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VARIABLE SPATIAL STRUCTURE OF SCHOOLING PELAGIC FISH OFF NAMIBIA: IMPLICATIONS FOR ACOUSTIC SURVEYS

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Schools of horse mackerel *Trachurus trachurus capensis*, sardine *Sardinops sagax* and round herring *Etrumeus whiteheadi* were surveyed by conventional echo-integration along systematic transects. The transects were surveyed twice, in opposite directions. Clupeoid biomass was concentrated in a few dense aggregations, whereas horse mackerel were less dense and distributed over larger areas. The influence of aggregation patterns of the different species on the precision of the acoustic estimates was analysed with respect to spatial variability and diurnal effects. Isotropic variograms computed from values of acoustic back-scattering strength showed little or no structure for all three species. Indicator variograms showed relatively large structures (>15 miles) for all three species at the lowest cut-off level, confirming the influence of high values on the variograms. The autocorrelation range decreased with an increase in cut-off value for horse mackerel, whereas variograms of sardine and round herring showed no structure at larger cut-off values. There were large variances in estimated biomass for sardine (77%) and round herring (90%) between surveys, whereas biomass estimates of horse mackerel were relatively similar between surveys.

Key words: abundance estimates, acoustics, geostatistics, spatial distribution

Several qualitative acoustic surveys are undertaken each year in Namibian waters to assess the biomass of the major pelagic fish stocks, sardine S*ardinops sagax*, anchovy *Engraulis capensis*, round herring *Etrumeus whiteheadi* and juvenile horse mackerel *Trachurus trachurus capensis*. These estimates of abundance form the basis for managing the stocks (Boyer and Hampton 2001). However, the precision of acoustic surveys is affected by several sources of error, including the behaviour of the targeted species (Olsen 1990, MacLennan and Simmonds 1992, Fréon and Misund 1999). The behaviour of pelagic fish has been studied both with respect to aggregation pattern and acoustic detectability (Olsen *et al.* 1983, Fréon *et al.* 1993, Maravelias *et al.* 1996, Massé *et al.* 1996, Misund *et al.* 1996, Petitgas and Levenez 1996, Misund 1997, Fréon and Misund 1999). Heterogeneity in spatial distributions of fish populations and diurnal influences on fish vertical distribution and level of aggregation all contribute to the overall variance of surveys (Gerlotto and Petitgas 1991, Fréon *et al*. 1993).

Generally, most of the biomass of a population of shoaling fish is contained in dense schools or aggregations. As a result, the imprecision of survey abundance estimates is usually caused by the "hit or miss" of these normally large schools, so the accuracy of surveys will depend greatly on encountering and sampling a sufficient number of schools (Aglen 1983, MacLennan and Mackenzie 1988, Marchal and Petitgas 1993, Petitgas 1993). This problem is compounded further when the stock size is small and the chance of detecting the few remaining schools is low (Barange and Hampton 1997, Petitgas 1998, Petitgas and Samb 1998). A combination of physical and biological processes is believed to contribute to spatial variance in the distribution of fish populations (Horne and Schneider 1997). It is therefore important to understand the dynamics of fish behaviour relevant to spatial variability and to characterize the underlying spatial structure of the populations being assessed. Such knowledge would provide insight towards developing effective survey strategies and optimizing research effort.

The aim of this paper is to quantify, by means of variograms, the spatial structure of aggregations of pelagic fish off Namibia, and to investigate their different strategies of space occupation. The influence of high-density areas on overall estimates of abundance and associated variance is also assessed, as is the effect of diurnal changes in fish behaviour on acoustic detectability of species and their aggregations.

