

Characterizing uncertainty in target-strength measurements of a deepwater fish: orange roughy (*Hoplostethus atlanticus*)

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The variability of ensemble 38 kHz, target-strength (TS_{38}) estimates for orange roughy (*Hoplostethus atlanticus*) (4.9 dB, factor of 3.1) in deep water (>600 m) limits the use of echo integration for absolute-biomass estimates. Orange roughy are high in oil content, have a wax ester swimbladder, and show an active-avoidance response to sampling gear. The interpretations of ensemble, *in situ* target strengths of orange roughy (range $\langle TS_{38} \rangle = -52.9$ to -51.0 dB for standard fish length $\langle SL \rangle = 35$ cm) are lower than previous model and surface-based measurements ($\langle TS_{38} \rangle = -48$ dB, $SL = 35$ cm). *In situ* TS measurements from individuals on the periphery of dense schools were processed to minimize uncertainties from single-target selection criteria, species composition, and active avoidance. Video and acoustic-tracking data quantified the variability in TS measurements arising from the variability in fish orientation. Multi-frequency acoustics and fish tracking are used to quantify *in situ* TS variability due to species identification and fish density. The Kirchhoff-ray mode backscatter model was used to illustrate the sensitivity of species-specific backscatter to assumptions of tilt-angle and material properties (density and sound-speed contrasts). We conclude that a remaining source of uncertainty for *in situ* TS measurements is the assumption that dispersed targets are representative of the survey population.

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Introduction

The life-history characteristics of exploited, deepwater (>600 m) fish species such as orange roughy (*Hoplostethus atlanticus*): long-lived, late age of maturity, slow growth, and low fecundity (Koslow *et al.*, 2000), are different from those of most continental-shelf species. Orange roughy fisheries have existed in New Zealand and Australian waters for the past decade and new ones have developed off Namibia, Chile, and on the high seas (Branch, 2001). Acoustic surveys are used in Australia, New Zealand, and Namibia on spawning aggregations to quantify stock abundance (Kloser *et al.*, 1996; McClatchie *et al.*, 1999; Boyer and Hampton, 2001). In Australia, a relative-acoustic index is used to monitor population trends (Bax, 1999), but the managers in New Zealand have requested absolute-biomass estimates with a target coefficient of variation of 30% (J. Annala, Ministry of Fisheries, personal

communication). Accurate, absolute-abundance estimates rely on accurate, target-strength (TS) measures when using the echo-integration technique (Dragesund and Olsen, 1965).

TS measurements of fish can be divided into *ex situ* (i.e., tethered experimental) and *in situ* (i.e., split-beam field) methods (Foote, 1991). *Ex situ* measurements of orange roughy TS are uncertain because of entrained air bubbles within the body and changes in the density and sound speed of lipids when fish are measured at the surface (Kloser *et al.*, 1997; McClatchie *et al.*, 2000; Barr, 2001). The direct *in situ* method of TS measurement is reported to be the best (Ehrenberg, 1983), although there are numerous acoustic and biological sampling uncertainties that need to be resolved. *In situ* TS measurements require that a single fish be located within the pulse-resolution volume. This is traditionally obtained by lowering the transducer to within 50–100 m of the targets (Kloser *et al.*,

1997) and using short pulse lengths. Unfortunately, the single-fish classification algorithms (Soule *et al.*, 1995) will accept multiple targets even at close range. To minimize single-target classification error, TS measurements may be compared with volume reverberation in order to filter multiple-target acceptances (e.g. Sawada *et al.*, 1993; Gauthier and Rose, 2001). Single- and split-beam fish tracking can also be used to ensure that single fish are being resolved (Demer *et al.*, 1999).

In situ TS measurements need to reflect fish size, sex ratio, and maturity-stage characteristics of the surveyed population. It is best to obtain *in situ* TS measurements at the same time and location as the acoustic survey. Are TS measurements of fish at the periphery of schools representative of the species and sizes of fish within schools? This problem occurs particularly in deep water, where schools of orange roughy are often associated with deep-scattering layers of micronekton (i.e., small fishes, crustaceans, and squid). Lantern fishes (Myctophidae) are the most numerous component of the micronekton. Small individuals (<10 cm total length (TL)) have the same TS at 38 kHz as orange roughy (35 cm standard length (SL)) as a consequence of the resonant scattering of the gas-filled swimbladder at depth (Kloser *et al.*, 2002).

