Comparing acoustic model predictions to in situ backscatter measurements of fish with dual-chambered swimbladders

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Lavunun Mirogrex terraesanctae have a dual-chambered swimbladder and are the dominant fish species in Lake Kinneret, Israel. Bi-monthly acoustic assessments are used to monitor lavunun abundance but the relation between the amount of reflected sound and organism morphology is not well described. Predictions from Kirchhoff-ray mode (KRM) backscatter models show a sensitivity of echo amplitude to fish length and fish aspect. Predicted mean KRM target strengths matched maximum in situ target strength measurements of eight tethered fish within 2.5 dB at 120 kHz and within 7 dB at 420 kHz. Tilt and roll of lavunun during tethered measurements increased variance of backscatter measurements. Accurate abundance and length frequency distribution estimates cannot be obtained from in situ acoustic measurements without supplementary net samples.

Key words: acoustic backscatter; cyprinid; lavunun; Mirogrex terraesanctae; swimbladder; target strength.

INTRODUCTION

Lavunun Mirogrex terraesanctae (Steinitz)=Acanthobrama terraesanctae is an endemic cyprinid that dominates the pelagic fish community in sub-tropical Lake Kinneret, Israel (Walline et al., 1993). Like other cyprinids, lavunun are physostomes with a dual-chambered swimbladder connected by a duct that attaches to the back of the oesophagus (Alexander, 1970). Unlike other commercially important fishes, this zooplanktivorous species (Gophen et al., 1990) is managed to maintain water quality in a resource that supplies up to 50% of Israel’s drinking water (Walline et al., 1993; Berman, 1994). Acoustic surveys have been conducted bi-monthly since 1987 to estimate lavunun abundance (Walline et al., 1992), but influences of organism size and behaviour on acoustic measurements have not been quantified.

The use of acoustic data to estimate abundance requires a quantitative relation between the amplitude of returned echoes and organism length. The amount of sound returned to an acoustic transducer by an animal is measured as the
Table I. Lavnun (*Mirogrex terrae sanctae*) total lengths ($L_T$, mm), number of 120 kHz target strength measurements, observed mean and maximum 120 kHz target strengths (dB), KRM 120 kHz predicted mean target strengths (dB), and difference between mean and maximum observed target strengths and KRM predicted backscatter amplitudes (dB). KRM predicted mean target strengths are based on 15 fish.

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<th>No. of targets</th>
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<th>Predicted 120 kHz</th>
<th>Difference (mean 120 kHz)</th>
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Backscattering cross sectional area ($\sigma_{bs}$, m$^2$). When packing densities of animals are too high to resolve individuals, relative densities are converted to numeric density estimates by dividing the total reflected sound (i.e. integrated echo) by the echo intensity from a representative animal (Dragesund & Olsen, 1965). Population abundance is estimated subsequently by multiplying the numeric or mass density by the volume of water in the survey area (MacLennan & Simmonds, 1992). Therefore the accuracy of any population abundance estimate is influenced directly by the choice of a representative backscattering cross section.

Backscattering cross section or its logarithmic transformation—target strength ($S_T$, dB), can be measured for any species using caged or tethered animals, measured in situ using dual or split beam echosounders, or modeled using numeric backscatter models (Table I; Horne & Clay, 1998). Experimental measures of acoustic backscatter and individual fish lengths can be used to derive empirical relationships between target strength and fish length at dorsal aspect (Love, 1971; Nakken & Olsen, 1977; Foote, 1987) or incorporating fish aspect angle (Foote, 1980; Olsen, unpubl. data). An alternate approach uses numeric models to estimate acoustic backscatter and to quantify the relative importance of biological and physical factors that influence magnitudes and variation of backscattered echoes.

This study uses a Kirchhoff-ray mode model to estimate acoustic backscatter from lavnun as a function of fish length, aspect, and acoustic wavelength. Model estimates are compared to in situ tethered and free swimming backscatter measurements, examining the sensitivity of backscatter predictions to sources of biological and physical variation, and quantifying variation among in situ target strength measurements. It is not known if the presence of two swimbladder chambers influences backscatter differently from the presence of a single chamber of equivalent volume. When combined with length frequency samples, a better understanding of how swimbladder shape and volume influences backscatter increases the ability to measure lavnun behaviour acoustically. An improved lavnun target strength to length relationship may improve the size
classification of fish targets, which is needed to estimate abundance and size-dependent bioenergetic parameters such as food consumption.