MATERIAL AND METHODS

Data collection

Data used for the study were from acoustic records of

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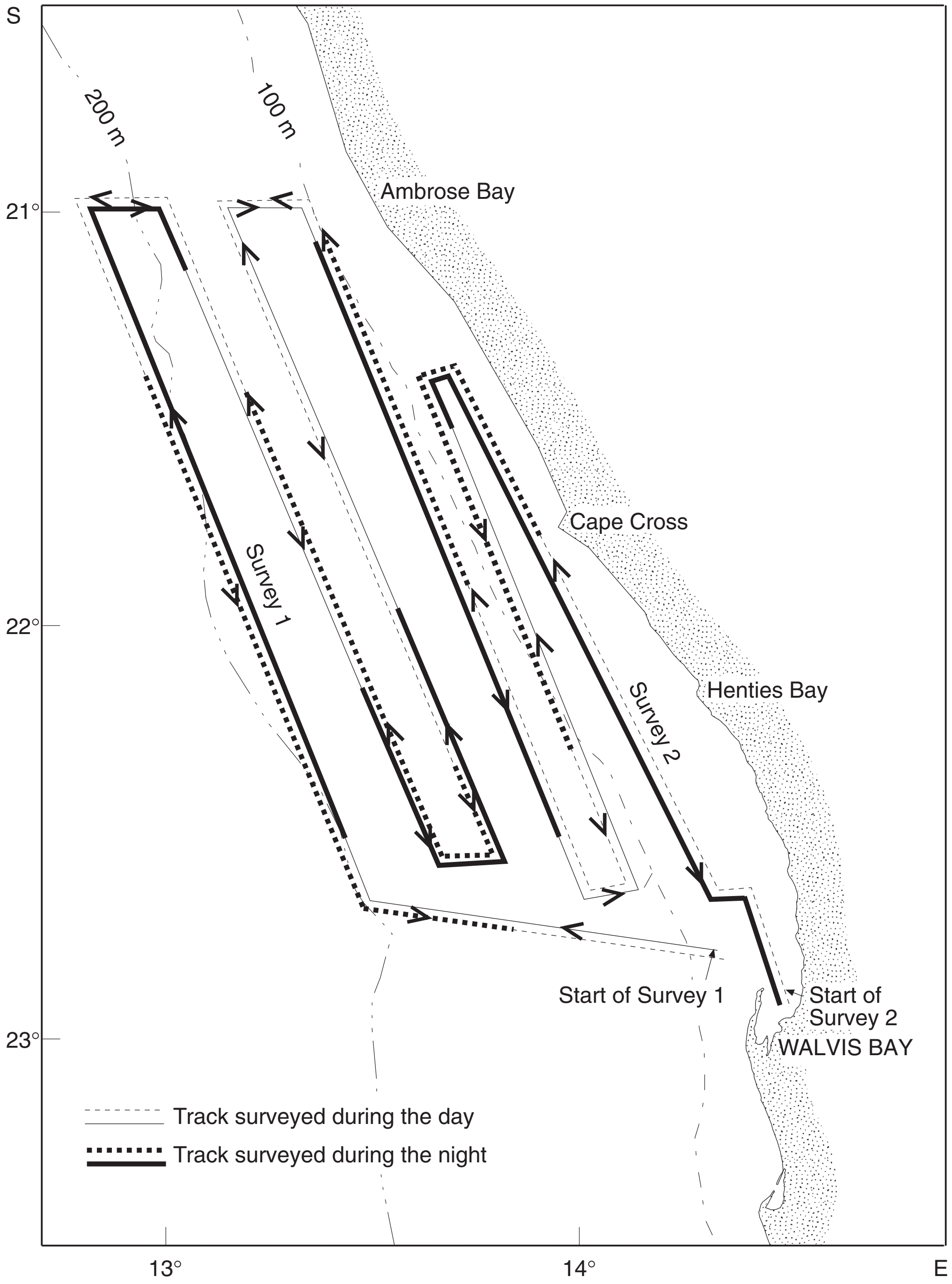

Fig. 1: Cruise tracks surveyed by day and night between Walvis Bay and Ambrose Bay during both surveys

Table I: Density estimates (g m^{-2}) for each survey calculated from 1-mile samples

