

Day–night differences in Cunene horse mackerel (*Trachurus trecae*) acoustic relative densities off Angola

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The assessment and the management of the Cunene horse mackerel in Angola rely heavily on abundance estimates from hydroacoustic surveys. Acoustic data collected from 1994 to 1999 were analysed to quantify diurnal variation in relative acoustic densities at 38 kHz. The nautical-area scattering coefficient (s_A , m^2 nautical mile $^{-2}$) was characterized by clear day–night differences: s_A values recorded during the day were significantly higher (mean s_A : 135 m^2 nautical mile $^{-2}$) than the corresponding night-time values (mean s_A 83 m^2 nautical mile $^{-2}$). This pattern is associated with differences in behaviour and horizontal and vertical distributions between day and night: by day, the fish school near the seabed, and by night, they move into the pelagic zone and disperse into wide-spread scattering layers. More than 40% of the total backscatter by day originated from the bottom 10 m, but at night this proportion decreased to <10%. The findings demonstrate considerable influences of behaviour and aggregation dynamics on acoustic measurements. Possible implications for the estimates of acoustic abundance are discussed in the light of the differences.

Keywords: abundance estimates, acoustics, Cunene horse mackerel, diurnal behaviour, vertical migration.

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Introduction

Off Angola, horse mackerel are harvested by industrial, semi-industrial, artisanal, and subsistence fleets and are the most important species for human consumption. Two species are found in Angolan waters: Cunene horse mackerel (*Trachurus trecae*) and Cape horse mackerel (*Trachurus t. capensis*). The former species is distributed along the entire coast of Angola, with aggregations of juvenile fish extending south into Namibian inshore waters, whereas the latter is found off southern Angola, Namibia, and South Africa, in the colder Benguela Current ecosystem (Duarte, 2001).

Annual acoustic surveys targeting Cunene horse mackerel, Cape horse mackerel, flat sardinella (*Sardinella maderensis*), round sardinella (*Sardinella aurita*), and sardine (*Sardinops sagax*) are carried out in Angolan waters by the RV “Dr Fridtjof Nansen”, and they provide abundance estimates of all principal pelagic fish stocks. The estimates obtained from the surveys form the primary basis for the assessment and management of pelagic stocks. The acoustic method enables large volumes of water to be sampled with relatively little effort and is therefore the generally preferred method of making direct estimates of the abundance of schooling pelagic fish (MacLennan and Simmonds, 1992). As for all methods, however, methodological limitations and sources of error exist (Anon., 2003, 2004), and acoustic estimates may be affected by both target availability and errors related to identification and the conversion from acoustic densities to biomass (Olsen, 1990; MacLennan and Simmonds, 1992; Fréon *et al.*, 1993a; Axelsen *et al.*, 2004).

Vertical migrations affect the target strength (TS) of fish (Foote, 1978; MacLennan and Simmonds, 1992) through compression/decompression of the swimbladder (Foote, 1980; Vabø, 1999) and changes in body posture (tilt-angle) of the fish relative to the transducer (Nakken and Olsen, 1977; Foote, 1987; Ona, 2001). Vertical migrations can also affect estimates indirectly through depth-dependent changes in availability and avoidance (Olsen *et al.*, 1983; Fréon and Misund, 1999; Vabø, 1999). As a result, TS can vary appreciably throughout a 24-h cycle, with potential impacts on abundance estimates. Better knowledge of the behaviour of the species involved is therefore important for developing effective survey strategies and optimizing sampling during acoustic surveys (Coetzee *et al.*, 2001). The overall aim of this paper is to analyse the patterns of variation in acoustic densities recorded for Cunene horse mackerel associated with diel vertical migrations and to evaluate their potential effects on the acoustic estimates of abundance.

