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A re-evaluation of relationships between fish size, acoustic frequency, and target strength

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There are many measurements of dorsal aspect target strength of fish, but relatively few studies compare estimation methods or attempt to combine data from different studies into general relations between fish size, acoustic frequency and target strength (or acoustic cross-section). We edited and updated earlier summary regressions relating fish size, acoustic frequency and acoustic cross-section. Experimental measurements on marine fish were separated into swimbladder and non-swimbladder species, model results compared with experimental data, target strengths of marine, and freshwater fish were contrasted, and previous and new target strengths of commercial New Zealand fish species were placed in the context of the new regressions. Analysis of variance was used to show significant effects of species, freshwater vs. marine, swimbladder vs. non-swimbladder fish, model vs. experimental, and dead vs. alive fish on the relationship between maximum dorsal aspect target strength and fish length. For experimental results on gadoids we found significant species and live vs. dead (or stunned) fish effects on the target strength to length relationship. The quadratic dependence of target strength on fish length was also tested and found to be the exception rather than the rule. Existing pitch tilt angle data was compiled and a normal distribution with standard deviation of at least 15° was required to describe most distributions.

Key words: acoustics, target strength, length, regression, orientation.

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Introduction

There are many experimental measurements of fish target strength (see Foote, 1991), but relatively few studies have compiled existing data into regressions to predict target strength (TS), or acoustic cross-section (σ) from fish size and acoustic frequency. The published regressions differ according to whether the dependent variable (TS or σ) was normalized by fish length (Love, 1971; Miyanohana *et al.*, 1990), acoustic wavelength (Haslett, 1965; Love, 1969, 1971, 1977; McCartney and Stubbs, 1971), or was unnormalized (Nakken and Olsen, 1977; Foote, 1980). Predicting target strength from regressions is necessarily imprecise due to pooling of data across species and frequencies. Foote (1979) used analysis of covariance to show that target strengths of different species had distinct relationships to length and frequency and should not be pooled. This makes the choice of wavelength or length-based normalization scheme immaterial. Both normalization schemes suffer from the compounded ratio problem where the occurrence of the same variable on both axes affects the correlation on the plot (Atchley *et al.*, 1976). The magnitude of the compounded ratio effect depends upon the relative variance of the dependent and independent variables.

When there are no other estimates of target strength for a species, it is tempting to use such regressions to predict target strength for use in acoustic surveys. The usefulness of predictive equations was addressed in a series of papers in the late 1970s and early 1980s (Foote, 1979, using data of Nakken and Olsen, 1977, edited by Foote and Nakken, 1978; Foote, 1980; MacLennan, 1981). Misuse of predictive regressions for target strength can produce large errors in acoustic estimates of abundance (Foote, 1980). We re-examine at what level, if any, data may be pooled and still remain useful for predicting maximum dorsal aspect target strength. This

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is a useful exercise, first, because a large amount of new data has been gathered in the last 15 years, and second, because we are obtaining new target strength data on New Zealand species which we want to place in the context of the existing work on other species.

Foote (1980) emphasized that regressions of target strength on length and frequency are only useful for fisheries surveys if TS is averaged with respect to the correct fish orientation distribution and the transducer beam pattern (Foote, 1980) although Miyanohana (1990) demonstrated that averaging the beam pattern makes very little difference for half-beam widths less than 15°. Even without averaging, we consider that regressions of target strength on length and frequency can serve a useful purpose – that of summarizing a large amount of data to place new information in context. For example, if we discover that certain New Zealand species fall outside the data envelope, we may then focus on the unique features of these species. Unusual features affecting target strength of New Zealand species include the bony head plates and oil filled swimbladder of orange roughy, *Hoplostethus atlanticus*, and an unusually high total length to swimbladder length ratio in hoki, *Macruronus novaezelandiae*, as compared to cod or pollack.

In this study, we extended regressions relating acoustic cross-section to fish length and acoustic frequency by editing earlier data sets (Haslett, 1965; Love, 1971) and adding selected, more recent results. Our coverage of the data is intended to be representative rather than compendious. In Haslett (1965) and Love (1971), freshwater and marine target strength data were presented together, swimbladder fish were combined with non-swimbladder species, no distinction was made between dead and alive fish, and no model results were included. Following Foote's (1979) example, we used analysis of variance to determine at what level the data might usefully be combined. The influence of selected independent variables on maximum dorsal aspect target strength was determined: the variables were species, presence or absence of the swimbladder, freshwater vs. marine, model vs. experimental, and stunned (or dead) vs. live fish. We used the experimental data for gadoids (*Pollachius pollachius*, *Pollachius virens*, *Gadus morhua*), which were assumed to be an homogeneous subset of species, to examine the effect of species and stunned (or dead) vs. alive fish. We also review new and published estimates of target strength of New Zealand commercial fish species in the context of trends in the regressions. Orange roughy were excluded because maximum dorsal aspect target strengths were not available. The assembled data sets were then used to address the validity of quadratic dependence of target strength on fish length. Last, we examined the available fish orientation data known to us in the context of using tilt angle distributions to average target strength.

Methods

Acoustic cross-section, fish size, and acoustic frequency

In this paper we consider only measurements of maximum dorsal aspect target strength (TS_{max}). We carefully selected TS_{max} data rather than the target strengths estimated from fish normal to the beam, because swimbladders are generally offset to the body axis. TS_{max} was used partly because it was used in the original papers (Haslett, 1962, 1965; Love, 1971), but also because the method of averaging target strength with respect to orientation of the fish varies in the literature and so increases the variance of the data.

Target strength data were digitized from graphs in the original publications. In cases where only part of the data set was readable, we recorded the number of digitized data points and compared it to the expected sample size calculated from information reported by the authors (Table 1). The core data sets came from the wavelength-normalized regressions of acoustic cross-section on fish size (Haslett, 1962, 1965; Love, 1971). Certain of the core data sets were excluded: one paper because we were unable to convert the units (Shishkova, 1964), three Japanese papers because we were unable to interpret their results from the English translations (Hashimoto and Maniwa, 1955, 1956a,b), and one paper because we were unable to identify the three species of fish used (Yudanov *et al.*, 1966). Data on sticklebacks and guppies (Haslett, 1962) were excluded because they are a suite of species (*Poecilia* spp.) that could not be separated to genus. These data were collected at very high (MHz) frequencies and so are not particularly relevant to this study. Minnows were also excluded because they are a group of species (Haslett, 1965). We decided to include a limited number of data from cod with artificially inserted swimbladders (Cushing *et al.*, 1963) because we were interested in the contrast between live and dead fish.