**MATERIALS AND METHODS**

Adult lavnun were collected from commercial purse seine catches during November 1998 and transferred to surface holding tanks prior to acoustic measurements and radiographs. Additional length-frequency distributions were tabulated from fish caught in commercial purse seines. Unfed lavnun were supplied with ambient Lake Kinneret water (c. 23°C) prior to acoustic measurement. All in situ backscatter measurements were extracted from trace tracking records measured on 1 December 1998 using a BioSonics 102 echosounder fitted with 120 kHz dual-beam transducer (7° and 18° half-power beam widths). The echosounder was calibrated using a tungsten-carbide calibration sphere (Foote et al., 1987) prior to acoustic measurements and all backscatter amplitudes were corrected for location in the acoustic beam. Expected backscatter values from the calibration sphere were checked using Anderson’s fluid sphere model (Anderson, 1950). To measure backscatter amplitudes from eight live fish, a hook and 12 cm leader were attached to the roof of the mouth and then fish were suspended from monofilament fishing line at a range of 6-7 m from the transducer. Fish were allowed to swim freely while tethered and were monitored visually from the surface. Fish tilt angles were not measured during tethering experiments. Target strength data were checked for systematic bias over time and as a function of angle from acoustic axis.

To compare tethered target strength measurements with those of free swimming fish, in situ targets were tracked when the boat was stationary. Individual fish remained in the acoustic beam for longer periods when the boat was stopped, compared with when the boat was sampling along transect lines. Single targets (i.e. fish) were identified using computer-generated echograms of digitized echo data (BioSonics ESP Dual-Beam Echogram Viewer/Editor, ver. 3.0). Only targets that did not change depth, that could be resolved individually, and that were tracked for 20 or more consecutive pings were included in analyses.

A group of 15 live lavnun was transported to a veterinary facility, anaesthetized, and radiographed at dorsal and lateral orientations using a Dongmun Model 31HR100P (exposure: 60 Kvp, 30 mA, 0-03 s). Acoustic backscatter amplitudes of the 15 lavnun were estimated using a Kirchhoff-ray mode (KRM) backscatter model. The KRM model uses digitized images of the fish body and swimbladder chambers to estimate total backscatter from a fish. Dorsal and lateral radiographs were converted to digital data files by tracing the silhouettes of bodies (not including fins) and swimbladders, scanning the traces, and then digitizing graphic files electronically at 1 mm resolution. Digital files of the fish body and swimbladders were smoothed using a three point triangular average. Digitized fish were rotated so that the sagittal axis of the body, paralleling the vertebral column, was aligned with the snout and the tip of the caudal peduncle. When calculating backscatter, the fish body is represented by a set of contiguous fluid-filled cylinders surrounding two sets of gas-filled cylinders that represent anterior and posterior swimbladder chambers. Backscatter from anterior and posterior chambers was estimated separately for each fish. Backscatter from each cylinder is added coherently to estimate total backscatter as a function of standard length ($L_s$, m), fish dorsal aspect relative to the transducer face ($\theta$, degrees), and acoustic wavelength ($\lambda$, m). The acoustic wavelength is a function of the speed of sound in water ($c$, ms$^{-1}$) and the transmitting frequency ($f$, Hz) (i.e. $\lambda = c f^{-1}$). Values for the speed of sound through water, a fish body, and a swimbladder were set at 1485, 1575 and 345 ms$^{-1}$. The density of fish flesh (1080 kg m$^{-3}$) was greater than of water (1000 kg m$^{-3}$) while swimbladder density was less than water at 2.64 kg m$^{-3}$ (Clay, 1991). Backscatter amplitudes were calculated for individual fish based on the body and swimbladder digital files. Fish lengths were scaled to the group mean length (115 mm) when calculating backscatter to compare among animals. Full details of the model can be found in Clay & Horne (1994), Jech et al. (1995), or the appendix in Horne & Jech (1999).
Backscatter estimates from the KRM model match field measurements (Clay & Horne, 1994; Jech et al., 1995; Trevorrow, 1996) and the model has been applied to other species over a range of acoustic carrier frequencies (Jech et al., 1995; Trevorrow, 1996). To quantify variation in backscatter amplitudes among lavnun, mean and standard deviation backscatter of the 15 modelled fish were predicted as a function of fish length, aspect, and acoustic wavelength. Echo amplitudes are plotted as reduced scattering lengths \( L_{RS} \), a non-dimensional measure of scattering length \( L_{bs}, m \) divided by fish length (i.e. \( L_{RS} = \frac{L_{bs}}{L} \)).