Material and methods

The acoustic-survey data collected in Angola by RV “Dr Fridtjof Nansen” from 1994 to 1999 were analysed using the standard echo-integration method (MacLennan and Simmonds, 1992). The surveys covered the area between the Congo (06°00'S) and Cunene Rivers (17°15'S), with transect lines running perpendicular to the coast. The transect lines were spaced ~6 nautical miles (hereafter miles) apart, extending offshore from 20 to 500 m bottom depth (Figure 1). Only data collected north of 12°S were

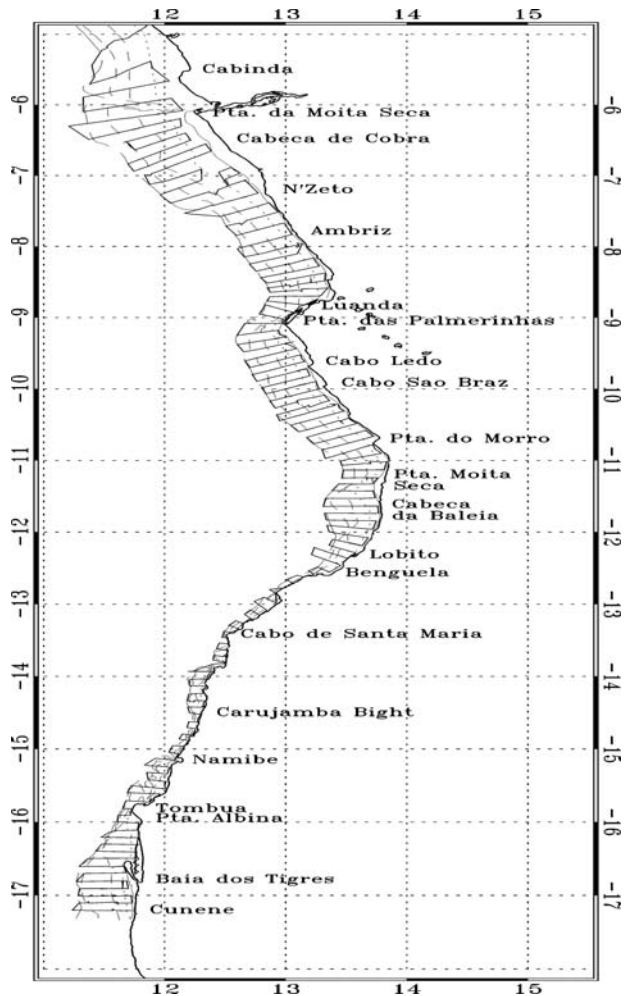


Figure 1. Course track surveyed (day and night). Latitude is shown in °S and longitude in °E.

included in the analysis, to exclude data from regions in which the distributions of Cunene and Cape horse mackerel overlap.

Values of the nautical-area backscattering coefficient s_A (m^2 nautical mile $^{-2}$; definitions in MacLennan *et al.*, 2002) were obtained using a Simrad EK 500 echosounder, running a keel-mounted 38-kHz transducer with seven nominal alongships and athwartships beam angles. The echosounder operated at a transmission power of 2000 W, ~ 1.0 pings s^{-1} , a 1-ms pulse duration, and 3.8 kHz reception bandwidth. Acoustic data were logged and post-processed using the Bergen Echo Integrator (BEI) system (Knudsen, 1990). The elementary sampling distance unit (ESDU) was set at five miles. Net samples of acoustic targets were obtained using pelagic (Akrehamn, 10–12 m vertical opening) and demersal (Gisund Super, 5 m vertical opening) sampling trawls.

Analysis

Vertical migration in pelagic fish is closely related to the diel solar cycle (Fréon *et al.*, 1993b). As the data were gathered at various times of the year, the correlation between recorded time (UTC) and solar time was not constant between surveys, so recorded time was converted to solar time. For each observation, the time of sunrise and sunset at the given date and position were

computed using standard astronomical formulae, as provided by Meeus (1998). The time-stamps of each ESDU were then standardized into the solar scale, sunrise corresponding to 06:00 and sunset to 18:00. Each day was further divided into four periods, “dawn” from 30 min before sunrise to 30 min after sunrise, “day” from 30 min after sunrise to 30 min before sunset, “dusk” from 30 min before sunset to 30 min after sunset, and “night” from 30 min after sunset to 30 min before sunrise.