Many more recent data sets were added (Foote, 1979, using data of Nakken and Olsen, 1977, edited by Foote and Nakken, 1978; Mukai *et al.*, 1993; Clay and Horne, 1994) (Table 1), but some data were not included, e.g. where an unspecified species of cod was measured in fresh water (Fedotova and Shatoba, 1982) or data were not available to us at reasonable cost (Buerkle and Sreedharan, 1981; Yudanov and Kalikhman, 1981). We did not include data from wide band systems (McCartney and Stubbs, 1971; Kjaergaard *et al.*, 1990). We also excluded *in situ* measurements (Traynor and Ehrenberg, 1979, 1990; Halldórsson and Reynisson, 1982; Dawson and Karp, 1990; Guillard and Gerdeaux, 1993; Barange and Hampton, 1994) or encaged fish experiments (Edwards and Armstrong, 1982; Edwards *et al.*, 1984; Goddard and Welsby, 1986; MacLennan *et al.*, 1990) where the length of individual fish could not be matched to target strength. In other cases, we had to exclude sources that reported

Table 1. Fish species used in the wavelength normalized regressions of maximum dorsal aspect target strength on fish length, including the source of the data, whether fish have a swimbladder (y) or not (N), are marine (F) or freshwater (M), and whether data come from experimental measurements (0) or model estimates. For model estimates, the type of model is given: 1=mapping method; 2=Do and Surti (1990); 3=Clay and Horne (1994); 4=Stanton (1989). The number of fish and number of frequencies used in experiments or model calculations is given if reported. In some cases overlapping points prevented all data being digitized and the number of digitized points (OBS) is compared to the number of points expected (EXP=number of fish × number of frequencies) to estimate the number of points not included (DIFF=OBS − EXP).

Species	Swim	Fr/Mar	Model	Source	Fish	Freq	EXP	OBS	DIF
Bay anchovies *Anchoa mitchilli*	y	M	0	(Love, 1971)	6	8	48	41	− 7
Atlantic menhaden *Brevoortia tyrannus*	y	M	0	(Love, 1971)	1	8	8	5	− 3
Goldfish *Carassius auratus*	y	F	0	(Love, 1971)	5	8	40	34	− 6
Herring *Clupea harengus*	y	M	0	(Nakken and Olsen, 1977)	41	2	82	76	− 6
Kandari *Collichthys lucidus*	y	M	0	(Mukai *et al.*, 1993)	9	2	18	16	− 2
Spotted seatrout *Cynoscion nebulosus*	y	M	0	(Love, 1971)	4	8	32	25	− 7
Yellow sea bream *Dentex tumifrons*	y	M	0	(Mukai *et al.*, 1993)	12	2	24	21	− 3
Mummichog *Fundulus heteroclitus*	y	M	0	(Love, 1971)	3	8	24	22	− 2
Striped killifish *Fundulus majalis*	y	M	0	(Love, 1971)	5	8	40	33	− 7
Atlantic cod *Gadus morhua*	y	M	3	(Clay and Horne, 1994)	4	2	8	8	0
Atlantic cod *Gadus morhua*			0	(Cushing *et al.*, 1963)	?	1	?	39	—
Atlantic cod *Gadus morhua*			0	(Foote, 1979)†	54	2	108	108	0
Atlantic cod *Gadus morhua*			0	(Midttun and Hoff, 1962)	11	1	11	11	0
Atlantic cod *Gadus morhua*			0	(Sothcott, unpubl.)*	?	2	?	26	—
Sticklebacks *Gasterosteus aculeatus*	y	F	0	(Haslett, 1962)	8	1	8	8	0
Belenger's jewfish *Johnius belengerii*	y	M	0	(Mukai *et al.*, 1993)	10	2	20	14	− 6
Whitefin crevalle *Kaiwarinus equula*	y	M	0	(Mukai *et al.*, 1993)	10	2	20	20	0
Hoki *Macruronus novaezelandiae*	y	M	2	(Do and Surti, 1990)	23	1	23	23	0
Atlantic silverside *Menidia menidia*	y	M	0	(Love, 1971)	6	8	48	43	− 5
Southern blue whiting *Micromesistius australis*	y	M	1	(McClatchie *et al.*, 1996)	10	2	10	10	0
Brown croaker *Miichthys miiuy*	y	M	0	(Mukai *et al.*, 1993)	9	2	18	16	− 2
Silver pomfret *Pampus argenteus*	N	M	0	(Mukai *et al.*, 1993)	9	2	18	18	0
European (river) perch *Perca fluviatilis*	y	F	0	(Harden Jones and Pearce, 1958)	10	1	10	10	0
Pollack *Pollachius pollachius*	y	M	1	(Foote and Ona, 1987)	13	4	52	52	0
Pollack *Pollachius pollachius*			0	(Foote 1979)†	38	2	76	76	0
Saithe *Pollachius virens*	y	M	1	(Foote and Ona, 1987)	2	4	8	8	0
Saithe *Pollachius virens*			0	(Foote 1979)†	51	2	102	102	0
Saithe *Pollachius virens*			0	(Midttun and Hoff, 1962)	2	1	2	2	0
Black crappies *Pomoxis nigromaculatus*	y	F	0	(Love, 1971)	6	8	48	30	− 18
Japanese butterfish *Psenopsis anomala*	y	M	0	(Mukai *et al.*, 1993)	8	2	16	15	− 1
Red cod *Pseudophycis bachus*	y	M	1	(McClatchie *et al.*, 1996)	3	2	6	6	0
Spotted mackerel *Scomber australasicus*	?	M	0	(Miyanohana *et al.*, 1990)	15	4	60	81	21
Chub mackerel *Scomber japonicus*	N	M	0	(Mukai *et al.*, 1993)	10	2	20	14	− 6
Atlantic mackerel *Scomber scombrus*	N	M	0	(Foote, 1980)	29	2	58	59	1
Yellowtail (Japan) *Seriola quinqueradiata*	y	M	0	(Miyanohana *et al.*, 1990)	10	4	40	35	− 5
Sprat *Sprattus sprattus*	y	M	0	(Nakken and Olsen, 1977)	29	2	58	60	2
Black scraper *Thamnaconus modestus*	y	M	0	(Mukai *et al.*, 1993)	9	2	18	18	0
Barracouta *Thyrsites atun*	y	M	1	(McClatchie *et al.*, 1996)	10	2	20	20	0
Yellowfin horse *Trachurus japonicus*	y	M	0	(Mukai *et al.*, 1993)	10	2	20	18	− 2
Horse mackerel *Trachurus trachurus*	y	M	0	(Barange and Hampton, 1994)	12	1	12	12	0