The concurrence of model predictions with measured target strengths was examined by plotting KRM predicted mean backscatter \( \pm 1 \) s.d. at 90° aspect for 120 kHz and then superimposing observed mean and maximum target strength values from the eight constrained lavnun. All field measurements and model estimates were averaged in the linear domain before being transformed logarithmically. Predicted lengths were calculated using standard lengths for insonified fish. Using the radiographed group of 15 fish as a reference set, standard length averaged \( 86.8\% \pm 1.9\% \) s.d. \( (r=0.983) \) of total fish length.

**RESULTS**

Lavnun are a physostomous, cyprinid species with a dual-chambered swimbladder located below the spinal column [Fig. 1(a)]. A narrow tube called the ductus communicans [Fig. 1(b)] joins the two chambers. Careful dissection of frozen specimens confirmed the presence of a pneumatic duct connecting the anterior surface of the posterior swimbladder chamber to the dorsal surface of the oesophagus. The pneumatic duct was often filled with gas in the frozen...
specimens but did not appear inflated in any radiographs of the 15 live fish. All swimbladder chambers of fish used in modelling experiments remained inflated during dorsal and lateral radiography.

Total lengths of the eight, tethered lavun used to measure dorsal target strengths were larger than the 15 modelled fish with lengths ranging from 120 to 148 mm (Table 1). Each backscatter measurement set contained originally several hundred observations. Target strengths varied by as much as 30 dB within measurement sets. Activity levels by fish decreased generally in the latter half of tethered measurement series but no consistent pulse-to-pulse backscatter amplitude trends occurred in the data records of each fish (Fig. 2). Target strength measurements of in situ tracked fish also varied with a $S_T$ range of up to 20 dB for a single animal (Fig. 3).

General shapes of KRM predicted backscatter response surfaces for individual fish were similar among the 15 modelled fish (Fig. 4). All fish were modelled at a standard length of 115 mm, through an aspect ($\theta$) range of 70° to 110°.
Fig. 3. Continuous 120 kHz in situ target strength (units dB) tracking of fish number, 3 (○), 4 (▲), 5 (△), 7 (■) and 10 (○) as a function of pulse number. Actual sizes of fish are not known.

(horizontal=90°, head up >90°), and over an acoustic frequency range of 12–420 kHz at 4 kHz intervals. If fish length is kept constant along the fish length to acoustic wavelength axis (L/λ−1) (Fig. 4), a higher L/λ−1 value corresponds to a higher acoustic carrier frequency. Keeping the frequency constant illustrates the effect of changes in fish length on echo amplitude. Overall, there is less influence of fish aspect on target strength at low L/λ−1 values. Throughout the L/λ−1 range, the response surface is symmetric about the peak echo amplitude. The quasi-periodic peaks and valleys along the maximum backscatter ridge correspond to areas of constructive and destructive interference between the body and swimbladder chambers. Along the fish aspect axis, predicted backscatter amplitudes were low at large head-up deviations from horizontal. Maximum echo amplitudes among the 15 modelled fish occurred over a θ range of 83–92° (Table II). Maximum echo amplitudes imply parallel alignment of the dorsal swimbladder surfaces to the transducer face. Absolute differences between predicted and observed mean target strengths among the eight fish used in the tether experiments averaged 2.24 dB (Table I).