Within each ESDU, the data were grouped into two sets: the bottom channel, covering the water column from the sounder-detected bottom up to 10 m above the bottom, and the pelagic channel, corresponding to the water column from 10 m above the bottom up to the upper integration limit set in the BEI software (13 m below the surface). The pelagic channel was further divided into 10 m subinterval depth strata. To determine the vertical variation in acoustic densities, the relative depth (RD) of the centre of mass of the echo recordings was computed for each ESDU:

$$\text{RD}_i = \frac{1}{D_i} \sum_j D_{i,j} \frac{s_{A_{i,j}}}{s_{A_i}}, \quad (1)$$

where $D_{i,j}$ is the mid-depth of depth stratum j of ESDU i , $s_{A_{i,j}}$ the s_A -value allocated to horse mackerel in depth stratum j of ESDU i , s_{A_i} the total s_A allocated to horse mackerel in ESDU i , and D_i the average bottom depth at ESDU i .

The proportion of the total echo allocated to horse mackerel in the bottom interval (PB) was calculated for each ESDU:

$$\text{PB}_i = \frac{s_{A_{i,b}}}{s_{A_i}}, \quad (2)$$

where $s_{A_{i,b}}$ is the s_A allocated to horse mackerel in the bottom channel of ESDU i , and s_{A_i} is the total s_A allocated to horse mackerel in ESDU i .

The acoustic densities may vary appreciably between consecutive ESDUs, given the characteristics of the geographic distribution of fish, so to recognize differences in acoustic densities recorded by day and by night, spatial variation in acoustic density had to be taken into account. A Relative Acoustic Density Index (RADI) was therefore calculated for each ESDU i :

$$\text{RADI}_i = \frac{s_{A_i} - \bar{s}_{A_{24i}}}{\bar{s}_{A_{24i}}}, \quad (3)$$

where s_{A_i} represents the s_A values allocated to horse mackerel in ESDU i , and $\bar{s}_{A_{24i}}$ indicates the average ESDU s_A -value allocated to horse mackerel during the 24-h period around the mid-time of the ESDU analysed.

To analyse time-patterns through the 24-h diel period, the relative indices derived from the ESDUs (RD, PB, and RADI) were binned in 2-h intervals. This interval length ensured that sufficient ESDUs were included to provide meaningful summary statistics, while maintaining an adequate time resolution. Differences in acoustic densities may also be related to patterns in the spatial aggregation (patchiness) and to behavioural modulation of the TS (Nakken and Olsen, 1977; Foote, 1978). To investigate the effect of time of day on the level of patchiness of the acoustic recordings of Cunene horse mackerel, the data were divided into intervals, and a Relative Presence Index (RPI) was calculated for

each interval:

$$RPI_j = \frac{P_j - P_{24j}}{P_{24j}}, \quad (4)$$

where P_j is the proportion of positive ESDUs in time-interval j , and P_{24j} is the proportion of positive ESDUs in the 24-h period centred on the midpoint of time interval j .

To test the diel-period effect, it was essential to compare only neighbouring day and night periods. The average s_A values obtained during each day were compared with the average s_A values from the nights immediately before and after, and the average values obtained during each night were compared with the average s_A from the two neighbouring days. Similarly, the proportion of positive ESDUs (RPI) in each day was compared with the same proportion in the preceding and following nights. The proportion of positive ESDUs in each night was also compared with the corresponding proportion in the two neighbouring days. The dawn and dusk periods, which were short and usually only included one ESDU each, were excluded from the analysis. For each survey, the endpoint day or night periods were excluded from the analysis, and only periods in which Cunene horse mackerel were present in at least one ESDU in a set of day and night periods were included.

To test the null hypothesis of no difference between RADIs by day and night, a paired-comparison randomization test was used (Manly, 2006). The test statistic was the number of positive differences between the average s_A recorded by day and the corresponding night period (sign test). The same methodology was used to test the null hypothesis of no effect of period (day–night) on the proportion of positive ESDUs (RPI).

Results

The diel variability in measured s_A indicates substantial day–night differences in s_A over the 24-h cycle. The RADI shows a pattern of increase from dawn, relative stability during the morning (up to 13:00), then a decrease in the afternoon to minimum values at night (Figure 2a). On average, s_A values measured by day were 12.5% higher than the corresponding night values ($p < 0.001$). The RPI showed a similar pattern, with mean value and variability increasing during the morning up to midday, and the lowest values at night (Figure 2b). The proportion of positive ESDUs observed by day was significantly (60%, $p < 0.001$) higher than the corresponding night-time values.

