

# Acoustic estimates of mesopelagic fish: as clear as day and night?

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The pelagic ecosystem on the Chatham Rise east of New Zealand has been monitored annually using acoustic surveys since 2001. Most of the acoustic backscatter comes from diurnally migrating mesopelagic fish, which are the major prey of hoki (*Macruronus novaezelandiae*) and other valuable commercial species. Mesopelagic schools and layers typically occur at 100–400 m depth during the day and migrate above 200 m depth at night. Previous acoustic estimates of the biomass of mesopelagic fish on the Chatham Rise were based only on night-time estimates from the upper 200 m and may significantly underestimate actual biomass. Paired day–night comparisons found that an estimated 20% of the total daytime backscatter migrates to depths of 0–14 m at night, where it is too shallow to be detected by hull-mounted acoustic instruments. In contrast, there is a positive bias associated with acoustic estimates of mesopelagic organisms during the day because they can occur close to the bottom mixed with demersal fish. Two alternative approaches for estimating biomass of diurnally migrating mesopelagic species are suggested. The first applies a correction based on the estimated proportion of backscatter migrating into the surface deadzone to night-time estimates of backscatter in the upper 200 m. The second uses night-time estimates of demersal backscatter, which remains deeper than 200 m at night, to correct daytime estimates of total backscatter. Both methods gave similar estimates of abundance and demonstrated that there was no statistically significant trend in mesopelagic fish biomass on the Chatham Rise over the past seven years.

**Keywords:** acoustic surveys, diurnal variation, mesopelagic fish, vertical migration.

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## Introduction

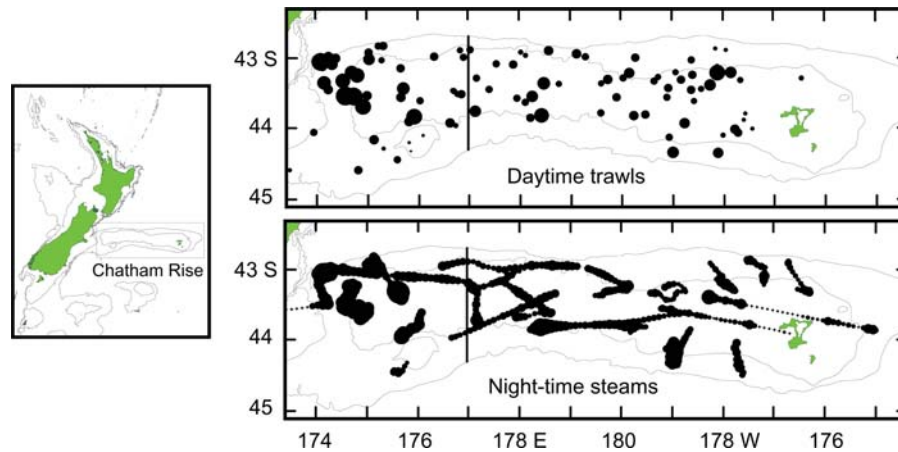
The Chatham Rise is a broad, bathymetric feature east of New Zealand (Figure 1). The subtropical convergence above it (Heath, 1985) creates a region of high primary productivity (Murphy *et al.*, 2001) that supports major commercial fisheries for hoki (*Macruronus novaezelandiae*), hake (*Merluccius australis*), ling (*Genypterus blacodes*), orange roughy (*Hoplostethus atlanticus*), and oreos (*Alloctytus niger* and *Pseudocyttus maculatus*). Hoki are the target of New Zealand's largest fishery, with annual catches of 100 000–250 000 t since 1986. The Chatham Rise is the major nursery ground for New Zealand hoki and one of the main adult feeding areas.

Annual bottom-trawl surveys for hoki and other species have been done on the Chatham Rise every January since 1992 (e.g. Livingston *et al.*, 2002). Acoustic data were recorded on most of these surveys since 1995. Initially, acoustic data were collected to help interpret trawl-survey results by, for example, investigating the vertical distribution of juvenile hoki (Bull, 2000) and to provide estimates of the ratio of acoustic vulnerability to trawl catchability for hoki and other species (O'Driscoll, 2003). However, since 2001, there has been systematic acoustic data collection covering the whole water column in recognition of the importance of monitoring the pelagic ecosystem.

Much of the acoustic backscatter on the Chatham Rise appears to be contributed by diurnally migrating mesopelagic fish (McClatchie and Dunford, 2003). Common species include myctophids (*Lampanyctodes hecteris*, *Symbolophorus* spp.) and the

sternoptychid (*Maurolicus australis*; Robertson *et al.*, 1978), which are the major prey of hoki and other valuable commercial species. Preliminary results from a continuing trophic study found that mesopelagic fish make up approximately half of the diet of hoki on the Chatham Rise (NIWA, unpublished data).