The effects of anatomical differences among conspecifics on backscatter amplitude can be discerned in the mean and standard deviation backscatter response surfaces (Fig. 5). Peak amplitude at any L/λ−1 value occurs near 90° and decreases symmetrically as aspect angles deviate from horizontal. In the upper contour plot, standard deviation values were highest along aspect angles approximating 90°, indicating high variation among swimbladder angles relative to the body. Variation in backscatter amplitude is low at aspects that deviate >10° from horizontal. To illustrate frequency-dependent effects of aspect angle on backscatter echo amplitudes, mean and standard deviation target strengths of the 15 modelled lavun were plotted as a function of fish aspect angle (Fig. 6).
The amplitude of the 120 kHz mean backscatter response curve peaked at c. 85°. All modelled lavun swimbladders tilted ventrally and toward the posterior of the body. A fish would have to be swimming head down at an aspect angle equal to the swimbladder tilt angle (i.e. −5°) to maximize backscatter measured by a 120 kHz echosounder. Slight variations in fish tilt from horizontal can influence backscatter amplitudes dramatically.

The fit of KRM backscatter predictions to measured target strengths was examined by plotting predicted and observed mean and maximum target strength values as a function of fish length (Fig. 7). Mean observed target strengths were less than those predicted by the KRM model. The difference between observed and predicted mean values is attributed, in part, to changes in aspect angle during fish backscatter measurements. Predicted mean backscatter values were calculated at fish aspect angles of 90°. Fish aspect angles were not measured during backscatter measurements. The upper points are an average of the 10 highest backscatter returns for each fish. Generally, these points lie within one standard deviation of the predicted mean backscatter from the KRM model.

KRM backscatter model estimates of body and swimbladder volume can be used also to infer buoyancy control by lavun. Estimates of fish body and swimbladder volumes are calculated by summing the volume of the 1 mm resolution cylinders used in KRM backscatter model calculations (Table III).
Lavun total swimbladder volume averaged 5.5% of the body volume, slightly higher than that reported for five species of marine and freshwater fish (Davenport, 1999). Total swimbladder volume was correlated with body weight \(r=0.94, n=15, P<0.0001\) and body volume \(r=0.92, n=15, P<0.0001\). Correlations between anterior or posterior chamber volumes and body weight or volume were less than total volume correlations (anterior chamber volume and weight, \(r=0.89, n=15, P<0.001\); posterior chamber volume and weight, \(r=0.58, n=15, P=0.024\)). In 13 of 15 cases fish body volumes (without swimbladder chambers) were equal to or greater than the measured weight of the fish. This result implies that these surface-adapted lavun were neutrally or positively buoyant even without the added buoyancy of the swimbladder. Unusually thin or oily fish were not observed among the group of 15 lavun. Weights of the 15 surface-adapted fish averaged 91% of predicted weight based on a length–weight equation developed for lavun \(W=0.00281 L^{3.43}\), Ostrovsky & Walline, 1999). If predicted weights are substituted for observed weights, then the fish would remain neutrally buoyant with an average estimated density (weight : fish body volume) of 0.99 g ml\(^{-1}\).

**DISCUSSION**

The purpose of assessing lavun abundance acoustically in Lake Kinneret is unique compared with the assessment of most other commercially harvested resources. Lavun are managed for their influence on water quality through...
Fig. 5. Kirchhoff-ray mode predicted mean and standard deviation reduced scattering lengths (linear unitless quantity) for 15 lavnun plotted as a function of fish aspect (θ, degrees), length (L, m), and acoustic wavelength (λ, m). Along the aspect axis, angles <90° are oriented head up. All fish were modelled at a length of 115 mm, an aspect range of 70-100°, and a frequency range of 12-420 kHz. The upper plot contours 1 s.d. from the mean. Original fish lengths are listed in Table II.

zooplankton consumption. In 1993, large adult lavnun disappeared from the population and were replaced by large numbers of sub-commercial size (<12 cm) lavnun (Gophen et al., 1999). The lack of large adults caused the commercial fishery to collapse. Fishery managers responded with a subsidized fishing programme to remove small lavnun. The primary goal of the programme was to increase water quality by reducing zooplankton consumption, which would increase predation pressure on phytoplankton by zooplankton (Gophen et al., 1999). The desire to measure the success of this dilution programme increased interest in the acoustic monitoring of lavnun.