The observed difference in average acoustic density between day and night was matched by a marked difference in depth (Figure 2c) and aggregation characteristics (Figure 3). Generally, Cunene horse mackerel concentrated in dense schools near the seabed by day, but at night they dispersed widely in the pelagic layers.

The observed differences in aggregation characteristics are reflected in the evolution of the RDs of horse mackerel by day (Table 1). The fish migrated from RDs of 20–40% at night (95% CI), corresponding to mean absolute depths of 42–46 m, to RDs of 70–80% by day (98–110 m). The proportion of acoustic densities recorded in the 10-m bottom channel followed a similar pattern. At night, 3–8% (95% CI) of the s_A attributed to Cunene horse mackerel was found in the bottom channel, increasing gradually to 35–40% by day.

Discussion

Consistently higher values of s_A were obtained for Cunene horse mackerel by day than by night when comparing consecutive day and night periods, a difference that can be attributed to diurnal changes in the vertical distribution and aggregation patterns. By day, Cunene horse mackerel tended to concentrate in dense schools near the seabed, but at night, they moved into the pelagic zone, dispersing into widespread scattering layers. The differences in acoustic density between day and night may be related to the lower packing density by night. However, the differences may also be attributable to changes in the angular orientation of the fish (Weston and Andrew, 1990; Pearre, 1997). Fish that are densely aggregated tend to polarize (Pitcher, 1983), with the result that tilt-angle distributions become more uniform (Blaxter and Batty, 1990; Axenrot et al., 2004). This maximizes the acoustic energy reflected back to the transducer (Foote and Nakken, 1978), increasing individual values of TS (Foote, 1987). Behaviourally induced changes in TS may therefore be one explanation for the relatively high values of s_A recorded by day.

Another explanation for the differences observed may be the movements of the fish into blind zones near the surface and seabed, reducing the availability of the fish to the echosounder and leading to the underestimation of their densities (MacLennan and Simmonds, 1992; Fr  on et al., 1993b). By day, fish tend to aggregate near the seabed, and some loss of signal may be caused by fish occupying the bottom dead zone (Ona and Mitson, 1996). Similarly, some loss of echo strength may be the result of targets entering above the upper blind zone (~13 m deep) at night. However, blind-zone errors are considered to be relatively low (<5%; Axelsen et al., 2004) for Cape horse mackerel in Namibia (Anon., 2003, 2004), so because bias effects would be negative for both daylight and night-time results, these should not have contributed much to the differences observed in the present study.

At night, horse mackerel generally aggregate less densely and are less polarized than by day (Pitcher and Parrish, 1993), resulting in reduced values of TS (Huse and Ona, 1996). Mesozooplankton rise at night, and pelagic fish and mesozooplankton therefore often form dense, mixed layers in the upper pelagic realm at night. These aggregations may produce strong echoes which, combined with the reduced TS of fish at night, may increase the probability of missing fish targets, according to Vaz Velho et al. (2006), who studied this effect and considered it to be moderate (Anon., 2003, 2004; Axelsen et al., 2004). The considerable differences reported here are therefore more likely to have been caused by changes in packing density, or TS between day and night, or a combination of both factors.

The main points of interest in this work are the causes of day–night differences, and how such effects impact the estimates of abundance. The results demonstrate the close link between behaviour and aggregation characteristics on the one hand, and the acoustic densities recorded on the other. Nevertheless, the differences are not necessarily indicative of the magnitude of the error in the estimates. In routine surveying, echo densities are averaged for both day and night periods. Similar proportions of daytime and night-time ESDUs are to be expected in the datasets (Table 1), and assuming no differences in TS between day and night, this should not lead to systematic errors in the abundance estimates. If the differences observed are primarily a consequence of night-time dispersion rather than to changes in TS , reduced