Species	Density (g m^{-2})							
	Survey 1				Survey 2			
	Mean	*CV*	*n*	$n > 0$	Mean	*CV*	*n*	$n > 0$
Sardine	10.59	0.58	764	121	2.53	0.35	781	56
Round herring	6.59	0.39	764	163	0.52	0.20	781	65
Horse mackerel	30.46	0.11	764	482	33.63	0.11	781	522

n = total number of samples
$n > 0$ = sample where density > 0

fish density collected off central Namibia during a 10-day survey in April 1998 on board the Norwegian research vessel *Dr Fridtjof Nansen,* using standard echo-integration methods (MacLennan and Simmonds 1992). The survey grid (Fig. 1) consisted of six transects running parallel to the coast and spaced 10 nautical miles (nm) apart. The positions of transects were determined from prior information on the distribution of sardine obtained from a survey conducted one month earlier. The survey grid was sampled once (Survey 1) and repeated in the opposite direction (Survey 2).

Measurements of back-scattering strength, expressed as S_a (m^2 nm^{-2}), were obtained with a Simrad EK500 echo-sounder operating at 38 kHz. The EK500 system was interfaced to the Bergen Echo-Integrator software (Knudsen 1990). Frequent midwater trawl sampling was conducted for identification of acoustic targets. The elementary sampling distance unit (ESDU), i.e. the distance over which the echo integral is accumulated to give one sample, was one mile.

Data processing

Contour maps of relative density were plotted for sardine, horse mackerel and round herring for each survey. This was done using linear kriging procedures of SURFER©. Experimental variograms were also computed to characterize the spatial structure of each species and to investigate the effect of aggregation patterns on the variation in fish density between species and surveys. This was done using estimation variance (EVA; Petitgas and Prampart 1993). An experimental variogram is the increase of the variance between points in space with increasing distance between them. In the present study, the variable S_a was used rather than the more conventional variable of fish density (g m^{-2}), thus avoiding having to make assumptions concerning the target strength function of each species. In order to calculate distances between S_a values, latitudes and longitudes were converted to miles. Isotropic (omnidirectional) experimental variograms were computed according to Matheron's (1971) variogram estimator:

$$\gamma(h)=\frac{1}{2N(h)}\sum_{i=1}^{N(h)}\left[Z(x_i+h)-Z(x_i)\right]^2 ,$$

where Z(x_i) is the density for the i^{th} data point and $N(h)$ is the number of pairs of points, which are a distance h miles apart.

To eliminate the effects of extreme values on the behaviour of the variograms and to investigate the nature of density effects, indicator variograms were computed (Petitgas 1993). This was done by grouping S_a values into density-classes, with cut-off values (z) of 1.0, 100 and 1 000. Each data point was then defined as 1 if $Z(x_i) \geq z$ and 0 if $Z(x_i) < z$. Models describing the behaviour of the variograms were then computed (see Cressie 1993) to compare spatial structures between species and surveys.

To investigate diurnal effects on fish density estimates, acoustic intervals were separated into day or night categories. Day was considered to be 05:00–17:00 (GMT), based both on the time of sunrise/sunset and sun radiation values. Sun radiation values generally increased sharply after 05:00, reached a peak at noon, then gradually decreased to a minimum between 17:00 and 18:00. For calculating mean hourly densities and depths, each hour was considered as being from half an hour before to half an hour after the specified hour. The vertical distribution of the fish, particularly their diel vertical migration, was investigated using the same 1-mile ESDU. The mean depth of fish for each ESDU was taken as the depth at which the vertical back-scattering strength (VBS) was at its maximum. Because the vertical sampling resolution was 5 m, it was necessary to set the depth of the maximum VBS to the midpoint of the vertical channel in which the echo return was strongest.