Numerous target-strength : fish-length relationships have been considered for the conversion of acoustic size to lavnun length (Fig. 8). Current lavnun acoustic assessments use a regression equation developed in 1993 by matching the peak in the target strength distribution (−48 dB at 70 kHz) with the peak in the
Fig. 6. Predicted KRM mean and standard deviation target strengths of a 115-mm herring plotted as a function of aspect angle at 120 kHz. Dotted lines represent 1 s.d. from the mean. Model estimates were calculated in the linear domain before logarithmic transformation. Angles <90° are oriented head down. n=15.

Fig. 7. Predicted and observed mean and standard deviation target strengths of herring plotted as a function of length at 120 kHz. Predicted target strengths were calculated at 90°.

length-frequency distribution of fish (10 cm) caught in commercial purse seines (Lindem & Sandlum, 1984). Since there was only one peak, the slope in the $S_T$-length equation was chosen to mimic the length frequency distribution observed in commercial catches. Despite the presence of more than one mode in $S_T$ and length frequency distributions in subsequent years, several difficulties remain if peak matching is used to determine $S_T$-length relationships: (1) selectivity of commercial purse seines prevents full sampling of fish <10 cm (even with a fine mesh codend liner); (2) the largest fish in the population (>15 cm) are rare and have never constituted a recognizable peak in $S_T$ or length distributions; (3) length and target strength ranges are not large (e.g. <10 cm and
a few dB); and (4) a single mode in the length distribution of a population can result in more than a single mode in the $S_T$ frequency distribution (Williamson & Traynor, 1984). Increasing the number of observations does not improve results because additional surveys suffer from the same sampling problems. Results from the 1998 surveys were consistent with the $S_T$-length relation ($S_T = 25\log(L) - 73$) used since 1994 and the conversion equation has been applied in all surveys.

The shape of the KRM target-strength: fish-length curve differs from the regression based models plotted in Fig. 8. Numeric backscatter models such as a KRM model are not used typically in acoustic abundance assessments of fish or zooplankton. Fisheries $S_T$-length regression models are based on measures of target strength from fish of known lengths or from literature values (Love, 1971). The KRM mean backscatter is based on the predicted reduced scattering lengths of 15 fish at 90° that were scaled linearly through the length range of interest. Allometric scaling of swimbladder and fish body is not incorporated into the KRM model, as it is not known how the swimbladder scales with body length. Another important difference between empirical regressions and the numeric backscatter model is the lack of behaviour included in KRM backscatter model estimates. Potentially, target strength measurements include variation in tilt and roll of each fish and of the transducer. Mean tilt angles of fish are species-dependent with observed angles ranging typically from 4° head down to 12° head up (Table I; Foote & Ona, 1987). Differences in the mean and maximum

<table>
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<tr>
<th>$L_T$</th>
<th>$W$</th>
<th>$W'$</th>
<th>$V_{SBA}$</th>
<th>$V_{SBP}$</th>
<th>$V_{SB}$</th>
<th>$V_{FB}$</th>
<th>$V_{FB} - V_{SB}$</th>
<th>$W(V_{FB} - V_{SB})^{-1}$</th>
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Fig. 8. Target strength-length relationships for Lake Kinneret lavnun at 120 kHz. The lines depict KRM (--
model results and three regression equations for fish ranging from 75 to 150 mm: (1) Love
(1971) (--), ST=19.1 log(L) - 63.9, (2) slope from Lindem & Sandlum (1984) and passing
through the point (○) (10, −48), ST=20 log(L, cm) - 68, (---) and (3) Walline, ST=25 log(L)
−73, currently in use in Lake Kinneret (---). Plotted points are from tethered fish mean in this
report (●), tethered maximum in this report (○), and lakewide survey mean ST and mean length
from purse seine hauls in November (▲) and June 1998 (■).

observed target strengths illustrate the influence of aspect on backscatter
amplitudes. To enhance the realism of the KRM model, probability density
functions of tilt and roll could be used to weight mean backscatter amplitudes of
fish species. At this time, it is not known how lavnun behaviour influences the
distribution of tilts and rolls.