†Data of Nakken and Olsen (1977) edited by Foote and Nakken (1978).

*Sothcott's unpublished data were presented by Haslett (1965).

mean rather than maximum dorsal aspect target strength (Goddard and Welsby, 1986).

Quadratic dependence of target strength on fish length

One method commonly used to compare length related differences in TS_{max} between taxa is to force the regression of target strength on length through a slope of 2, and then compare the regression intercepts (Foote, 1979). The rationale for this is the postulated quadratic relation between TS_{max} and length. This relation was tested by plotting the slope and standard error of the slope for 28 species, and comparing it to the expected value of 2. We then forced the regression slopes through 2 and compared the intercepts to determine whether morphologically similar and taxonomically related species grouped together.

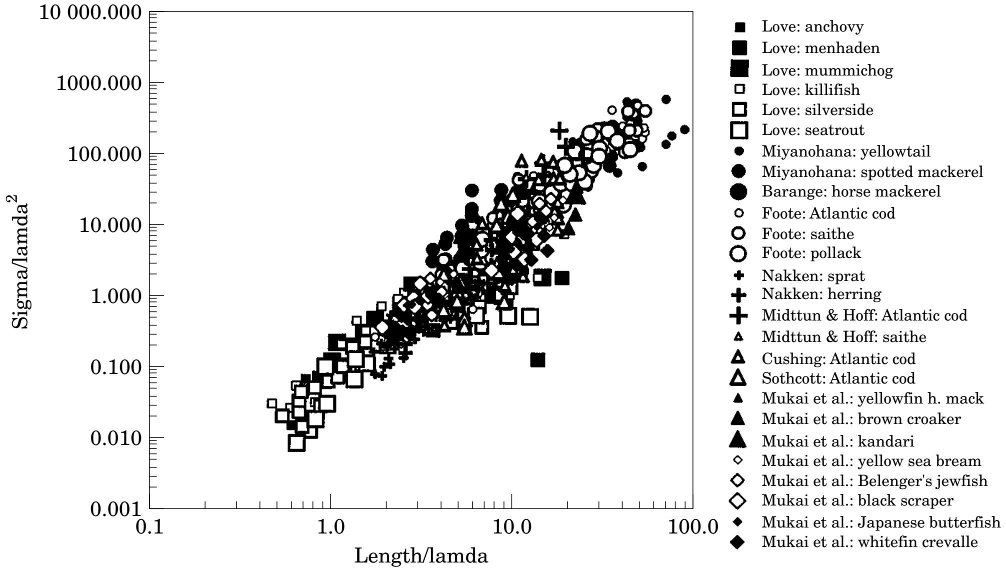

Figure 1. Wavelength normalized acoustic cross-section (sigma/lambda^2) plotted against wavelength normalized fish length (length/lambda) for experimental results on marine swimbladder fishes. All data are for single fish maximum dorsal aspect TS. See text for discussion of data set selection. Data sources and species names are given in Table 1.

Fish orientation

There are few data sets on the tilt angle (or pitch) of fish (Olsen, 1971; Beltestad, 1974; Carscadden and Miller, 1980; Foote, 1980, 1983; Angell, 1983; Ona, 1984; Long and Aoyama, 1985; Foote and Ona, 1987; Coombs and Cordue, 1995), and only one pertains to fish beneath a moving survey vessel (Olsen *et al.*, 1983). Although the parameters of tilt angle distributions were summarized by Foote (1987) the existing data have not been plotted together, so we have assembled them and added some results for hoki (A. MacDiarmid, unpubl. data). We did not include Long and Aoyama's (1985) data because their sample sizes were very small (5–7 individuals per species), and neglected data in one Norwegian thesis (Angell, 1983) because we lacked a translation. We obtained the data in another Norwegian thesis (Beltestad, 1974) from a figure in Nakken and Olsen (1977). Our aim was to illustrate the severe lack of fish orientation data. To determine if the spread of measured tilt angles is greater than that usually assumed when calculating tilt-averaged target strengths, a normal curve with standard deviations of 5° and 15° was superimposed on the data, centred on the mean of each frequency distribution.

Results

Acoustic cross-section as a function of fish size and acoustic frequency

By far the greatest number of target strength measurements have been made in experiments on marine fish with swimbladders (Fig. 1 and Table 1). Although the variability is high, acoustic cross-section clearly shows length and frequency dependence (as shown by Haslett, 1962 and others). Variability is generally greater for higher length/λ, as noted by McCartney and Stubbs (1971), because length/λ is the controlling factor for directivity.

We were only able to locate two data sets from experimental measurements on non-swimbladder fish (Fig. 2, Table 1). Although scattered data with very small sample sizes exist they were not included (Nakken and Olsen, 1977). As expected, the non-swimbladder fish generally fall below the trend line for swimbladder species. Variability of target strength from non-swimbladder species is greater than for swimbladder fish because length/λ is greater for the whole body than for a swimbladder alone. For a given length of fish and insonifying frequency (hence wavelength), the directivity of the non-swimbladder fish will be greater, thereby creating higher variability in the data.