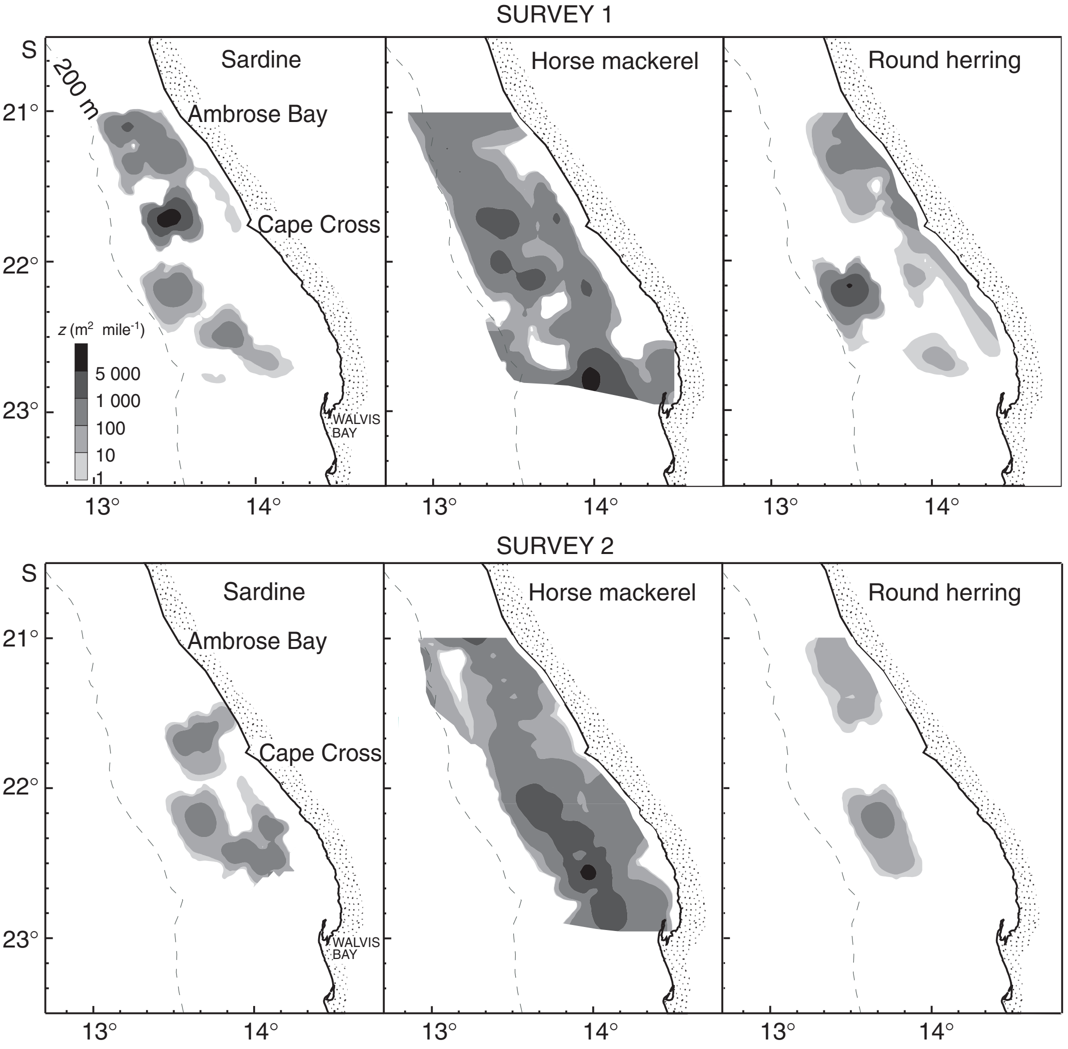

Fig. 2: Distribution and relative abundance of sardine, horse mackerel and round herring recorded during Surveys 1 and 2

RESULTS

The patchy distributions and relative densities of sardine and round herring differed between Surveys 1 and 2, whereas horse mackerel were distributed relatively evenly over the entire area during both surveys (Fig. 2). The mean densities of sardine and round herring decreased by 77 and 90% respectively between surveys, but the difference between horse mackerel densities was small (10%). The large *CV*s (Table I) can be attributed to the patchy nature of the distributions, with few large values markedly influencing either the mean density or the variance estimates of sardine and round herring.