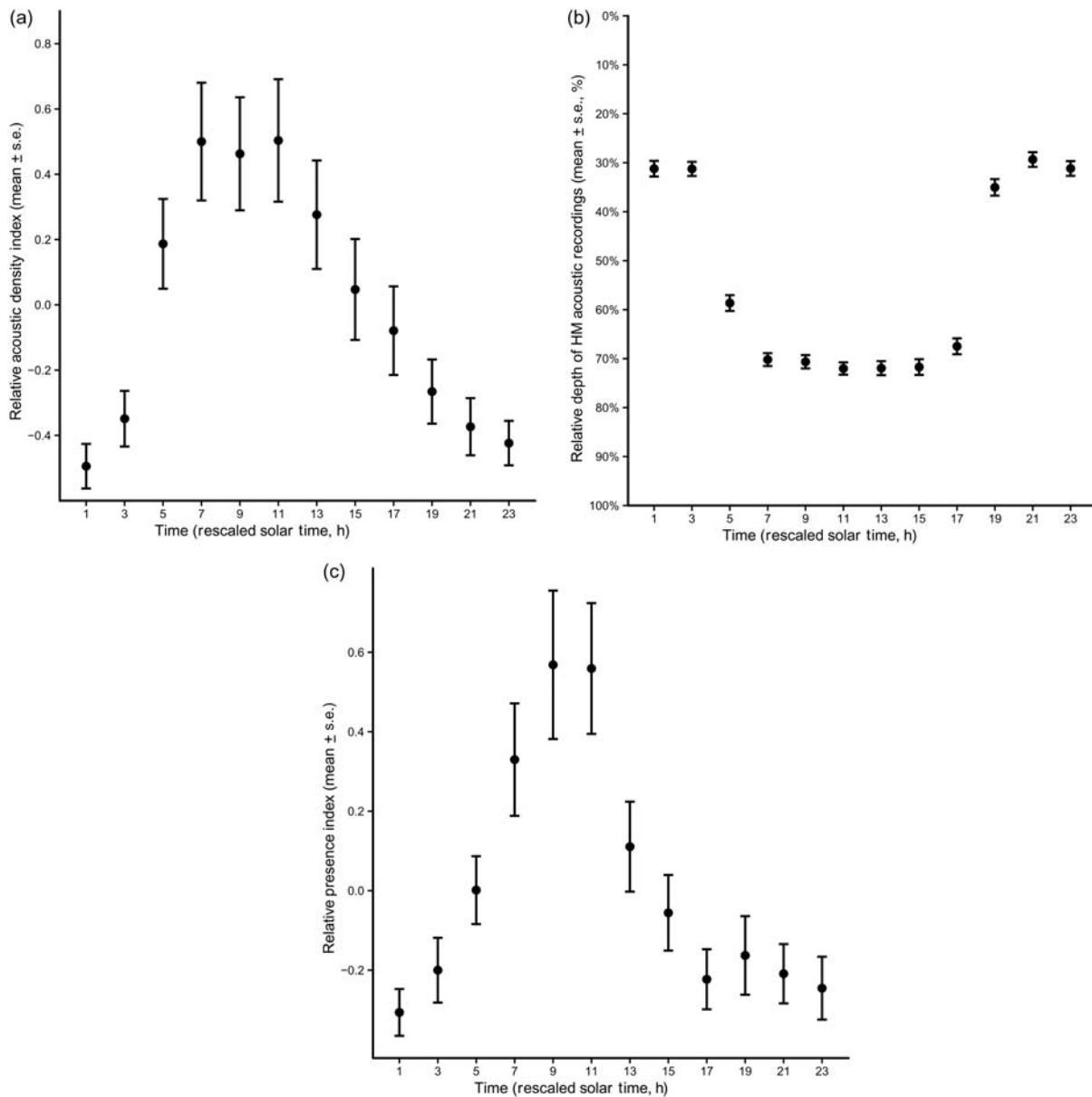


Figure 2. (a) Relative Acoustic Index (RAI), (b) RD, and (c) RPI of horse mackerel throughout the day, at 2-h intervals (solar time).