Model data from the mapping method (Foote and Ona, 1985; McClatchie *et al.*, 1996), equicylinder model (Do and Surti, 1990), deformed cylinder model (McClatchie *et al.*, 1996), and a modification of the Kirchhoff method (Clay and Horne, 1994) fall within the trend line for the experimental data (Fig. 3, Table 1). The target strengths for hoki based on the equicylinder model are lower than for other species of the same size. This may be due to the unusual morphology of hoki (discussed below).

There are few data for New Zealand species but, with the exception of slightly lower than expected target

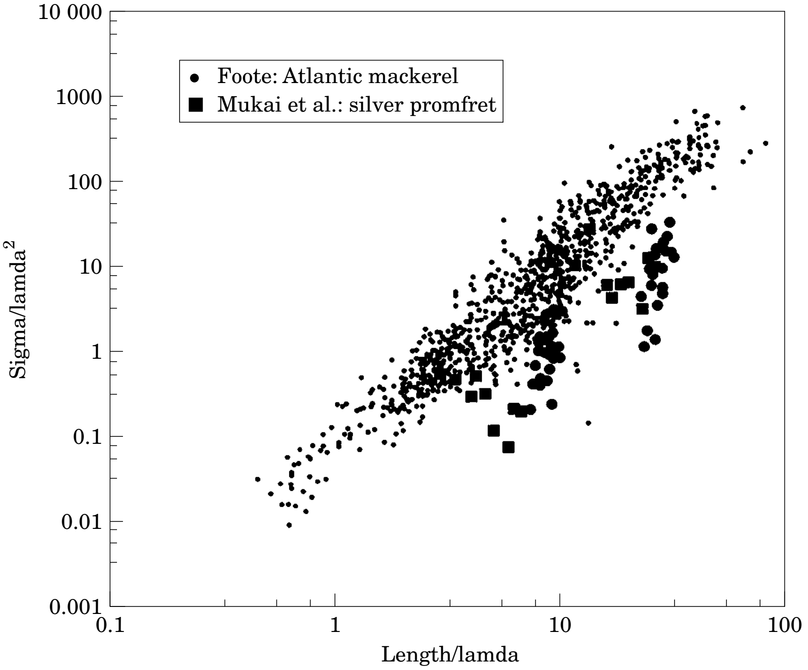

Figure 2. Wavelength normalized acoustic cross-section (sigma/lambda^2) plotted against wavelength normalized fish length (length/lambda) for experimental results on marine non-swimbladder fishes. Data from Figure 1 are plotted as dots for comparison. All data are for single fish maximum dorsal aspect TS. See text for discussion of data set selection. Data sources and species names are given in Table 1.

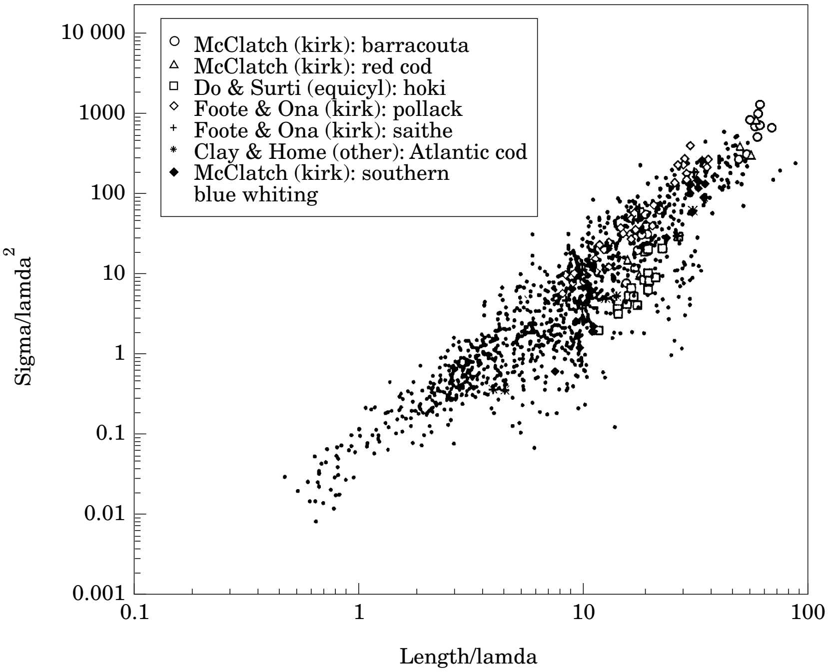

Figure 3. Wavelength normalized acoustic cross-section (sigma/lambda^2) plotted against wavelength normalized fish length (length/lambda) for selected modelling results on marine swimbladder fishes. Data from Figure 1 are plotted as dots for comparison. All data are for single fish maximum dorsal aspect TS. See text for discussion of data set selection. Data sources and species names are given in Table 1.

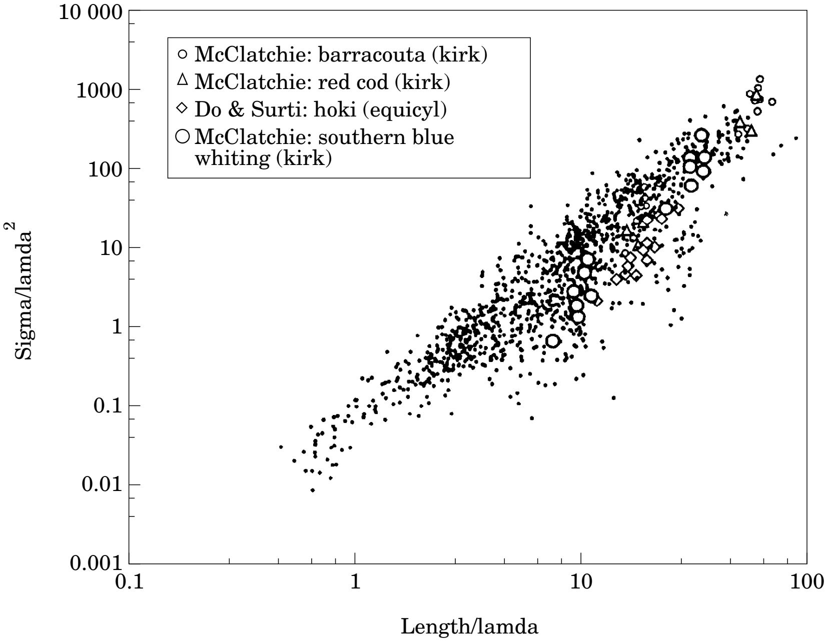

Figure 4. Wavelength normalized acoustic cross-section (sigma/lambda^2) plotted against wavelength normalized fish length (length/lambda) for New Zealand species. Data from Figure 1 are plotted as dots for comparison. All data are for single fish maximum dorsal aspects TS. See text for discussion of data set selection. Data sources and species names are given in Table 1.