The structure of the lavnun swimbladder (Fig. 1) is typical of other cyprinids
and closely resembles that of dace (Dobbin, 1941). The anterior and posterior
chambers are connected by a sphincter-like ductus communicans, which allows
chambers to change volume independently. The anterior chamber is in close
contact with the Weberian ossicles (Dobbin, 1941) which increases potentially
the range of sonic frequency reception (Myrberg, 1981). Enhanced aural
function by Weberian ossicles requires tautness in the anterior chamber wall
which is stiffened by the surrounding musculature and pressurized from within
(Alexander, 1959a). Also a pressurized chamber allows cyprinids to maintain
swimbladder volume as a fish changes depth. Constant pressure should preserve
the sensory characteristics of the swimbladder/Weberian ossicle system and
could maintain constant target strength over limited depth ranges if the dorsal
surface of the swimbladder is not distorted. Support for this conjecture is found
in bream Abramis brama L., a species with the highest internal swimbladder
pressures documented, where swimbladders only compress one quarter of that
expected for a free air bubble (Alexander, 1959a). Internal pressures of lavnun
swimbladders have not been measured but the structure resembles that of other
cyprinids, including bream.

The posterior chamber of the cyprinid swimbladder is connected to the back of
the oesophagus by a pneumatic duct. Since cyprinids are physostomes, they can
swallow air at the surface and force it into the swimbladder (Brawn, 1962;
Blaxter & Batty, 1984) to regulate buoyancy (Steen, 1970). An open system may allow the release of gas during vertical migration (Thorne & Thomas, 1990; Nøttestad, 1998) and may confer an advantage in predator-prey interactions when prey are avoiding (Harden Jones, 1952; Blaxter, 1985) or attempting to confuse (Nøttestad, 1998) predators. Lavun are not expected to release gas from the pneumatic duct, as they do not migrate vertically over large depth ranges. Lake Kinneret has a maximum depth of 40 m and fish are often restricted to the upper 15 m during extensive stratification and anoxic periods. Average volumes of posterior swimbladder chambers were larger than anterior chambers, but anterior volumes were more varied and had greater ranges than posterior chambers (Table III). This is consistent with the observation that anterior chambers are more extensible than posterior chambers (Alexander, 1959b) and with interaction between anterior chambers and Weberian ossicles. The presence of muscles surrounding the swimbladder and the potential pressurization of swimbladder chambers suggest that lavun and other cyprinids favour buoyancy regulation over sensory function. For lavun, enhanced buoyancy regulation may reduce the amount of energy expended to prevent sinking into anoxic waters below the seasonal thermocline.

The presence of two swimbladder chambers within a fluid-filled body has the potential to scatter sound as two damped bubbles. At carrier frequencies near resonance (c. 400 Hz for 1-cm radius bubbles, 2-1 cm apart) scattering from each chamber is omni-directional. The close proximity of the two chambers [Fig. 1(b)] decreases the resonance frequency of a single bubble by 17% and increases the scattering amplitude by c. 1 dB (R. Nero, pers. comm.). At frequencies above resonance, differences in size and shape reduce the probability of direct interaction between the two chambers as resonance frequencies would differ between the two chambers. The presence of two chambers does accentuate the constructive and destructive interference (i.e. peaks and valleys) observed in individual and mean scattering response surfaces (Figs 4 and 5). In this study, anterior and posterior swimbladder chambers were treated as two, non-interacting scattering bodies. Even though the dissected swimbladder shows a tissue connection between the two bladders, lateral X-ray images of 15 fish did not contain a visible connection between the two chambers or indicate the presence of a pneumatic duct. The KRM backscatter model calculates contributions of each swimbladder chamber and adds scattering components coherently.