To resolve species-identification difficulties, broadband or multi-frequency methods can be used to classify the dominant, acoustic-target groups (Barr, 2001; Kloser *et al.*, 2002). Matching TS samples with pelagic and demersal trawling in time and space is difficult because of the depth (600–1200 m) and ruggedness of the seabed (Kloser *et al.*, 1997; McClatchie *et al.*, 2000). Echograms show that orange roughy schools extend up to 150 m in the water column but are difficult to capture in midwater, presumably due to diving avoidance (Koslow *et al.*, 1995). The effect of diving on *in situ* TSs can lower the average TS by 3 dB (Kloser *et al.*, 2000). What is less certain is the effect of deep-towed acoustic sensors on *in situ* TS measurements. Fish may change their tilt angle without downward movement in the presence of the lowered transducer. This “passive” avoidance may differ from natural schooling-fish orientations encountered during acoustic surveys.

The uncertainty in frequency-dependent TS measurements introduced by variability in fish identification, size, species composition, and tilt distribution can be explored using backscatter models (e.g., Love, 1978; Clay and Horne, 1994). The interpretation of the model results relies on knowing the dominant-scattering species, their size, orientation, anatomy, and material properties. The sensitivity of backscatter models to sound speed and density changes may also influence the accuracy of model predictions (Chu *et al.*, 2000).

In this article, we combine *in situ* TS measurements, visual observations, and backscatter-model predictions to explore the effects of fish density, identification, tilt-angle

distribution, and material properties on the prediction of ensemble TSs of orange roughy at 38 kHz.

Methods

Sampling area

Frequency-dependent, *in situ* TS measurements, video observations, and species identification with targeted pelagic and demersal trawls were obtained from an orange roughy spawning aggregation located on the edge of a ridge known as St. Patricks Head (41°30'S 148°45'E, depth 800–1000 m) off the east coast of Tasmania in July 1999.

Biological sampling

Demersal and multiple-opening pelagic trawls were used to sample fish concentrations that had been located acoustically (Kloser *et al.*, 2002). The composition of each demersal catch was identified to species group based on body size and swimbladder type (Kloser *et al.*, 1997). Representative numbers, lengths, and weights of all groups were measured. The seven dominant species groups were: eels, morid cods, oreos, orange roughy, sharks, macrourids, and miscellaneous. Macrourids have large, gas-filled swimbladders, except for the dominant species, *Coryphaenoides subserrulatus*, which has a large, spongy-gas matrix bladder. Further analysis was only done for species groups that represented >1% of the total catch by numbers. Pelagic-trawl catches were treated in the same way but contained an extra group of small mesopelagic fishes (<10 cm TL) with gas bladdered species usually dominated by lantern fishes (Myctophidae).

Dissections, imaging, and sound velocity

Orange roughy components (swimbladder and body) were measured using Computerized Aided Tomography (CAT) scans in dorsal and ventral aspect and by dissection. Wax ester, swimbladder sound speed was measured at 0 m depth (1 atm) and temperatures between 5 and 22°C using the propagation time between two 2-MHz ultrasound transducers (cf. Kossoff *et al.*, 1973).

Acoustic instrumentation

The echosounder was a MUlti-Frequency, Towed Instrument (MUFTI) that included a 40° single-beam, 12 kHz, and 7° split-beam, 38 and 120 kHz transducers (Kloser *et al.*, 2002). The towed body also housed transmitters, preamplifiers, Falmouth Scientific conductivity, temperature and depth logger (CTD), and a “monitoring” pressure case. The monitoring pressure case measured tow-body pitch, roll, depth, and operating voltage. The acoustic system (SIMRAD EK500 version 5.3 software) was calibrated (at 1, 0.3, and 1 ms pulse durations for the 12, 38, and 120 kHz transducers) at depth using a 38.1-mm tungsten-carbide sphere, optimizing the two-way, beam-compensation

algorithm for a flat response (minimum standard deviation) for up to 5° off-axis.