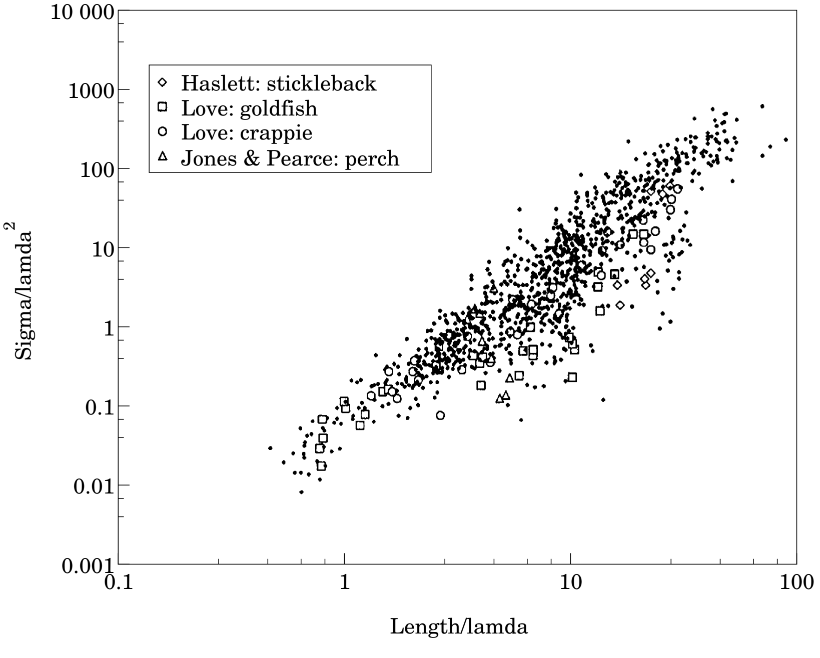

Figure 5. Wavelength normalized acoustic cross-section (sigma/lambda^2) plotted against wavelength normalized fish length (length/lambda) for experimental results on freshwater species. Data from Figure 1 are plotted as dots for comparison. All data are for single fish maximum dorsal aspect TS. See text for discussion of data set selection. Data sources and species names are given in Table 1.

Table 2. Analysis of variance for the entire TS_{max} data set testing the effect on TS_{max} of species, marine or freshwater, presence of a swimbladder, alive or dead (or stunned), and model applied.

	Sums of squares	df	Mean square	F	p-level
Species	98.06	32	3.064	38.3	<0.001
Swimbl	7.52	1	7.520	93.97	<0.001
Model	8.37	3	2.789	34.86	<0.001
Marine/freshwater	4.32	1	4.317	53.95	<0.001
Alive/dead	5.98	2	1.992	24.9	<0.001
Error	96.75	1209	0.080	—	—

Table 3. Analysis of variance for the gadoid TS_{max} data set testing the effect on TS_{max} of species and model applied.

	Sums of squares	df	Mean square	F	p-level
Species	2.12	2	1.058	18.8	<0.001
Model	2.02	2	1.012	17.98	<0.001
Error	23.97	426	0.056	—	—

strengths for hoki, the red cod and barracouta (McClatchie *et al.*, 1996) agree well with the trends for other species (Fig. 4, Table 1). Target strengths for southern blue whiting were variable, with some unexpectedly low values for swimbladder fish (McClatchie *et al.*, 1996). So far, the sample sizes for target strength measurements on any New Zealand species are small (3–23 fish, Table 1) and size ranges are relatively narrow.

The freshwater data are sparse compared to the marine and appear to be a little more variable (Fig. 5). The slope of the regression is less than that for marine fish. We would expect a difference between marine and freshwater target strengths of identical fish because the reflection coefficients between fish tissues and the water differs between marine and fresh water.

The results from analysis of variance strongly supported Foote's (1979) contention that the TS_{max} data are heterogeneous. For the entire data set, we found significant effects of species, marine or fresh water, live vs. dead fish, presence of a swimbladder, and the model applied (Table 2). The test was made across 33 species. F-values for all independent variables were significant at the 0.1% level. For the gadoid data alone, the effects of species and the model applied were highly significant ($p<0.001$) (Table 3). This test was made across three species (cod, pollack, and saithe) and three models.

Morphological considerations

Hoki differ in their morphology from Atlantic cod, pollack, barracouta and southern blue whiting. The ratio of swimbladder length to fish length for hoki contrasts with the other four species (Fig. 6) because hoki have a long, tapering tail so that, for a given size, they have a comparatively shorter swimbladder. This produces a lower target strength than would be estimated for a cod or pollack of the same size. The effect is more notable when using the equicylinder model (Do and Surti, 1990) compared to Stanton's (1989) model. Previous work (Midttun and Hoff, 1962) showed that the ratio of swimbladder length to height strongly influenced target strength, and caused species specific differences (e.g. between cod and saithe) that were a function of the different shapes of their swimbladders.

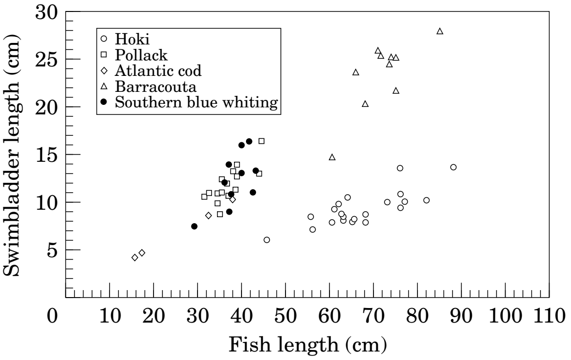

Figure 6. Swimbladder length to fish length ratios for hoki (*Macruronus novaezelandiae*) compared to Atlantic cod (*Gadus morhua*), pollack (*Pollachius pollachius*), barracouta (*Thyrsites atun*) and southern blue whiting (*Micromesistius australis*).