McClatchie and Dunford (2003) estimated a biomass of 665 000 t of mesopelagic fish on the Chatham Rise based on acoustic data collected during the 2001 trawl survey, but see caveats in their discussion. McClatchie *et al.* (2005) then examined the spatial distribution of mesopelagic backscatter from Chatham Rise surveys in 2001–2003 and inferred that hoki abundance and condition was correlated with the abundance of their mesopelagic prey. These previous estimates of mesopelagic fish abundance (McClatchie and Dunford, 2003; McClatchie *et al.*, 2005) were based on integration of acoustic backscatter from only the upper 200 m at night (19:00–05:00 New Zealand Standard Time, NZST). The rationale for this was that the mesopelagic fish of interest are mixed with semidemersal fish during the day, but migrate away and are separated from demersal fish at night (McClatchie and Dunford, 2003). Based on a subset of their data, McClatchie and Dunford (2003) concluded that night-time estimates in the upper 200 m (the nyctoepipelagic zone) adequately captured the scattering from vertically migrating mesopelagic fish, but acknowledged that the proportion of the total mesopelagic fish community biomass represented by the nyctoepipelagic component was unknown.



**Figure 1.** Map showing the location of the Chatham Rise off the east coast New Zealand and typical survey results (from 2006). Bathymetric contours are 500 and 1000 m. Plots on right show spatial distribution of total acoustic backscatter on the Chatham Rise observed during daytime trawl stations and night-time steams. Circle area is proportional to the acoustic backscatter (maximum symbol size =  $500 \text{ m}^2 \text{ km}^{-2}$ ). The vertical line separates western and eastern strata at  $177^\circ\text{E}$ .

The overall aim of this work was to develop a robust time-series of relative acoustic estimates for mesopelagic fish that could be used for ecosystem monitoring. We were concerned that the night-time estimates of the upper 200 m may not be representative of the total mesopelagic backscatter. Examination of echograms collected on the Chatham Rise specifically suggested that some of the backscatter migrates very close to the surface at night (Figure 2) and can move into the surface dead zone where it was not detectable by the vessel's downward-looking, hull-mounted transducer (e.g. Demer and Hewitt, 1995). In this study, we compare daytime and night-time estimates of total acoustic backscatter on the Chatham Rise in an attempt to estimate the proportion of backscatter in the nyctoepipelagic zone and the potential bias on account of the surface deadzone. Casey and Myers (1998) queried whether trawl catchability was as “clear as day and night?” and we found ourselves asking the same question for mesopelagic backscatter on the Chatham Rise.

## Material and methods

### Acoustic data collection

Acoustic data were collected during randomly stratified bottom-trawl surveys for hoki and other species on the Chatham Rise in 2001–2007. Survey dates were between 27 December and 25 January (e.g. the 2001 survey was from 28 December 2000 to 25 January 2001). All surveys were done from the 70-m research stern trawler RV “Tangaroa”. Data in 2004 were collected using an uncalibrated ship's echosounder only and are not considered here. The other six surveys were done using the same custom-built CREST acoustic system (Coombs *et al.*, 2003) with hull-mounted, Simrad, single-beam 12 and 38 kHz transducers. CREST is a computer-based “software echosounder”, which supports multiple channels. The transmitter had a nominal power output of 2 kW rms. Transmitted pulse length was 1 ms with 3 s between transmits. The 38-kHz transducer was calibrated regularly, at least once a year, with a 38.1 mm tungsten–carbide sphere following standard procedures (Foote *et al.*, 1987). It was not possible to calibrate the 12-kHz transducer, so these data were only used to make