In situ visual observations

A digital video camera, two 250-W incandescent lights, and a pitch/roll/depth monitoring package were deployed at 800 m depth and towed at approximately 0.25 m s⁻¹. Four lasers were used to provide scale to the imagery and a reference measurement (Barker *et al.*, 2001). The camera's field-of-view was calibrated using frame-grab images analysed using Laser Measure[®] and Optimus software. Fish behaviour (stationary, slow, and fast movement) and orientation (horizontal, 5 to -5°; head-down, -5 to -30°, -30 to -60°; head-up, 5-30°, 30-60°) were scored every 5 s. Fish orientation relative to the seafloor and recorded camera orientation could only be estimated within wide confidence limits because of changing fish aspect and density.

In situ TS sampling

The MUFTI towed body was lowered to 750 m (50–100 m above schooling orange roughy) while the vessel drifted. The TS-selection criteria were: target threshold, -65 dB; normalized pulse duration, 0.7–1.5 ms; maximum one-way gain compensation, 6 dB; and phase deviation 10° at 38 kHz, 0.3 ms pulse duration, the phase deviation criterion was not used. Multi-frequency, backscatter mixing at 12, 38, and 120 kHz was used to accentuate the low concentration regions dominated by orange roughy (Kloser *et al.*, 2002). For each region, *in situ* TS data were divided into four 10-m depth layers, referenced from the seabed, to observe depth bias and to include orange roughy concentrations up to 20 m above the seafloor. The mean TS was calculated within two off-axis acceptance intervals (0–2.5° and 0–5° from the transducer axis), and four, maximum-TS filter settings (-46, -44, -42, and -40 dB). TS filters were used to examine the bias introduced by the presence of large, gas-bladdered fishes (Kloser *et al.*, 2000). The lower TS threshold was set at -65 dB.

At high, pulse-repetition rates (>2 s⁻¹) when drifting, it is possible to track individual fish using the split-beam, SIMRAD EK500 echosounder (Ona and Barange, 1999). Acoustic-depth measurements of tracked fish were corrected for vessel heave by subtracting heave-induced variations in the detected seabed echo. To be accepted as a valid fish track, a minimum of five successive TS values had to be recorded within a vertical range less than 0.11 m. Only one missing target between two successive detections was allowed in a valid fish track. The mean TS, number of TS values, and standard deviation of each tracked fish were calculated using a 0–2.5° off-axis filter.

Backscatter modelling

Backscatter amplitudes were estimated using a Kirchhoff-ray mode (KRM) model (Clay and Horne, 1994) param-

eterized for orange roughy. KRM backscatter estimates are based on digital outlines of the body and swimbladder compiled from CAT-scan images. Digitized fish images are rotated so that the sagittal axis of the body is aligned with the snout and the tip of the caudal peduncle. The fish body is represented by a set of contiguous, fluid-filled cylinders surrounding a set of contiguous, wax ester cylinders representing the swimbladder. The digital resolution of the body and swimbladder was set at 1 mm. Backscatter from each cylinder in the body and the swimbladder is computed and added coherently to estimate total backscatter as a function of fish length (L, units in metres), aspect relative to the transducer face (θ , units in degrees), and acoustic wavelength (λ , units in metres). The measurements for lipids by Yayanos *et al.* (1978) provided the basis for the sound-speed and density ratios used in estimating the backscatter amplitudes of the swimbladder, while the fish-body properties are based on measurements by McClatchie and Ye (2000) and Barr (2001). Backscatter was calculated over a frequency range 12–120 kHz and a tilt range $\pm 60^\circ$ off horizontal at 38 and 120 kHz. The echo intensities were calculated as reduced-scattering lengths (RSL). The non-dimensional RSL is the backscattering length (L_{bs}) divided by the fish length (L). The usual target strength is then $TS = 20 \log(RSL) + 20 \log(L_{cm})$.

To examine the sensitivity of the KRM-model predictions to material properties, the density (ρ) and sound speed (h) ratios were systematically changed as model inputs. Contrasts in sound speed (c) and density (ρ) are used to form reflectivity coefficients, relative to seawater ($c = 1490 \text{ m s}^{-1}$ and $\rho = 1031 \text{ kg m}^{-3}$), at each interface within the fish (fish body $c = 1535 \text{ m s}^{-1}$, $\rho = 1050 \text{ kg m}^{-3}$; swimbladder $c = 1525 \text{ m s}^{-1}$, $\rho = 903 \text{ kg m}^{-3}$). Ranges of sound speeds and densities of seawater, fish bodies, and swimbladders were based on water properties during our acoustic survey and values published in Barr (2001) and McClatchie and Ye (2000). Reference values (g_o , h_o) were set at the midpoints of each variable's range. Combinations of g and h ratio values were determined by dividing the range of each variable into 11 equal increments. Thus a total of 121 KRM models were run at each combination of g and h for the fish body, swimbladder, and whole fish (Table 1). The change in TS relative to that at (g_o , h_o) was contoured over the full range of g and h values (cf. Chu *et al.*, 2000).