Quadratic dependence of target strength on fish length

We found that most species do not conform closely to the quadratic dependence of target strength on fish length (Fig. 7). Silver pomfret and sprat show the closest agreement to quadratic dependence, although confidence limits are very wide for silver pomfret. The mean slope for most species falls between 1.5 and 2.5. Horse mackerel and brown croaker show the largest deviation from the quadratic rule. Twenty of 26 species have slopes less than 2. The gadoids (Atlantic cod, saithe and pollack) all have slopes greater than 2. The gadoids have mean slopes ranging between 2.15 and 2.48 with narrow confidence limits (Fig. 7).

Forcing the slope through 2, and comparing the intercepts of the target strength–length regressions (Foote, 1979) produces both reasonable and curious groups of species. The intercepts for gadoids group with intercepts for yellowtail, spotted mackerel, yellowfin horse mackerel, and chub mackerel (Fig. 8, Table 1). Yellowfin horse mackerel (*Trachurus japonicus*), yellowtail (*Seriola quinqueradiata*), and chub mackerel (*Scomber japonicus*) are all swimbladder species but we

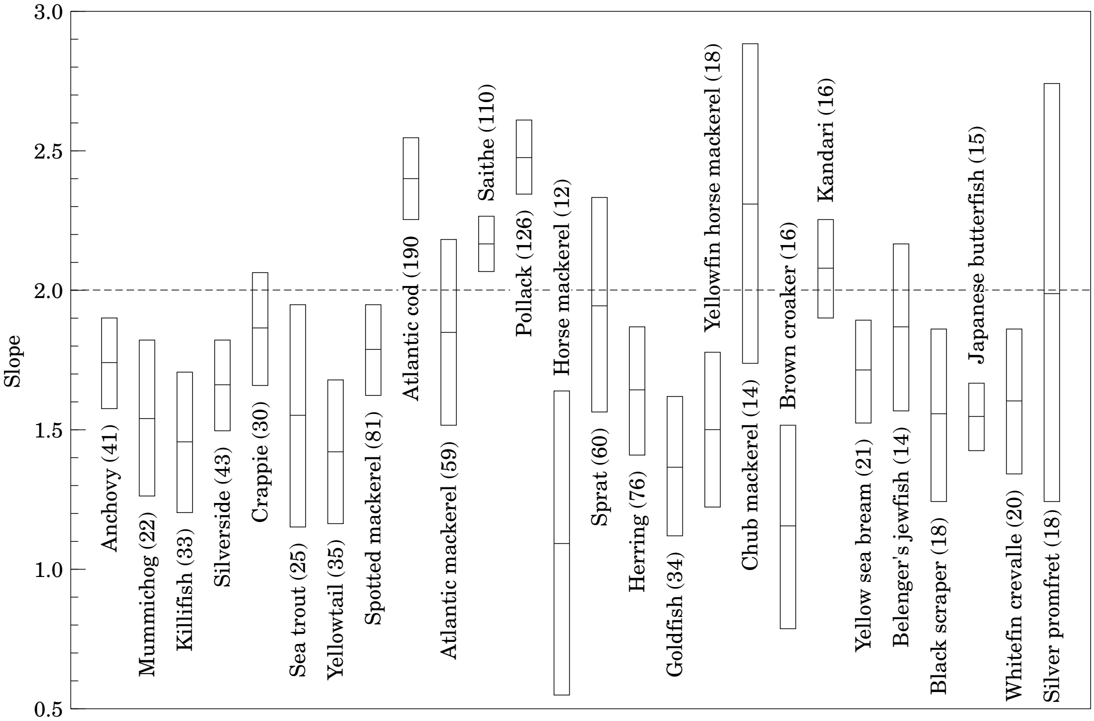

Figure 7. Slope and 95% confidence limits for the slope of regressions relating maximum dorsal aspect target strength to fish length for species and data listed in Table 1. Numbers in brackets are the numbers of individual fish.

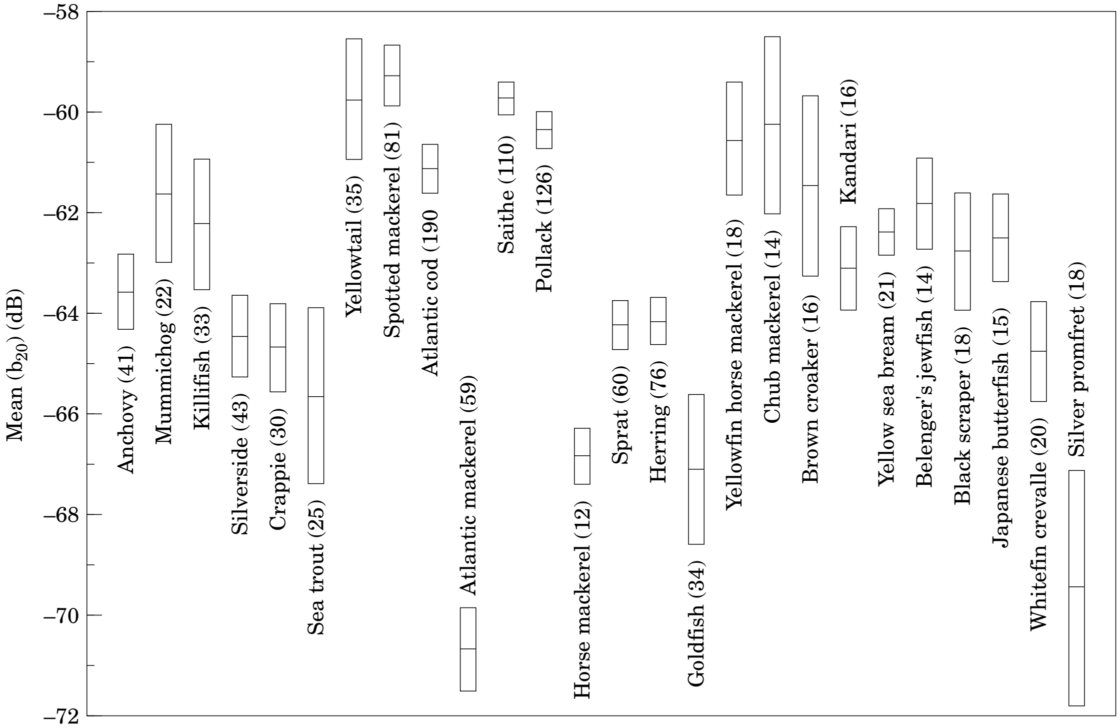

Figure 8. Intercept and 95% confidence limits for the intercept of regressions relating maximum dorsal aspect target strength to fish length for species and data listed in Table 1, where the slope has been forced to reflect quadratic dependence. The intercept, b_{20}, was estimated from $TS_{max}=20 \log \text{Length}+b_{20}$.