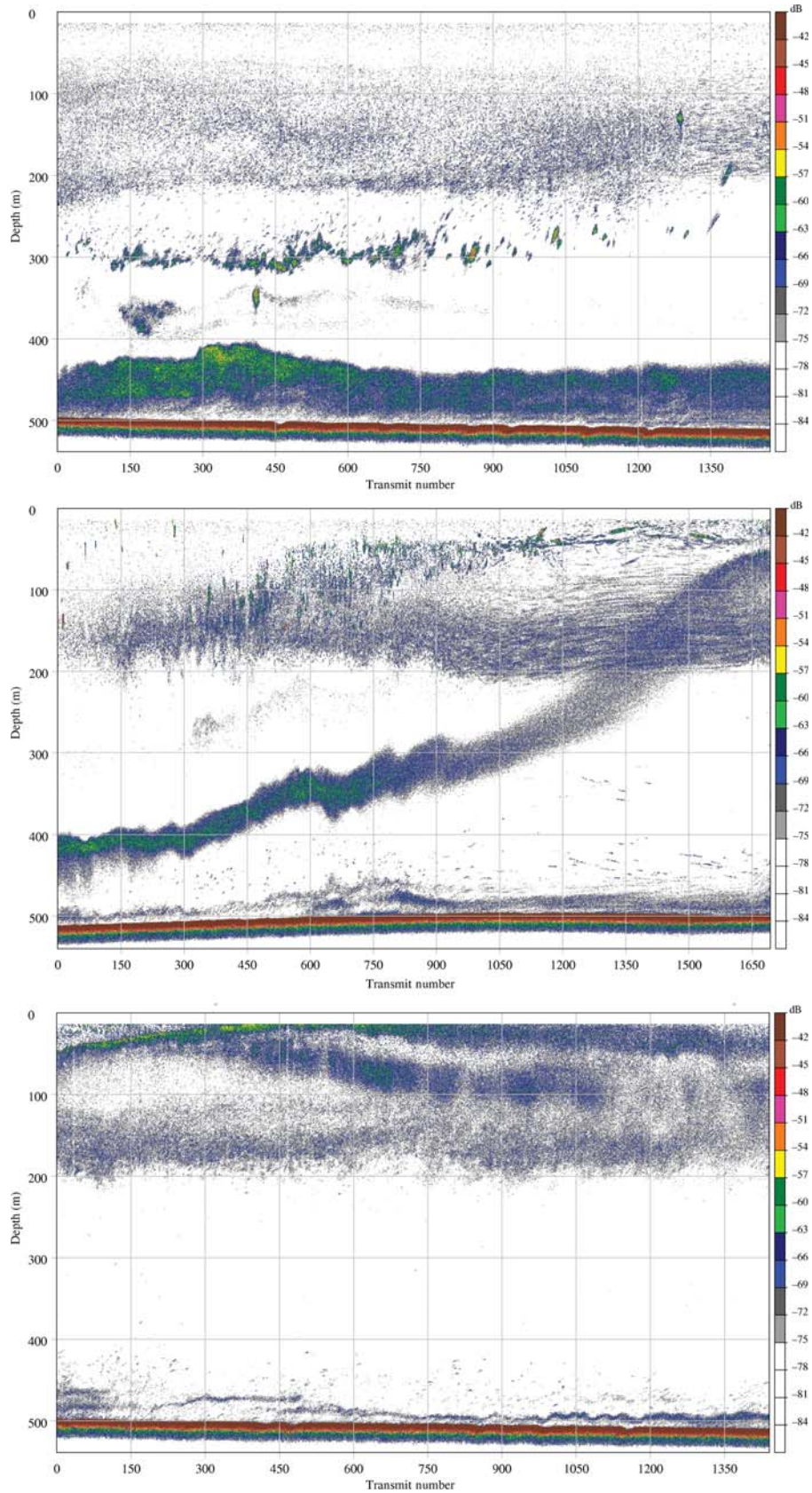
visual comparisons with the 38-kHz data and were not analysed quantitatively.

Bottom-trawl surveys typically had 96–119 random stations, stratified by depth and area, with a minimum distance between any two stations of 5.5 km. At each station, the bottom trawl was towed for 5.5 km at a speed over the seabed of 3.5 knots. Bottom trawls were only done during daylight with all trawling taking place between 05:00 and 20:00 NZST. Acoustic data were collected during bottom trawls and while steaming, typically at 8–10 knots, between trawl stations, by day and night.

At night, vessel officers surveyed some of the areas to be trawled the subsequent day by transiting over the anticipated trawl paths and checking that the seabed in each was suitable for bottom trawling. This resulted in paired daytime and night-time acoustic recordings for a subset of trawls. There was also a short experiment on bottom-trawl catchability in 2002, where the last bottom trawl of the day was repeated at night. Because the daytime and night-time trawls were run in the same direction and the vessel steamed back along the trawl path at dusk, we had comparable daytime, dusk, and night-time recordings of the same trawl path on ten occasions from this experiment (Figure 2).

### Midwater trawling

Limited trawling was done in 2005–2007 to identify the acoustic targets using a midwater “myctophid trawl” manufactured by Motueka Nets New Zealand Limited. This trawl was based on a scaled-down version of a commercial design, with a 15-m circular opening and 10-mm codend. All mark-identification trawling was done at night to avoid interfering with the bottom-trawl survey. Tows were targeted at individual marks or discrete depth layers. Tow speeds averaged 3.5 knots (range 2.5–4.7 knots), and tow lengths were between 0.9 and 3.7 km (average 1.9 km). For each trawl, all items in the catch were sorted and weighed on Seaway, motion-compensating electronic scales accurate to  $\sim 0.1$  kg. Where possible, finfish, squid, and crustaceans were identified to species level. The quality of the species identification varied between trips, depending on the staff on board, so catches were summarized at a higher (usually family) taxonomic level to ensure consistency.



**Figure 2.** Series of repeated transects over the same area in daylight (17:04–18:18 NZST), at dusk (19:18–20:42), and at night (20:43–21:55) showing ascent of mesopelagic layers.