Table 1. Reference (o) and range (min, max) of density (g) and sound-speed (h) contrasts for orange roughy (*H. atlanticus*) bodies and swimbladders used in KRM backscatter sensitivity modelling.

Body part	g_o	g_{min}	g_{max}	h_o	h_{min}	h_{max}
Body	1.018	0.969	1.068	1.030	1.017	1.051
Bladder	0.876	0.862	0.886	1.023	1.013	1.034

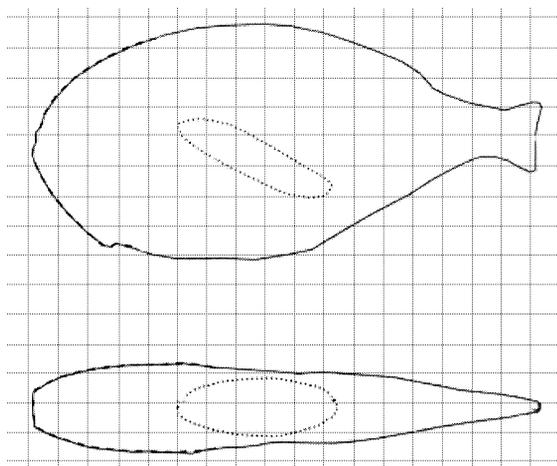


Figure 1. Schematic of orange roughy (*H. atlanticus*) anatomy from dissections and CAT-scan images for a spawning male (SL 35 cm) showing dorsal and lateral views. Grid squares are 2 cm.

Results

Morphology and swimbladder sound velocity

Dissection and CAT scans of orange roughy were used to obtain dorsal and ventral measurements of the body and swimbladder from a 35 cm SL spawning male and female fish (Figure 1). Because of the large ovaries of the females the shape of the swimbladder was distorted. Other hard body parts, such as the ossified head, backbone, and small but dense otoliths were not measured. The average sound speed at atmospheric pressure, in 40, wax-ester, swimbladder samples varied from 1507 m s^{-1} at 5°C to 1460 m s^{-1} at 22°C . This contrasts with seawater, where the sound speed varies from 1442 m s^{-1} at 5°C to 1501 m s^{-1} at 22°C . The sound speeds in orange roughy swimbladders and seawater are therefore equal at approximately 16°C . Adjusting our measurements by 27 m s^{-1} (McClatchie and Ye, 2000) to compensate for the spawning depth (750 m) and temperature (7°C) results in a sound speed of 1525 m s^{-1} for a wax-ester swimbladder at depth. Our swimbladder, sound-speed measurements over the same temperature range and ambient pressure are approximately 18 m s^{-1} higher than those for the body lipids of orange roughy measured by McClatchie and Ye (2000).

Biological sampling

The mean SL of orange roughy (97.5% of the catch by number) from catches $>1000 \text{ kg}$, in seven targeted demersal trawls at the site of *in situ* TS measurement was 34.9 cm ($n = 401$, standard deviation (s.d.) = 2.7 cm) with 84% males (male mean length 34.4 cm, female mean length 37.0 cm). Bycatch species (2.5% of the catch by number) were dominated (80%) by macrourids (*Coryphaenoides subserrulatus*), a large, gas-bladdered species with a mean TL of 32.5 cm (s.d. = 2.3 cm, $n = 200$); the remaining

species were oreos (*Alloctytus* sp.). A pelagic tow at the same site, targeted 50 m from the seabed, caught 277 small mesopelagic animals (fishes, crustaceans, and squid). Approximately half of the catch was fish (47.3% by number), of which 80% were large, gas-bladdered species (79% macrourids) and 17% were small, gas-bladdered species (16% myctophids).

Visual sampling

The analysis of video observations from the *in situ* TS site showed that orange roughy were the dominant species in 432 of the 1453 analysed 5-s video segments. Orientations of orange roughy within these frames showed that 62% were horizontal ($\pm 5^\circ$), 34% were head-down, and the remaining 4% were head-up. Observed behaviours were categorized as 71% maintaining position, 25% fleeing (i.e., actively swimming away from the camera), and 4% swimming slowly. Of the head-down fish, 40% were fleeing (active avoidance) and 59% were stationary. Little difference was observed in the head-up fish: 39% fleeing and 61% stationary.