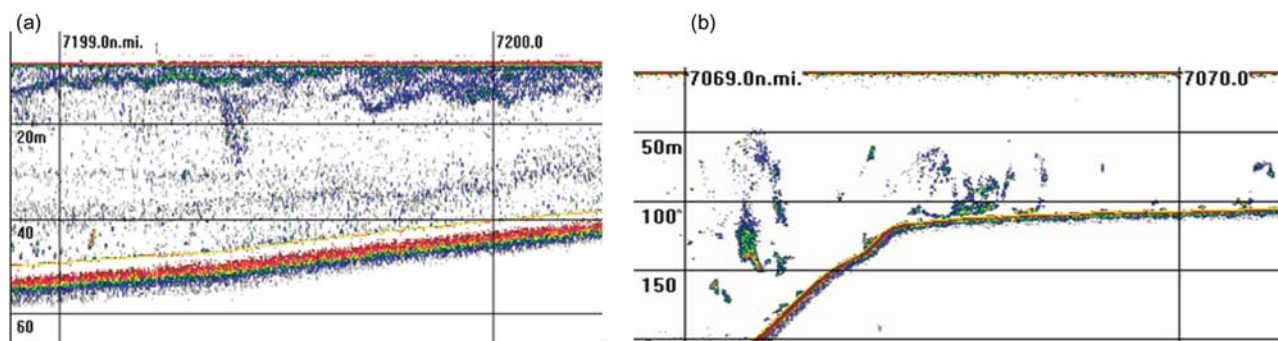


Figure 3. Typical acoustic recordings of horse mackerel by (a) night, and (b) day.

Table 1. Mean \pm s.e. of Cunene horse mackerel acoustic recordings during the four diel periods.

Parameter	Dawn	Day	Dusk	Night
Number of valid ESDUs	534	3 281	506	3 158
RADI	0.14 (\pm 0.183)	0.31 (\pm 0.068)	-0.10 (\pm 0.110)	-0.42 (\pm 0.036)
RPI	0.06 (\pm 0.110)	0.35 (\pm 0.064)	-0.28 (\pm 0.080)	-0.25 (\pm 0.052)
RD	0.49 (\pm 0.002)	0.71 (\pm 0.006)	0.54 (\pm 0.021)	0.31 (\pm 0.007)
Proportion of total s_A allocated to bottom channel	0.15 (\pm 0.016)	0.36 (\pm 0.006)	0.18 (\pm 0.019)	0.05 (\pm 0.005)
Proportion of s_A allocated to upper pelagic channel	0.015 (\pm 0.016)	0.05 (\pm 0.003)	0.09 (\pm 0.011)	0.18 (\pm 0.006)
Proportion of ESDUs with all the Cunene horse mackerel recordings in the upper pelagic layers	0.05 (\pm 0.009)	0.01 (\pm 0.002)	0.04 (\pm 0.008)	0.10 (\pm 0.005)

acoustic densities resulting from dispersion at night could be compensated for by correspondingly larger distribution areas.

If the *TS* differs between day and night, however, the estimates of abundance may be affected. The *TS* used in the surveys was first derived for clupeids (Foote *et al.*, 1986), and has been applied to both clupeids and carangids in the Benguela region (Anon., 2003, 2004). The implicit assumption in employing this *TS* is that it reflects an average situation for the species to which it is applied. If the *TS* is different between day and night, the main question concerns the extent to which the *TS* employed is representative of the day or night situation. For datasets containing equal proportions of day and night data, the bias would correspond to the deviation between the *TS* conversion applied and the actual daytime and night-time average *TS* values.

Particularly dense patches are sometimes encountered by day, and datasets obtained only by day may be characterized by a few very high values that may influence the mean values significantly. For sardine (*Sardinops sagax*) and round herring (*Etrumeus whiteheadi*), Coetzee *et al.* (2001) found that the biomass estimates may decrease by up to 25% and the variance by 90% if a single very high value is removed. Extreme patchiness is often associated with low levels of abundance (Pitcher, 1983), which is the case for the Cunene horse mackerel (Anon., 2007). The amplitude of this type of error may therefore increase as stock levels fall.

A larger proportion of zero s_A values was recorded by night than by day, but the proportion of ESDUs where Cunene horse mackerel was detected in the upper pelagic layers was greater by night. This suggests an underestimation of how much aggregation patterns of Cunene horse mackerel differ by day and night or that fish are more difficult to detect by night. For this reason, we regard the differences in acoustic densities as being associated primarily with differences in *TS* and in aggregation pattern, rather than packing densities.

Ideally, therefore, values recorded by day and by night should be converted separately. However, this would require knowledge of the differences in *TS* and probability of detection between day and night, and this question still needs to be answered. As horse mackerel vertical distribution varies considerably in the course of a 24-h cycle, the effects of depth and time of day need to be evaluated separately. Future studies should investigate more closely the *TS* of horse mackerel, and in particular the possible effects of depth and time of day (Vabø, 1999; Axelsen, 2007).

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