### Acoustic abundance estimation

Acoustic data collected during the survey were analysed using standard echo-integration methods (Simmonds and MacLennan, 2005), as implemented in NIWA's Echo Sounder Package (ESP2) software (McNeill, 2001). All echograms were visually scrutinized and the seabed was detected by a combination of an in-built, bottom-tracking algorithm and manual editing. Pings with data obviously degraded by bubble attenuation were removed. Only files with >90% of good (i.e. not degraded) pings were considered of acceptable quality for echo integration. Data were integrated in two ways: (i) from 14 m below the surface, where 14 m was the approximate depth of the surface deadzone for our 38 kHz transducer mounted at 6 m depth, in 50-m depth bins down to the detected bottom (i.e. surface-referenced integration); and (ii) in 5-m depth bins up to 50 m from the detected bottom (i.e. bottom-referenced integration).

Night-time estimates were based on data recorded while steaming between 20:00 and 05:00 NZST. This differed slightly from McClatchie and Dunford (2003), who defined night as 19:00–05:00 NZST. Times of sunset and sunrise on the mid-Chatham Rise in the middle of January are 20:15 and 05:02 NZST. The horizontal integration unit for night-time data was 500 pings (25 min), which was equivalent to 6–8 km at typical steaming speeds of 8–10 knots. This unit was chosen because it was approximately equivalent to the length of the acoustic recordings during daytime trawls. Mean area-backscattering coefficients were estimated for each 500 ping unit ( $s_{a,\text{night},500}$ ), as plotted in Figure 1).

To estimate abundance, we treated each night as a single random transect. The assumption of randomness was at least to some extent valid because the vessel was steaming random trawl stations. The night-time transects typically ranged in length from 30 to 160 km and there were between 17 and 27 nights with suitable acoustic data in each survey year. Mean area-backscattering coefficients were calculated for each transect ( $s_{a,\text{night},\text{transect}}$ ). Then, an overall survey estimate and variance was obtained using the formulae of Jolly and Hampton (1990), as described by Coombs and Cordue (1995). The Chatham Rise was divided into two strata (east and west of 177°E) based on consistent observations of higher acoustic backscatter in the west (McClatchie *et al.*, 2005). Note that our boundary between east and west strata differs slightly from the boundary of 176°E used by McClatchie and Dunford (2003), which was based on only one year's data.

Daytime estimates of abundance were based on data recorded while bottom trawling only. Daytime steams between stations were not considered. Acoustic recording was started when the trawl doors entered the water and stopped when the gear was hauled off the bottom. This resulted in short (6–8 km) recordings at each random trawl location. Mean area-backscattering coefficients were estimated for each trawl recording ( $s_{a,\text{day},\text{trawl}}$ ) and these were treated as random point samples to estimate survey mean and variance. As for night-time recordings, the Chatham Rise was divided into east and west strata at 177°E. Between 86 and 117 daytime acoustic point estimates were available from each survey.

All acoustic abundance estimates were based on estimates of total mean area-backscattering coefficients ( $s_a$ ), partitioned by depth, but not by mark type. Depth zones were defined as: (i) nyctoepipelagic—occurring from 14 to 200 m at night;

(ii) nyctobathypelagic—occurring deeper than 200 m, but more than 50 m above the detected bottom at night; (iii) demersal—occurring within 50 m of the detected bottom at night. In this paper, we use  $s_a$  as a proxy for biomass (after McClatchie *et al.*, 2005). One relationship between  $s_a$  and biomass for mesopelagic fish on the Chatham Rise is derived by McClatchie and Dunford (2003), but there is still considerable uncertainty associated with the species involved, their size distributions, and their acoustic target strengths.

### Paired day–night comparisons

The subset of night-time data that corresponded to daytime trawl paths ( $s_{a,\text{night},500} \approx s_{a,\text{day},\text{trawl}}$ ) was selected using the criteria of 2 km and 12 h maximum separations between sample midpoints. Where more than one  $s_{a,\text{night},500}$  datum fulfilled these criteria, the one closest (in distance) to the trawl path was chosen. Data selected for paired comparisons were reintegrated at much greater vertical resolution (2-m depth bins).

Paired daytime ( $D_i = s_{a,\text{day},\text{trawl},i}$ ) and night-time ( $N_i = s_{a,\text{night},500,i}$ ) values were used to estimate the proportion of the total backscatter ( $p$ ) that remains in the acoustic-detection zone (deeper than 14 m) at night. Let  $D_i = T_i \varepsilon_i$  and  $N_i = p T_i \tau_i$ , where  $T_i$  is the true value of the backscatter, and  $\varepsilon_i$  and  $\tau_i$  are random errors both with mean 1. This assumes that the random variability around the true value is proportional to the true backscatter (i.e. larger values have greater variability). Then,  $\log(D_i) = \log(T_i) + \log(\varepsilon_i)$  and  $\log(N_i) = \log(p) + \log(T_i) + \log(\tau_i)$ , so  $\log(N_i) - \log(D_i) = \log(p) + \log(\tau_i) - \log(\varepsilon_i)$ . Because both random errors have means = 1:

$$\log(p) = \left( \log \left( \frac{N_i}{D_i} \right) \right). \quad (1)$$

We estimated uncertainty on values of  $p$  by bootstrapping. The data were resampled (with replacement) 1000 times, each time selecting a sample of the same size as the original dataset. Values of  $p$  and associated values were calculated for each bootstrapped sample and 95% confidence intervals were generated.