Acoustics

Prior to the video and trawl observations, measurements were taken at 12, 38, and 120 kHz using the MUFTI towed body at 60 m above the seabed. A calibration sphere was suspended 15 m below the transducers. During the MUFTI drift, four regions were identified as containing low densities of orange roughy adjacent to the seabed (up to 20 m) based on three-frequency mixing. Potential orange roughy regions were associated with high volume reverberation at 120 kHz relative to low 38 kHz ($\sim -5 \text{ dB}$) and 12 kHz ($\sim -2 \text{ dB}$) using a three-colour, composite-echogram image (Kloser *et al.*, 2002). The mean TS_{38} (TS at 38 kHz) of individual targets in these regions ranged from -48.4 dB ($n = 6101$, s.d. = 2.0) for the -40 dB upper threshold to -51.0 dB ($n = 4737$, s.d. = 0.7) for the -46 dB upper threshold. The mean TS_{38} of tracked fish for the -40 dB upper threshold (-48.2 dB , 238 tracks, 2248 TS values) and the -46 dB upper threshold (-51 dB , 168 tracks, 1604 TS values) did not differ from the mean TS_{38} using all measurements. The similarity between the tracked and non-tracked mean TS_{38} indicates minimal bias associated with the single-target, detection algorithm used in this study.

ΔTS_{38-120} , the TS difference of the tracked fish (94 tracks, 1821 TS values) between 38 kHz ($\langle\text{TS}_{38}\rangle = -47.1 \text{ dB}$, s.d. = 5.6) and 120 kHz ($\langle\text{TS}_{120}\rangle = -49.1 \text{ dB}$, s.d. = 6.6), ranged from -8 to $+16 \text{ dB}$ (Figure 2). Identifying orange roughy based on ΔTS_{38-120} being -2.5 to -7.5 dB , from Sv differences observed in schooling fish (Kloser *et al.*, 2002), resulted in a mean TS for orange roughy of -52.9 dB (13 tracks, 201 TS values). Including data for all ΔTS_{38-120} and applying a -46 dB upper threshold increased $\langle\text{TS}_{38}\rangle$ by 1.9 dB (-51.0 dB , s.d. 4.4, 67

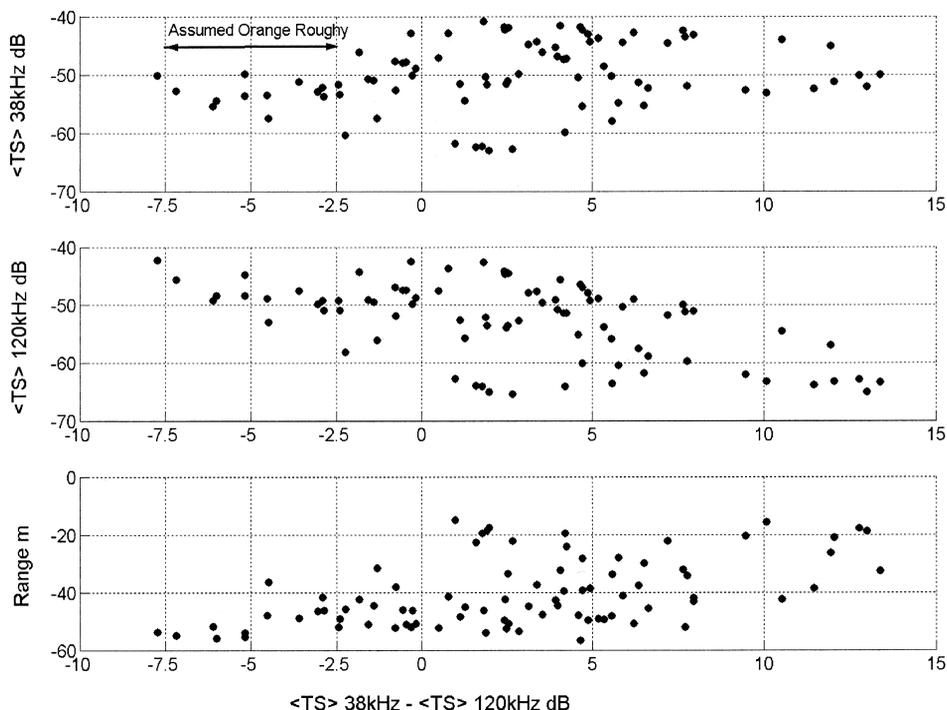


Figure 2. Ensemble averaged *in situ* target strength of tracked orange roughy (*H. atlanticus*) at 38 and 120 kHz. A ΔTS_{38-120} difference (lower panel) of -5 ± 2.5 dB is interpreted as originating from orange roughy (Kloser *et al.*, 2002).