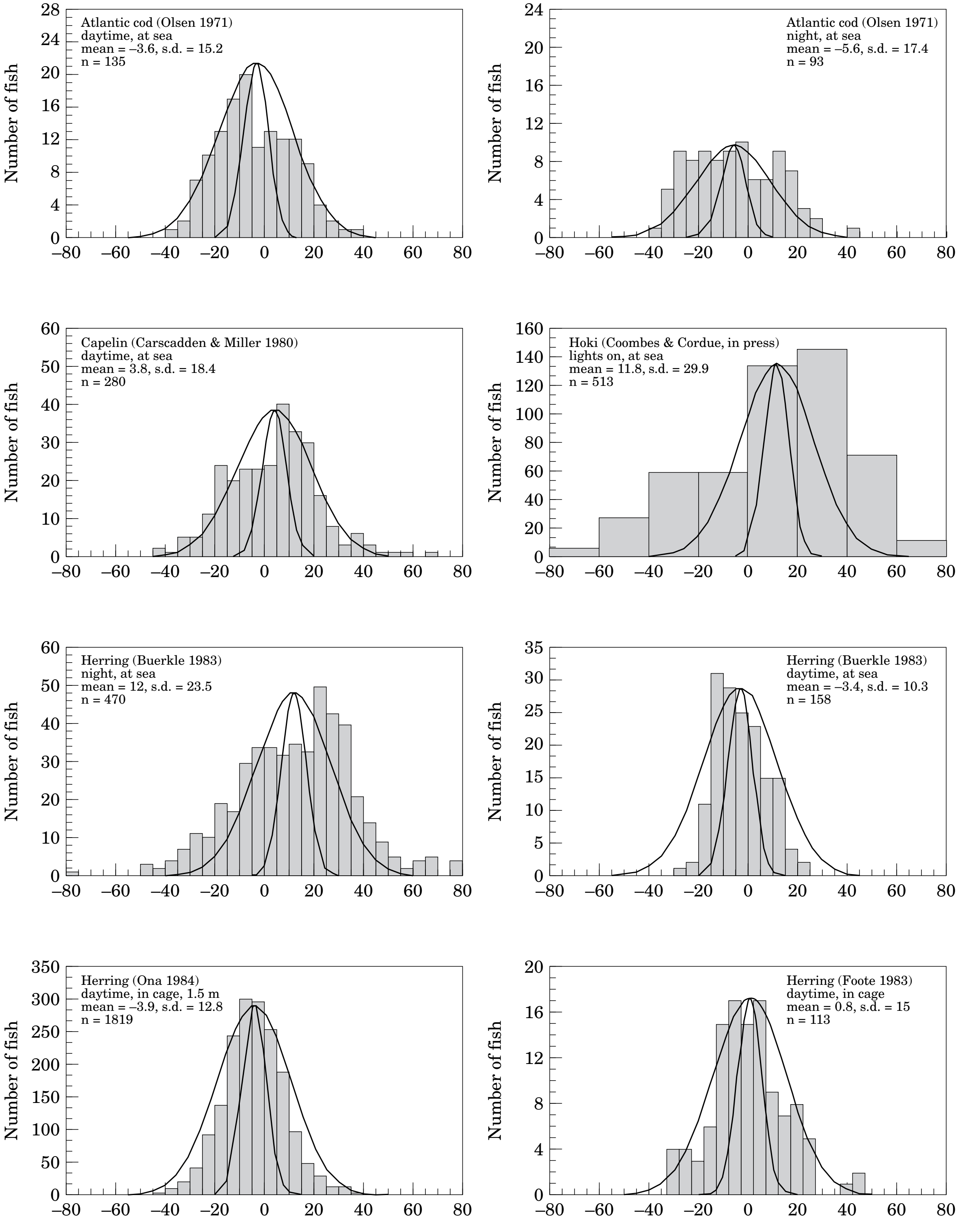
Atlantic cod (Olsen 1971)
daytime, at sea
mean = –3.6, s.d. = 15.2
n = 135
Atlantic cod (Olsen 1971)
night, at sea
mean = –5.6, s.d. = 17.4
n = 93
Capelin (Carscadden & Miller 1980)
daytime, at sea
mean = 3.8, s.d. = 18.4
n = 280
Hoki (Coombes & Cordue, in press)
lights on, at sea
mean = 11.8, s.d. = 29.9
n = 513
Herring (Buerkle 1983)
night, at sea
mean = 12, s.d. = 23.5
n = 470
Herring (Buerkle 1983)
daytime, at sea
mean = –3.4, s.d. = 10.3
n = 158
Herring (Ona 1984)
daytime, in cage, 1.5 m
mean = –3.9, s.d. = 12.8
n = 1819
Herring (Foote 1983)
daytime, in cage
mean = 0.8, s.d. = 15
n = 113
Number of fish
–80
–60
–40
–20
0
20
40
60
80

Figure 9.