We attempted to correct night-time estimates for loss of backscatter into the surface deadzone by assuming that backscatter in the dead zone (0–14 m) was equivalent to the observed area-backscattering coefficient in the equivalent region immediately below the dead zone (i.e. 14–28 m from the surface). Surface-corrected, night-time values,  $N_{i,sc} = N_i + N_i^{14-28m}$ , were calculated and compared with daytime values to estimate a surface-corrected value for  $p$  ( $p_{sc}$ ). If the surface correction was sufficient to account for the reduction in backscatter at night, we expected  $p_{sc}$  to equal 1.

Estimates of the average proportion of the total backscatter in the three different depth zones at night were obtained by scaling the observed vertical distribution of night-time backscatter (from  $s_{a,\text{night},\text{transect}}$  values) in each survey by  $p$ . A correction factor (CF) was then calculated to scale up the observed nyctoepipelagic backscatter to account for the estimated missing backscatter ( $1-p$ ):

$$\text{CF} = \frac{(1-p) + p\text{NE}}{p\text{NE}}, \quad (2)$$

where pNE is the estimated average annual proportion of total backscatter in the epipelagic zone at night.

## Results

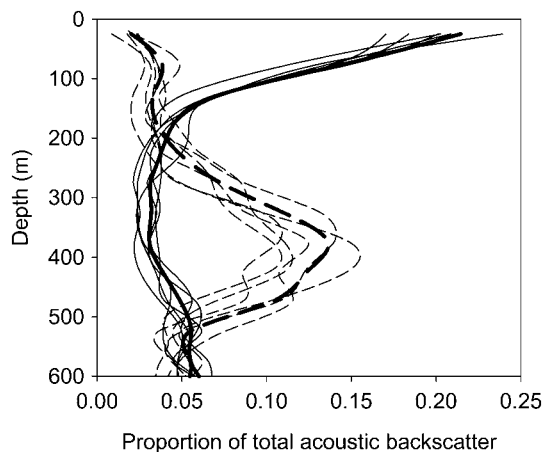
### Trawl data

A total of 65 species or species groups was caught in 41 night-time midwater trawls in 2005–2007. Catches from 19 trawls in the upper 200 m (nyctoeipelagic zone) averaged 5.73 kg total weight and were dominated by myctophid fish (64.3% by weight, genera identified included *Lampanyctodes*, *Lampanyctus*, *Diaphus*, *Symbolophorus*, and *Electrona*) and gelatinous zooplankton (17.3% by weight, mainly salps). Catches were lower in the 21 trawls deeper than 200 m (nyctobathypelagic zone), averaging 3.39 kg, with fewer myctophids (44.3% by weight) and larger proportions of squid (19.1%) and decapods (8.9%, mainly prawns).

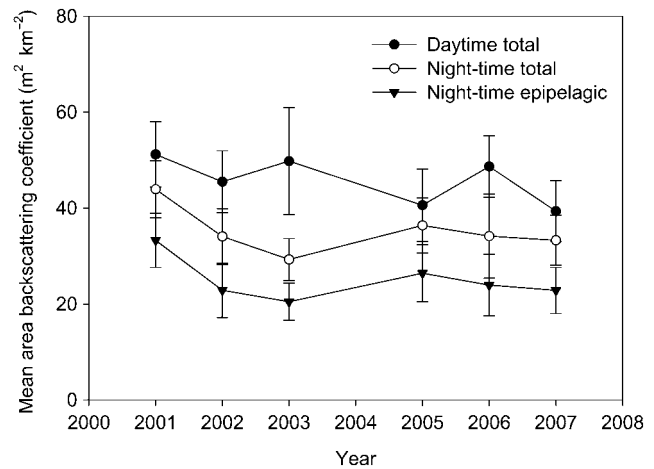
### Acoustic abundance estimates

Similar patterns of diurnal vertical migration were observed in all years (Figure 3). Most acoustic backscatter was concentrated at 200–500 m depth during the day and migrated into the upper 200 m at night (Figure 3). This vertically migrating component was assumed to be dominated by mesopelagic fish (see McClatchie and Dunford, 2003 for rationale and caveats). Mean acoustic backscatter in the upper 14–200 m at night displayed a similar pattern between surveys to total night-time backscatter (Figure 4). In individual surveys, 67–76% of the total night-time backscatter was in the top 14–200 m, indicating that the nyctoeipelagic component was the dominant source of acoustic backscatter on the Chatham Rise. Mesopelagic schools and layers were often close to the bottom by day (Figure 2). This meant that daytime estimates in the bottom 50 m were 2.5–5.0 times higher than night-time estimates. The component of backscatter that remained within 50 m of the bottom at night was assumed to be dominated by demersal fish and made up only 9–14% of the total night-time backscatter.