tracks, 1322 TS values). This increase is presumably a result of the inclusion of other species with gas bladders in the calculation. If ΔTS_{38-120} is used to classify orange roughy, then the mean *in situ* TS_{38} for orange roughy is -52.9 dB.

The equal and higher TS at 38 kHz relative to 120 kHz is consistent with models of resonance scattering by small- to medium-sized fishes with gas-filled swimbladders (Kloser *et al.*, 2002). Fishes with gas-filled swimbladders collected by trawls included macrourids (*Coryphaenoides subseriulatus*) (mean TL, 32.5 cm; s.d., 2.3 cm; $n = 200$) and myctophids (*Lampanyctus australis*) (mean TL, 12.0 cm; s.d., 0.6 cm; $n = 17$). A cluster of ΔTS_{38-120} greater than 8 dB is consistent with strong, resonant scattering at 38 kHz from a very small, gas-bladdered lantern fish (3.6 cm TL, $n = 2$) that was captured in the targeted pelagic tows.

Backscatter modelling

The TS at 0° tilt (i.e., horizontal) for the 35 cm, male- and female-spawning orange roughy shows cyclic changes with frequency (see also Barr, 2001). For the same frequency, TS rapidly increases or decreases with tilt angle, making amplitude prediction at any specific angle difficult. For male- and female-spawning fish at 38 kHz, the TS peaks over a broad range of tilt angles from approximately 20° head-down to 5° head-up (Figure 3a). The TS of both fish follows the same undulating pattern. The TS difference between the fish is typically <1 dB for head-down aspects

but is consistently more for the male fish around the maximum TS, and alternates between ± 5 dB for head-up aspects. At 120 kHz (Figure 3b), the same general pattern is observed but even greater changes in predicted backscatter occur over narrower-aspect ranges. In the contour plot, predicted 38 kHz TSs differed by as much as -10 dB from the reference value used for the male-spawning orange roughy (Figure 4a). The near-vertical contours suggest that density contrasts (g) were influencing the reflectivity of sound at interfaces more than sound-speed contrasts (h). The largest TS differences occurred at low values of g and h . This pattern is consistent with contours for 12 kHz (not shown), but not at 120 kHz, when the contours formed “c” shaped arcs (Figure 4b), indicating that TS differences were equally influenced by density and sound-speed contrasts at high and low h values.

The sensitivity of the tilt-averaged TS of orange roughy (male and female) at 38 kHz was examined using Gaussian, tilt-angle distributions with s.d. of 5 and 15° . TS curves were generally flat (less than 1 dB variability) through 5° head-up to 20° head-down at 5° s.d. (Figure 5). In all cases, the TS dropped up to 5 dB from the maximum when fish were 10 – 15° head-up. Male average TS is greater than female average TS except at extreme, head-down orientations. The tilt-angle distribution of orange roughy assessed *in situ* by video was inserted into the male and female shape, KRM model with male $TS = -50.8$ dB and female $TS = -53.6$ dB. The male and female orange roughy TS