This interpretation is also shown in the shape of the curves depicting the cumulative contribution of ranked density-classes relative to mean fish densities (Fig. 3). For horse mackerel, the curve rises smoothly, with smaller density values contributing as much to the

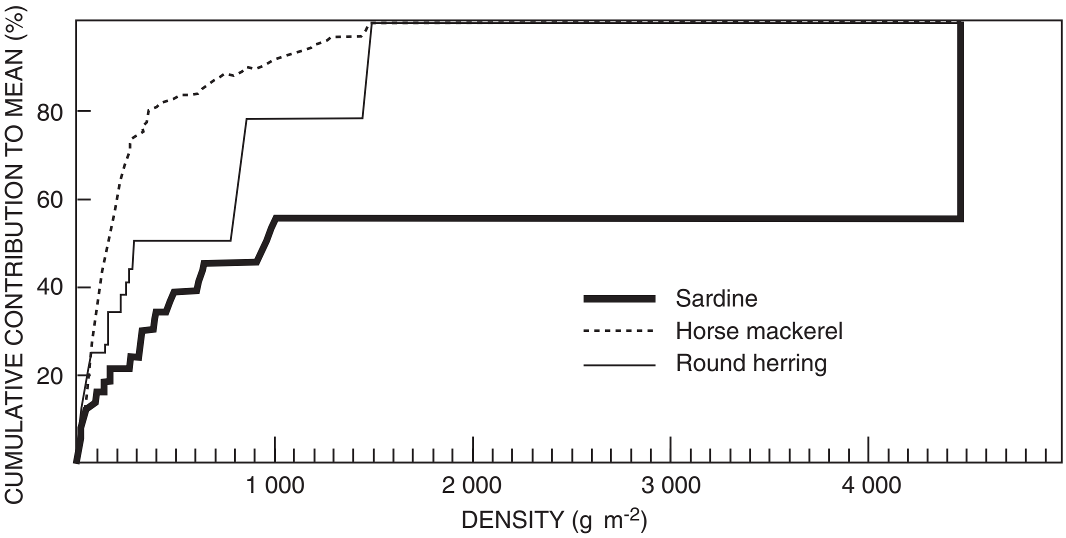

Fig. 3: Cumulative percentage contributions of ranked densities to the estimated mean survey density of sardine, round herring and horse mackerel. Observations for both surveys are combined

mean density as larger values. Both sardine and round herring distributions were extremely positively skewed. For sardine, the highest value recorded added some 45% to the total biomass. As the shape of the curves also reflects the dispersion characteristics of the populations being assessed, inferences can be made about the different shoaling patterns of the three species. The horse mackerel curve is smoother and more convex

Table II: Contribution to overall mean S_a (m^2 nm^{-2}) and variance of each of the cut-off indicator variables for each survey. Also shown are the proportion (P) of observations that fall into each density-class and the probabilities $Pz(x)$ of values exceeding the cut-off levels (z)

Species	Cut-off (z)	P	$Pz(x) \geq (z)$	Mean (%)	Variance (%)
		Survey 1			
Sardine	1	1	0.156	100	99.6
	100	0.3	0.049	98.3	99.6
	1 000	0.08	0.013	91.3	99.5
Round herring	1	1	0.213	100	99.3
	100	0.2	0.043	95.7	99.2
	1 000	0.06	0.013	88.4	99.1
Horse mackerel	1	1	0.630	100	95.9
	100	0.6	0.380	98.2	93.6
	1 000	0.18	0.115	71.4	92.6
		Survey 2			
Sardine	1	1	0.072	100	99.0
	100	0.48	0.034	96.5	99.0
	1 000	0.09	0.064	69.5	95.9
Round herring	1	1	0.083	100	97.1
	100	0.28	0.023	74.4	92.6
	1 000	–	–	–	–
Horse mackerel	1	1	0.668	100	96.7
	100	0.58	0.389	97.4	94.5
	1 000	0.18	0.119	75.5	93.6