Daytime estimates of total acoustic backscatter over the Chatham Rise were consistently higher than night-time estimates (Figure 4). In the six survey years, night-time estimates of total



**Figure 3.** Vertical distribution of total acoustic backscatter integrated in 50 m depth bins on the Chatham Rise observed during the day (dashed lines) and at night (solid lines) in 2001–2007. Thin lines show data from individual years. Thick lines are averages over the 6 years.



**Figure 4.** Total acoustic-abundance indices for the Chatham Rise based on (strata-averaged) mean area backscatter ( $s_a$ ). Error bars are  $\pm 2$  s.e.

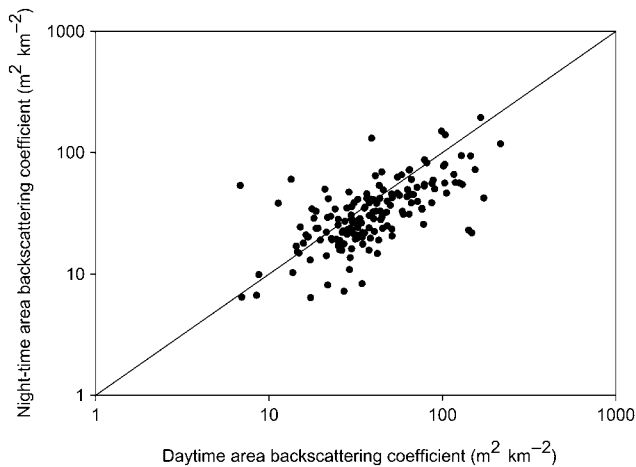
backscatter (expressed as mean  $s_a$ , averaged over the entire survey area) were 59–90% of daytime estimates. In some years (e.g. 2003), the difference between daytime and night-time estimates was to some extent explained by sampling error, because daytime and night-time estimates were based on different survey designs (Figure 1). For example, in 2003, there was one very high point estimate of total backscatter from a daytime trawl. This led to an increased difference between daytime and night-time estimates in 2003, and is reflected in the increased uncertainty associated with the daytime estimate from this year (Figure 4). However, the consistent trend of lower observed backscatter at night could not be explained by survey design alone and was related to bias in night-time estimates.

### Paired day–night comparisons

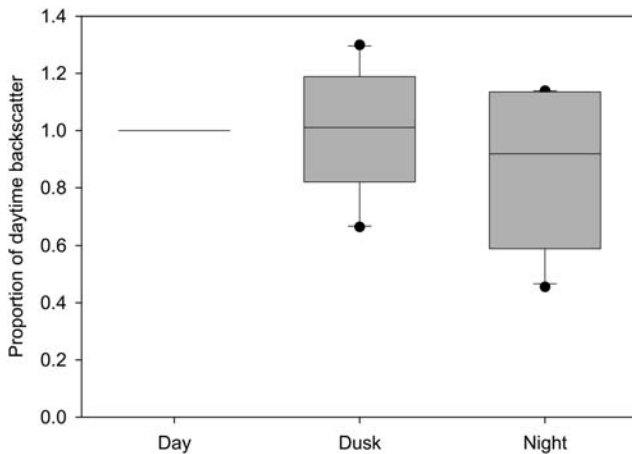
Besides the ten values from the 2002 experiment, another 150 day–night pairs were selected. Although daytime and night-time observations were relatively close in time (<12 h apart) and in space (<2 km apart), there was considerable variability between paired data (Figure 5). Night-time estimates were lower than daytime estimates in 110 of 160 pairs.

The estimate of the proportion of total backscatter observed at night,  $p$ , from all paired data was 0.80 (95% CI 0.74–0.85). The estimated mean proportion varied between surveys from 0.71 (0.60–0.82) in 2005 to 0.89 (0.77–1.01) in 2007. Surface-deadzone corrections based on extrapolating the average density 14–28 m below the surface into the surface deadzone (upper 14 m) were insufficient to account for the reduction in total backscatter at night. The estimate of  $p_{sc}$  from all years combined was 0.89 (95% CI 0.83–0.95). To obtain  $p_{sc} = 1$ , we had to assume that average density in the upper 0–14 m was 2.2 times the average density from 14 to 28 m.

To further investigate the transition between daytime and night-time estimates, we considered the ten experimental tows from 2002 when we had daytime, dusk, and night-time recordings over the same path. Although not statistically significant, these data suggested that acoustic backscatter at dusk, while the mesopelagic layers were migrating upwards, but before they had reached the surface (Figure 2), was similar to daytime estimates, but that backscatter decreased at night (Figure 6).



**Figure 5.** Comparison of night-time and daytime estimates of total mean area backscatter ( $s_a$ ) from 160 day–night paired comparisons in 2001–2007. Solid line shows equality.



**Figure 6.** Comparison of daytime, dusk, and night-time estimates of total mean area backscatter ( $s_a$ ) from ten repeated transects in 2002. Daytime values were scaled to 1. Box plots show lower and upper quartiles divided by the median, whiskers are tenth and 90th percentiles, and points are minimum and maximum values.