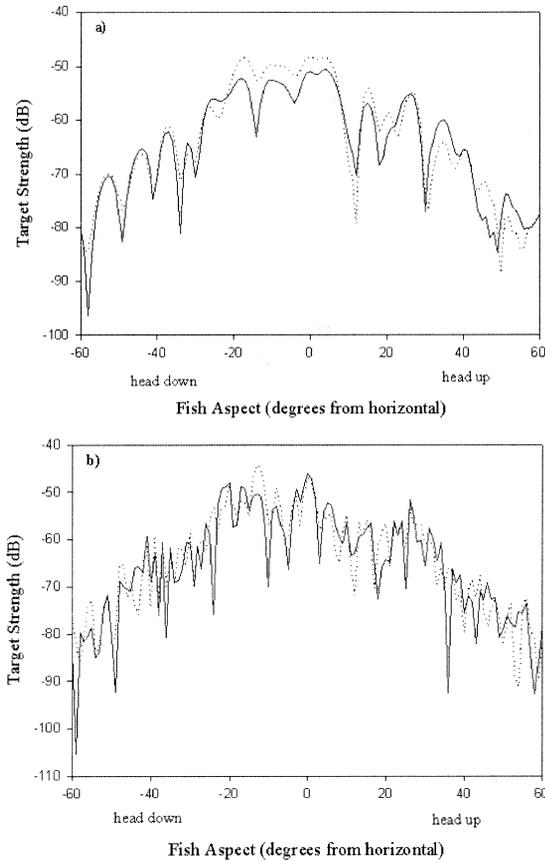


Figure 3. KRM backscatter model output for 35 cm SL spawning male (solid line) and female (dashed line) orange roughy (*H. atlanticus*): (a) dorsal aspect 30–150° at 38 kHz and (b) dorsal aspect 30–150° at 120 kHz.

model predictions using video observations of tilt-angle orientations are consistent (within 1 dB) with the Gaussian tilt-angle orientations through 5° head-up to 20° head-down (Figure 5). ΔTS_{38-120} averaged over the unimodal tilt-angle distribution with s.d. = 15° for orange roughy (male and female) was negative (range 1 to -3 dB) for head-down (0 to -30°) and negligible (range 1.4 to -1.3 dB) for head-up (0–10°) orientations. ΔTS_{38-120} for the female orange roughy was negative (-1 to -2.8 dB) over the tilt-angle range 10 to -30°.

Discussion

Orange roughy is one of the hardest commercial deep-water fish stocks to survey acoustically, given their low TS, active and, perhaps, passive avoidance behaviour, and co-location with small, gas-bladdered fishes. Diving avoidance observed during acoustic measurements can lower *in situ* TS by 3 dB at 38 kHz (Kloser *et al.*, 2000), a reduction

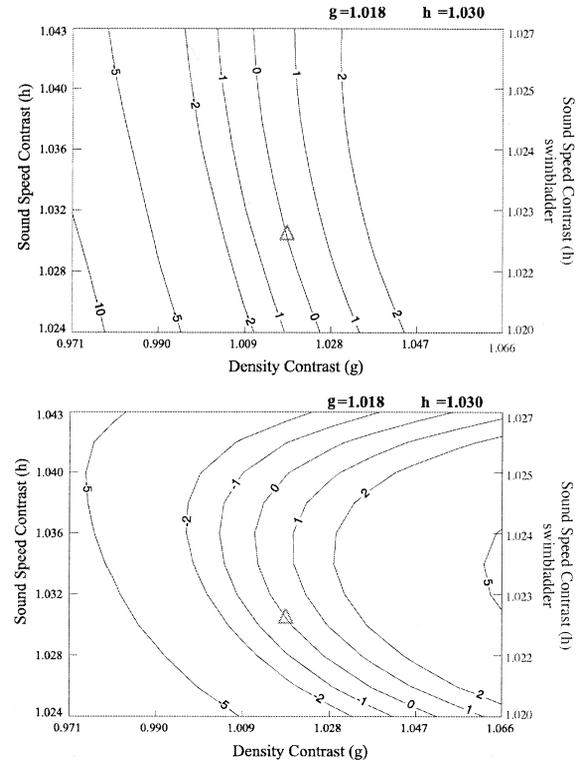


Figure 4. The sensitivity of the KRM backscatter model to variation in density (g) and sound speed (h) contrasts (Table 1) for a 34.8 cm SL orange roughy (*H. atlanticus*) at (a) 38 kHz and (b) 120 kHz. Open triangles indicate the g_0 and h_0 reference values.

consistent with the average 2.5 dB decrease shown by near-surface *ex situ* TS measurements (McClatchie *et al.*, 2000). Our tracked *in situ* measurements show that an active diving response could decrease the TS of orange roughy by 7 dB at 38 kHz. Video observations show that 34% of fishes were oriented head-down (5–30°) and this may be considered “passive” avoidance, as average TS values would decrease. The KRM model predicts that orange roughy TSs at 38 kHz vary minimally between 5° head-up to 25° head-down orientations. Using our video observations of tilt-angle distribution in the KRM model gave similar results (within 1 dB). Barr (2001) also showed that the impact of orientation change on TS model predictions is small. We conclude, based on KRM-model results, that potential passive avoidance or natural variation in orientation observed by video will have less than 1 dB impact on the TS of orange roughy.