The 15 fish radiographed and used in the KRM backscatter models were less dense than water (Table III). KRM modelled fish also weighed less than predicted by the Ostrovsky & Walline (1999) length-weight regression. Positive buoyancy observed among the 15 lavun is attributed to weight loss. All fish were kept in a 1-m deep tank for several weeks prior to radiography and were assumed acclimated to near surface pressures. Fish were not fed but unfiltered lake water was circulated continuously through the tank. Fish density, buoyancy, and swimbladder volume estimates suggest that swimbladder volumes were not reduced proportionate to reductions in body mass. Seasonal change in body condition is another factor that potentially reduces precision of target-strength : fish-length relations and accuracy of acoustic biomass estimates (Ona, 1999).
Body composition may affect target strength if body density changes and swimbladder volumes compensate to maintain neutral buoyancy. Since fish density may change seasonally with body composition, target strength may also change with season. The amount of lipid and gonad tissue varies seasonally in the lavnun body (I. Ostrovsky, pers. comm.). But variations in cyprinid fat content have not been shown to influence swimbladder volume (Alexander, 1959c). In contrast, variations in herring fat content reduce swimbladder volume from 5% to <2% of body volume (Ona, 1990). Ontogenetic changes in bone content due to ossification may be more important than variations in fat content when determining cyprinid density. Changes in body density with growth, in swimbladder volume as a percentage of body volume or mass, and in behaviour manifested through aspect and roll angles are all potential factors that could influence the target-strength:length relationship more among juvenile fish than adults. Accuracy of population abundance and biomass estimates may be reduced if conversion of target strength to fish length is size dependent.

Echo amplitudes recorded from tethered and in situ tracked lavnun varied by up to 20 dB among fish, and even between successive measurements on the same fish [Fig. 3(b), fish 4]. Large amplitude fluctuations are caused potentially by tilt or roll of the fish, movement by the transducer at the water surface or a combination of the two. Wriggling motions when fish are hooked increase the amount of roll and tilt by the fish relative to the transducer and will alter the angle and amount of swimbladder surface area exposed to the incident wave front. Individual and mean backscatter model response surfaces show a large sensitivity to the angle of sonic incidence formed between the sound source (i.e. transducer face) and the sagittal axis of the fish body. From model predictions, a change in incidence angle of <10° results in up to three orders of magnitude change between minimum and maximum reduced scattering length from a single animal (Table II). Average target strength estimates differ by up to 12 dB within 10° of the maximum predicted amplitude (Fig. 6). Sensitivity of echo amplitude to fish aspect angle is enhanced because of differences in aspect angles of the two swimbladder chambers. Angles of posterior chambers are more likely to deviate from fish body sagittal axes than aspect angles of anterior swimbladder chambers. Target strength variation observed among tethered and tracked lavnun backscatter measurements was equal to or greater than those measured for several species including Atlantic cod Gadus morhua L. (Nakken & Olsen, 1977; Rose & Porter, 1996), salmon Oncorhynchus sp. (Drew, 1980; Dawson & Karp, 1990), threadfin shad Dorosoma petenense (Günther) (Dawson & Karp, 1990; Jech et al., 1995), and striped bass Morone saxatilis (Walbaum) (Dawson & Karp, 1990).

The observed and predicted variation in backscattered echo amplitudes may impact the assessment and management of lavnun or other pelagic fish stocks. The KRM model predicts a non-monotonic increase in target strength with fish length (Fig. 7). The shape of the predicted $S_T$-length curve differs from that used traditionally to convert target strength to fish length (Fig. 8). If fish lengths are acoustically indistinguishable, then accurate length frequency distributions cannot be obtained from in situ target strength data collections. Fishery managers often categorize biomass distributions in size classes, so the inability to segregate medium from large fish may influence quota allocation of a target
species to the fishery or reduce the ability to distinguish species in heterogeneous fish communities. Fortunately, fish behaviour and additional net sampling can be used to minimize bias in abundance estimates. When fish congregate, they tend to associate with similar sized animals (Ranta & Lindström, 1990; Ranta et al., 1992) and maintain similar orientations (Partridge et al., 1980; Aoki, 1984). The near uniform length and aspect angle distribution among individuals within schools minimizes variation of backscattered echo amplitudes and increases precision of acoustic assessments. Supplementary net samples used to document species occurrence and length frequency distributions should continue as routine components of acoustic surveys.

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