### Corrected abundance indices

Estimates of the average annual proportion of the total backscatter in different depth zones at night are given in Table 1. Over all surveys, 56% of the total acoustic backscatter on the Chatham Rise is nyctoepipelagic, 15% is nyctobathypelagic, and 9% is demersal. The remaining 20% ( $1-p$ ) of the total backscatter is missing at night and we have assumed that this component had migrated into the surface deadzone. Values of the annual correction factor necessary to scale the observed nyctoepipelagic backscatter to account for missing backscatter ranged from 1.18 in 2007 to 1.57 in 2005 (Table 1). Annual correction factors were applied to night-time abundance estimates from the wide area surveys (corrected night-time values in Figure 7).

An alternative method of correcting for mesopelagic backscatter missing in the surface deadzone at night does not use the paired day–night data at all. If we assume that the daytime acoustic estimates provide an unbiased estimate of true total backscatter across

the entire Chatham Rise, then by subtracting the observed backscatter component that remains deeper than 200 m at night (i.e. the nyctobathypelagic and demersal components), we get an estimate of the migrating nyctoepipelagic component including the surface deadzone (corrected daytime values in Figure 7).

Both methods give similar values, which are an average of 40% higher than the uncorrected estimates of nyctoepipelagic backscatter (Figure 4). Both corrected series suggest that there has been no significant trend in mesopelagic fish biomass on the Chatham Rise over the past seven years (Figure 7).

### Discussion

Estimates of total acoustic abundance were lower at night than during the day on the Chatham Rise. In six survey years, night-time estimates of total backscatter (expressed as mean  $s_a$ , averaged over the entire survey area) were 59–90% of daytime estimates. In 160 paired day–night recordings, the average proportion of daytime backscatter detected at night was 80% (95% CI 74–85%).

Hjellvik *et al.* (2004) suggested that there are three hypotheses to explain diurnal variation in total acoustic backscatter: (i) fish hiding in the bottom or surface deadzones; (ii) variation in fish target strength (TS) because of diurnal variation in the tilt-angle distribution; and (iii) variation in fish TS because of pressure-related changes during vertical migration.

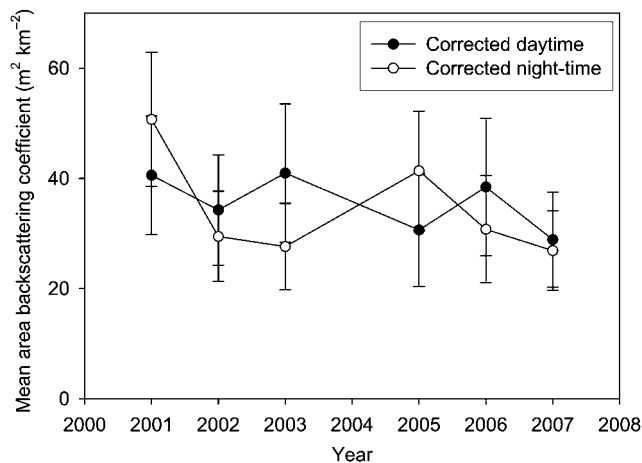
Mesopelagic fish are a diverse group and have a range of swimbladder morphologies, including some species with reduced or absent swimbladders. Swimbladder morphology can also change relative to fish size (e.g. Yasuma *et al.*, 2003). For species with a swimbladder (e.g. *Maurolicus australis* and *Lampanyctodes hectoris*) to maintain a constant swimbladder volume throughout their vertical range of hundreds of metres would require extensive daily gas secretion and absorption. Alternatively, the fish would need to be negatively buoyant at depth. Assuming constant tilt-angle distribution, this would lead to lower TS estimates and consequently reduced observed backscatter, by day. This is the opposite pattern to that observed, so it seems unlikely that the diurnal change in backscatter was a consequence of pressure-related changes in TS.

Both remaining hypotheses, variation in TS attributable to changes in tilt-angle distribution or fish ascending into the dead zone, could explain the reduction in acoustic backscatter at night observed in the current study. Many models and experiments have demonstrated the relationship between TS and tilt-angle (Simmonds and MacLennan, 2005). Reduction in average TS at night could be caused by systematic changes in the orientation of individual fish TS or by increased variability in tilt-angle distributions for a group of fish (McClatchie *et al.*, 1996). There are usually behavioural changes in mesopelagic fish orientation and organization during the diurnal cycle (Gjøsaeter and Kawaguchi, 1980), and additional work is required to monitor their effects on acoustic TS (Benoit-Bird and Au, 2001). However, visual examination of echograms (Figure 2), vertical profiles (Figure 3) and the results from a limited number of comparable recordings at dusk (Figure 6) all suggest that the main bias was as a consequence of migration into the surface deadzone at night. At dusk, mesopelagic fish were actively migrating upwards (Figure 2), and for that reason, we would expect their orientation (and TS) to have changed. However, total acoustic backscatter at dusk was similar to that in daytime recordings, and backscatter only reduced at night, when fish were close to the surface (Figure 6).

