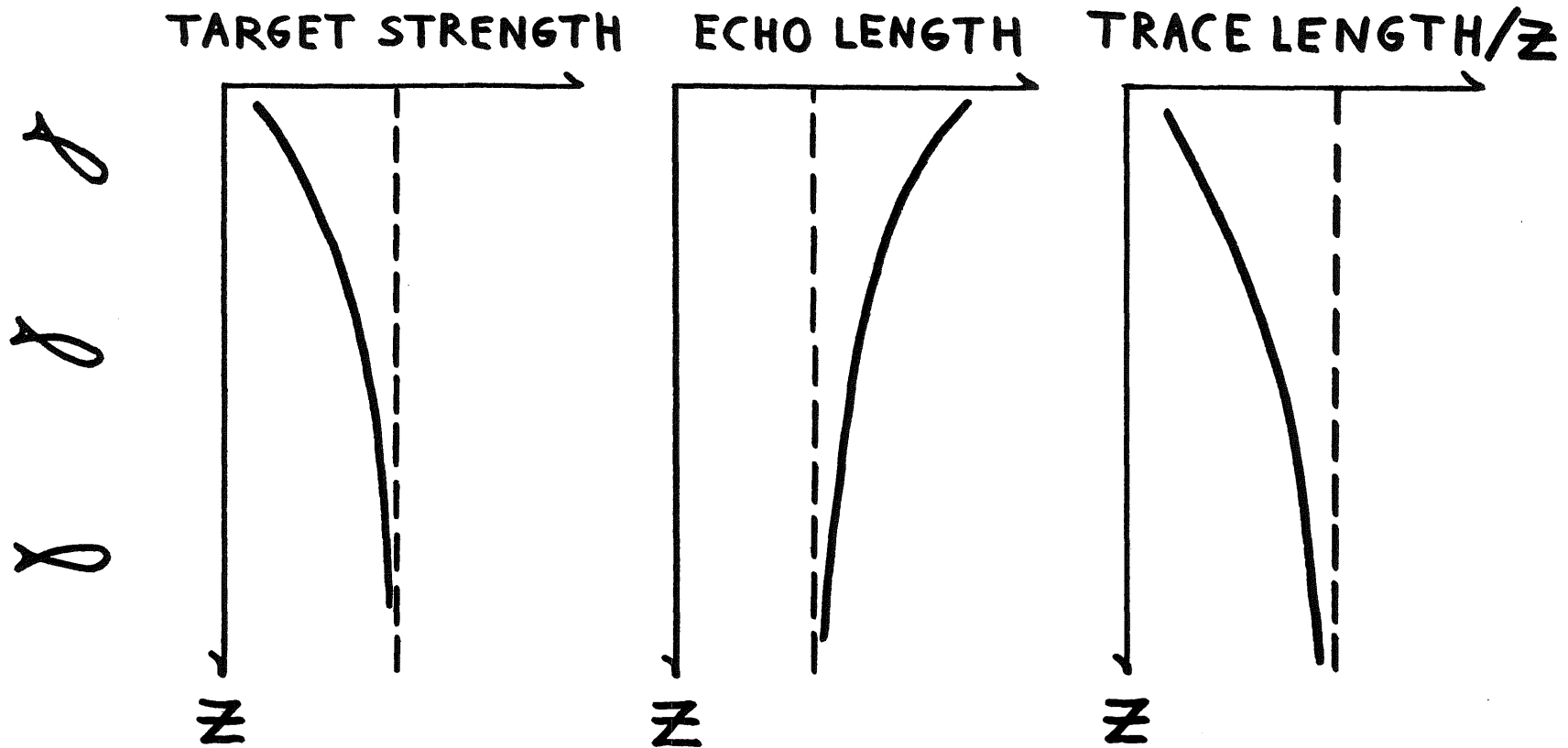


Fig. 4. Comparison of three acoustic methods for detecting avoidance reaction. Mean quantities are plotted against depth z , with and without avoidance reaction.