Interpreting single-frequency, ensemble-averaged, *in situ* TS measurements of orange roughy is uncertain (4.5 dB) because of the potential mis-classification of targets. Thresholding of *in situ* TS data was used to eliminate large TS, gas-bladdered fishes. Modelling results support an upper TS threshold for *in situ* targets of -46 dB, with which the maximum observed TS was -48.2 dB (male) and -50.6 dB (female) for orange roughy.

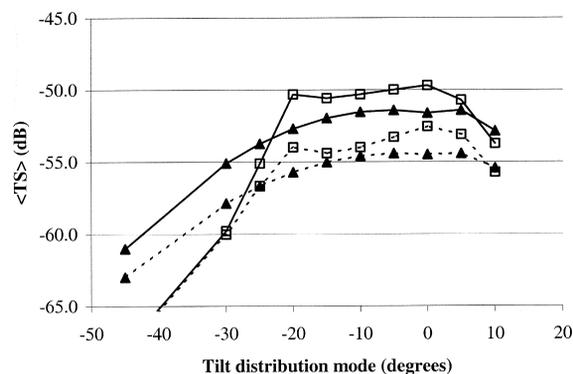


Figure 5. KRM backscatterer model predictions of TS at 38 kHz averaged over Gaussian tilt-angle distributions (s.d. 5° (open square) and 15° (closed triangle)) for 35 cm SL male (solid) and female (dashed) orange roughy (*H. atlanticus*). A head-up tilt is positive.

Frequency differencing of tracked targets further supports the -46 dB upper TS threshold. Results from frequency-difference analyses show that the -46 to -65 dB range includes small, gas-bladdered fishes (mostly myctophids) that coexist with orange roughy. Including these species increases the mean TS by 1.9 dB. It is noteworthy that our KRM-model predictions, using a wide range of tilt distributions ($+10$ to -30°), do not support the -5 ± 2.5 dB range of ΔTS_{38-120} suggested for orange roughy. We base our classification of orange roughy on the -5 dB ΔTS_{38-120} difference observed on schools ensounded at 150 -m range (Kloser *et al.*, 2002). The disagreement between experimental and model frequency difference methods used to identify individually tracked orange roughy should be investigated further. Our lower, orange roughy ensemble, *in situ* TS results ($\langle TS \rangle = -52.9$ dB; SL, 35 cm; s.d., 2.7 cm), based on multi-frequency fish tracking, are 4.9 dB (factor of 3.1) lower than the mean TS recommended for the New Zealand acoustic surveys (McClatchie and Ye, 2000). We assume that the targets selected on the periphery of dense, orange roughy schools are representative of the population at the time of the survey. The uncertainty in this assumption is unknown, but is explored using our modelling of changes in the material properties. KRM-model predictions of orange roughy backscatter are sensitive to changes in material properties. Slight changes in density or sound-speed contrasts can dramatically increase or decrease backscatter amplitudes. The difficulty in measuring sound speeds within fish bodies at depth and the omission of other scattering structures in the model (e.g., backbone, ossified head) potentially combine to reduce the accuracy of model estimates. Annual gonad production will also influence the sound speed and density contrasts within the fish body. The resulting changes in the reflectivity coefficients will have the greatest impact on backscatter-model predictions for species without swimbladders or those with wax-ester/lipid-invested swimbladders such as orange roughy. The validity of

adjusting our near-surface, lipid, sound-speed measurements for pressure effects at depth has not been quantified. Material property measurements at appropriate pressures and temperatures are needed to refine the modelling and identification of mesopelagic fishes.

The uncertainty in interpreting deepwater, *in situ* TS measurements of orange roughy is dominated by questions of targets being representative of the population and, to a lesser extent, issues of species identification and avoidance. Backscatter modelling reinforces concerns about the TS variability due to density and sound-speed contrasts. Despite the uncertainty associated with acoustic samples from the field and backscatter models, it is encouraging that the combination of modelling, acoustic measurements, visual observation, and net captures provides repeatable interpretations of TS, fish size, and acoustic-abundance indices for the estimation of schooling populations.

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