**Table 1.** Estimates of the average proportion of the total backscatter in different depth zones at night.

Year	Night-time depth zone				
	Missing (0–14 m)	Epipelagic (14–200 m)	Bathypelagic (>200 m)	Demersal (bottom 50 m)	Correction factor (CF)
2001	0.28 (0.14–0.42)	0.54 (0.44–0.65)	0.11 (0.09–0.13)	0.06 (0.05–0.08)	1.52 (1.25–1.77)
2002	0.16 (0.07–0.25)	0.56 (0.50–0.63)	0.18 (0.16–0.20)	0.10 (0.09–0.11)	1.29 (1.12–1.45)
2003	0.20 (0.02–0.34)	0.56 (0.46–0.68)	0.14 (0.12–0.17)	0.10 (0.08–0.12)	1.35 (1.04–0.61)
2005	0.29 (0.18–0.40)	0.51 (0.44–0.60)	0.12 (0.10–0.14)	0.07 (0.06–0.09)	1.57 (1.35–1.77)
2006	0.17 (0.04–0.29)	0.58 (0.50–0.68)	0.15 (0.13–0.18)	0.10 (0.08–0.11)	1.28 (1.06–1.50)
2007	0.11 (0.00–0.23)	0.61 (0.53–0.69)	0.16 (0.14–0.18)	0.12 (0.11–0.14)	1.18 (0.98–1.37)
All	0.20 (0.15–0.26)	0.56 (0.52–0.60)	0.15 (0.13–0.17)	0.09 (0.08–0.10)	1.36 (1.26–1.46)

The missing fraction is estimated as  $1-p$ , where  $p$  is the average proportion of total backscatter observed at night from paired day–night acoustic data. Estimates for other depth zones calculated from observed vertical distribution along night-time transects scaled by  $p$ . The correction factor is the value used to scale observed nyctoepipelagic backscatter to account for the missing backscatter if we assume that the missing component is all in the surface deadzone. 95% confidence intervals in parentheses are from bootstrapping.



**Figure 7.** Acoustic-abundance indices for mesopelagic fish on the Chatham Rise. Corrected daytime estimates were derived from daytime estimates of total backscatter minus the night-time bathypelagic and demersal components, which remain deeper than 200 m at night. Corrected night-time estimates were based on night-time estimates of epipelagic backscatter (14–200 m), with a correction for the estimated proportion of backscatter migrating into the surface deadzone (Table 1). Error bars are approximate 95% confidence intervals from bootstrapping.

Regardless of the causal mechanism, there appears to be a significant bias in night-time estimates of mesopelagic backscatter. Conversely, it is not possible only to survey during the day because mesopelagic layers are mixed with demersal fish close to the bottom and we are not yet able to separate these acoustically. Conventional dead zone corrections based on extrapolating the average density 14–28 m below the surface into the surface dead zone (upper 14 m) were insufficient to account for the reduction in total backscatter at night. Our results indicated that densities in the surface deadzone have to be a factor of two higher than densities in the zone immediately below to explain the reduction in backscatter. We proposed two alternative methods to calculate nyctoepipelagic backscatter that utilized both daytime and night-time recordings. Of these, the method that subtracts night-time estimates of the backscatter that remains deeper than 200 m (i.e. the nyctobathypelagic and demersal components) from daytime estimates of total backscatter (corrected daytime estimates in Figure 7) is probably the more robust, because it combines data over the entire survey area. The major source of uncertainty

with this method is the relatively low precision of daytime acoustic estimates (Figure 4). The alternative method (corrected night-time in Figure 7) uses paired day–night comparisons to estimate the proportion of backscatter migrating into the dead zone to correct night-time estimates. This method is sensitive to the relatively small number and variability of paired data available from a survey and also depends on tow paths being surveyed at night, which is becoming less critical as the areas of trawlable ground on the Chatham Rise become better defined. Both correction methods gave similar results for the first seven years of this study.

Because the nyctoepipelagic backscatter as a proportion of the total backscatter has been reasonably constant over time (Table 1), similar relative trends in abundance are obtained using uncorrected night-time backscatter from 14 to 200 m (Figure 4) and the two corrected indices (Figure 7). In this respect, the assumption of McClatchie and Dunford (2003) that night-time estimates in the upper 200 m were representative of the scattering from nyctoepipelagic fish on the Chatham Rise is vindicated. However, our corrected estimates are less biased and consequently provide a better representation of actual (absolute) abundance.

The Chatham Rise survey time-series is continuing. Future work will link spatial and temporal patterns in mesopelagic fish abundance with abundance and condition of demersal-fish predators and also with climate and oceanographic conditions. Much more extensive targeted trawling is also planned to improve knowledge of mesopelagic species composition, with associated *ex situ* and model estimates of acoustic TS being developed for key species.

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