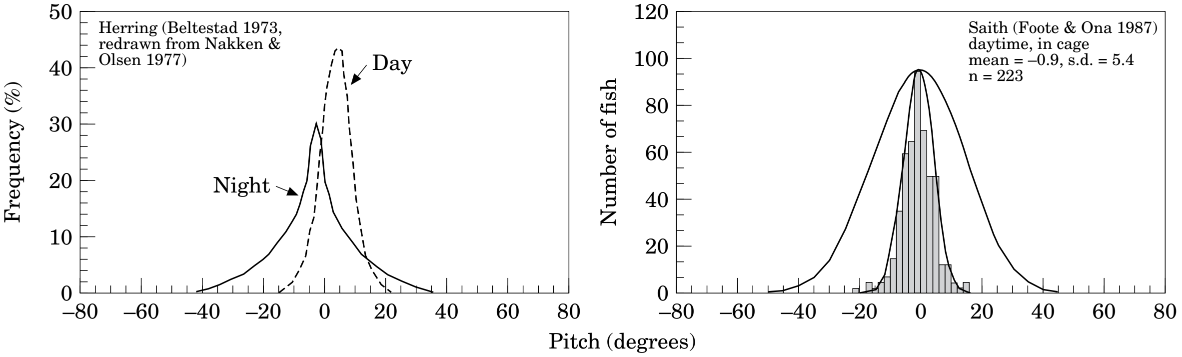

Figure 9. Pitch plane distribution of tilt angles from the literature for Atlantic cod (*Gadus morhua*), Capelin (*Mallotus villosus*), hoki (*Macruronus novaezelandiae*), herring (*Clupea harengus*) and saithe (*Pollachius virens*). Normal curves with standard deviations of 5° and 15° are centred on the mean of each tilt angle distribution. Data source, mean tilt angle, standard deviation and number of fish comprising the distribution are given on each graph.

were unable to determine whether spotted mackerel (*Scomber australasicus*) has a swimbladder. Despite the three mackerels having a swimbladder they are morphologically very different from the gadoids. Two non-swimbladder species (Atlantic mackerel and silver pomfret) group together, again despite major differences in body form. Although chub mackerel (*Scomber japonicus*) and Atlantic mackerel (*Scomber scombrus*) are closely related species, chub mackerel have a swimbladder and Atlantic mackerel do not (Collette and Nauen, 1983). The intercepts of the forced target strength–length regression fall on opposite ends of the range for these species, as expected. These groupings predominantly appear to reflect the presence or absence of a swimbladder and indicate that comparing intercepts after forcing the slope through 2 may not be sensitive to target strength differences between species, although it is a useful method for gadoids (Foote, 1979).

Fish orientation

Data on fish orientation are scarce and we have assembled virtually all of them in this paper. The existing data on fish orientation strongly suggest that the tilt angle distributions of fish measured by stationary or slowly towed cameras can be quite different to that in shallow fish schools beneath a survey vessel. Mean tilt angle for the 10 distributions measured with cameras range from 12° (head up from horizontal) to $-5.6°$ (head down) (Fig. 9). Standard deviations for tilt distributions range from 10.3–29.9° (Fig. 9). In sharp contrast, a mean tilt angle of $-27.5°$ was measured for herring at 40–50 m diving beneath a survey vessel travelling at 11 kn (Olsen *et al.*, 1983). Apart from these diving herring, which were apparently uniformly fleeing the ship and so had a narrow standard deviation of tilt angles (S.D. = 5°), the standard deviation of tilt angle distributions is generally wider than 5°. For cod, herring, capelin, and hoki orientation, the standard deviation was closer to 15°. The exception was the narrow distribution measured by Foote (1983) on saithe in a cage (Fig. 9). We do not mean to suggest here that avoidance behaviour is inherent, although there is evidence that fish may avoid a noisy vessel if the vessel is too close (Mitson, 1993).

Discussion

Dead or stunned fish have different target strengths from swimming fish but most experiments have been done on moribund fish (MacLennan, 1981). Many experimental data are from one season and neglect the important effects of feeding state, gonad development and pressure (or depth) on the volume of the swimbladder, and, hence, target strength in many fish (Ona, 1990). The relationship between target strength and swimbladder distortion due to compression by the stomach or gonads has been quantified only approximately (Ona, 1990). Fat content of fish is a diurnally and seasonally variable factor related to both feeding and gonad development. Normalizing target strength by the fat content might reduce the variability of target strength because swimbladder volume is less variable in relation to fish size when volume is normalized by fat content (Ona, 1990). This cannot be done because fat content is not generally reported.

Our analysis supports Foote's (1979) assertion that, for the purposes of prediction, target strength should not be pooled across taxa. This holds even within groups of morphologically similar, closely related species such as gadoids. The effect on TS_{max} of species, marine or freshwater, presence of a swimbladder, being alive or dead, and the modelling method applied are all highly significant. Within the gadoids, both the species and the modelling method have significant effects. This shows that each species has to be dealt with separately, but even within species care should be exercised in comparing TS_{max} from different models. Comparisons between species using the intercept of target strength–length regressions forced through a slope of 2 only appears to be useful within groups such as the gadoids.

The fact that we can present virtually the entire data set for tilt angle distributions of fish on a single page underlines the need for more information (Foote, 1980). The data also show that using a normal curve with standard deviation of 5° to average target strength is inappropriate because the pitch tilt distributions generally have a standard deviation of 15° (or larger for hoki). For some fish such as orange roughy, which are strongly flattened in the dorso-ventral plane, the roll tilt distribution may be more important than the pitch tilt distribution. These data are even more uncommon than the pitch distributions, and need to be measured if we are to model target strength accurately for these species.

Conclusions

(1) Analysis of an extensive data set* showed that the relationship between target strength and fish length is species specific, depends upon presence of the swimbladder, and is affected by whether fish are freshwater or marine, and alive or dead. These results are in agreement with Foote (1979). A more limited analysis showed that target strength depends on the model used to estimate it.
(2) Recent estimates of target strength for New Zealand species presented in the context of the global data revealed that hoki (*Macruronus novaezelandiae*) morphology leads to lower than expected target strengths.
(3) Using the intercepts from regressions of the form *target strength=20 log length+a* is an inappropriate way to compare target strength of different species.
(4) A compilation of published and new fish orientation distributions showed that the normal distribution with a standard deviation of at least 15° should be used to average target strengths for use in acoustic surveys.

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*Data available as a text file from National Institute of Water and Atmosphere FTP site: http://www.niwa.cri.nz (contact s.mcclatchie@niwa.cri.nz)

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