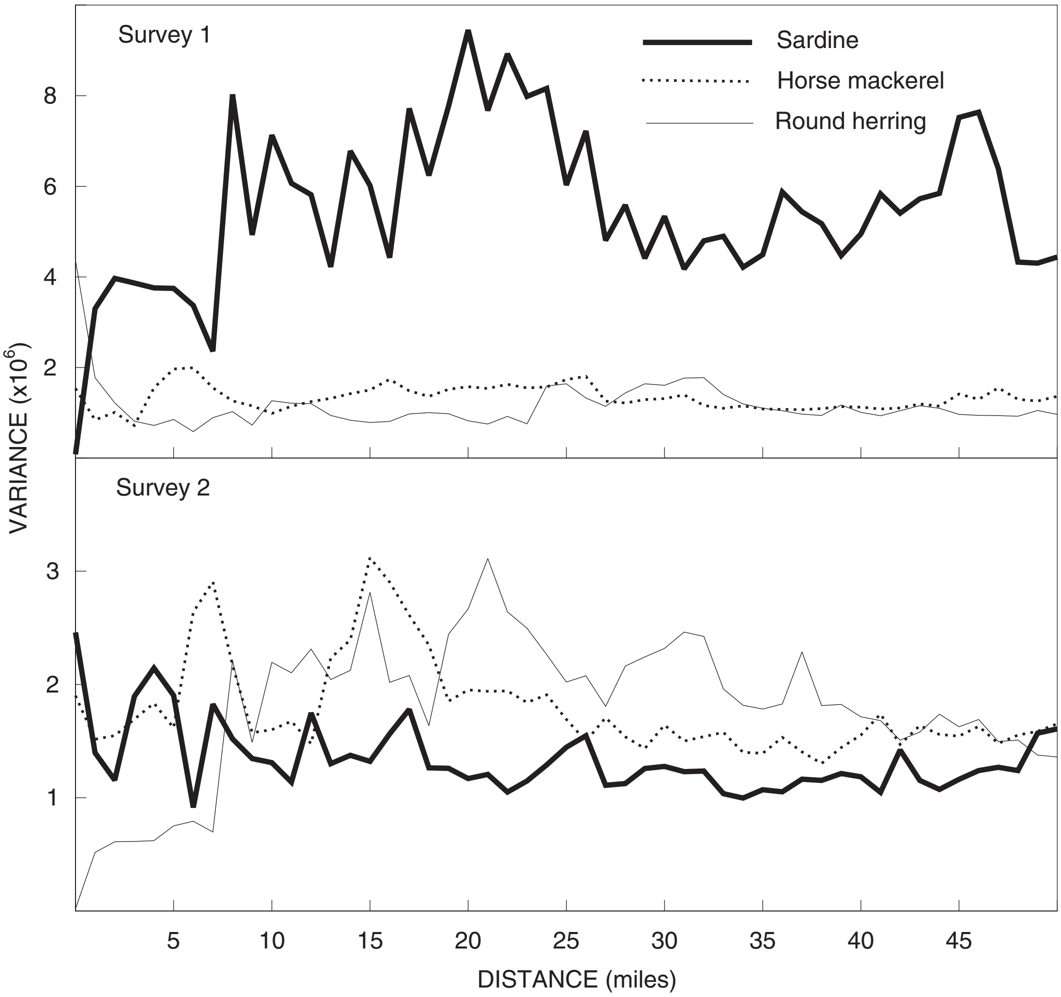

Fig. 4: Isotropic variograms for each species from data collected during Surveys 1 and 2

than the other two curves, indicating greater dispersion of that species compared to sardine and round herring. In contrast, sardine and round herring typically form dense aggregations, most of their biomass being made up of a few dense concentrations over relatively small areas.

Isotropic variograms computed from the S_a values detected little (for sardine in Survey 1) or no structure in the distributions of any of the species during either survey (Fig. 4). The variograms were generally irregular, with no linear increase in variance with distance. Because all distributions were positively skewed, the influence of high-density values dominated the behaviour of the variograms, and no inferences of the underlying structure could be made. Because samples were collected continuously along the ship's track, isotropic (omnidirectional) variograms were dominated by the longshore effects, given the different sampling effort in both directions. Anisotropic (directional) variograms were also computed, but the small number of pairs of points in the cross-shelf direction precluded rigorous analysis of the underlying structure.

To investigate the effects of fish density on the variograms, indicator variograms were also computed. Table II shows that a small proportion of S_a values are in the highest cut-off category ($z \geq 1\ 000$), but that

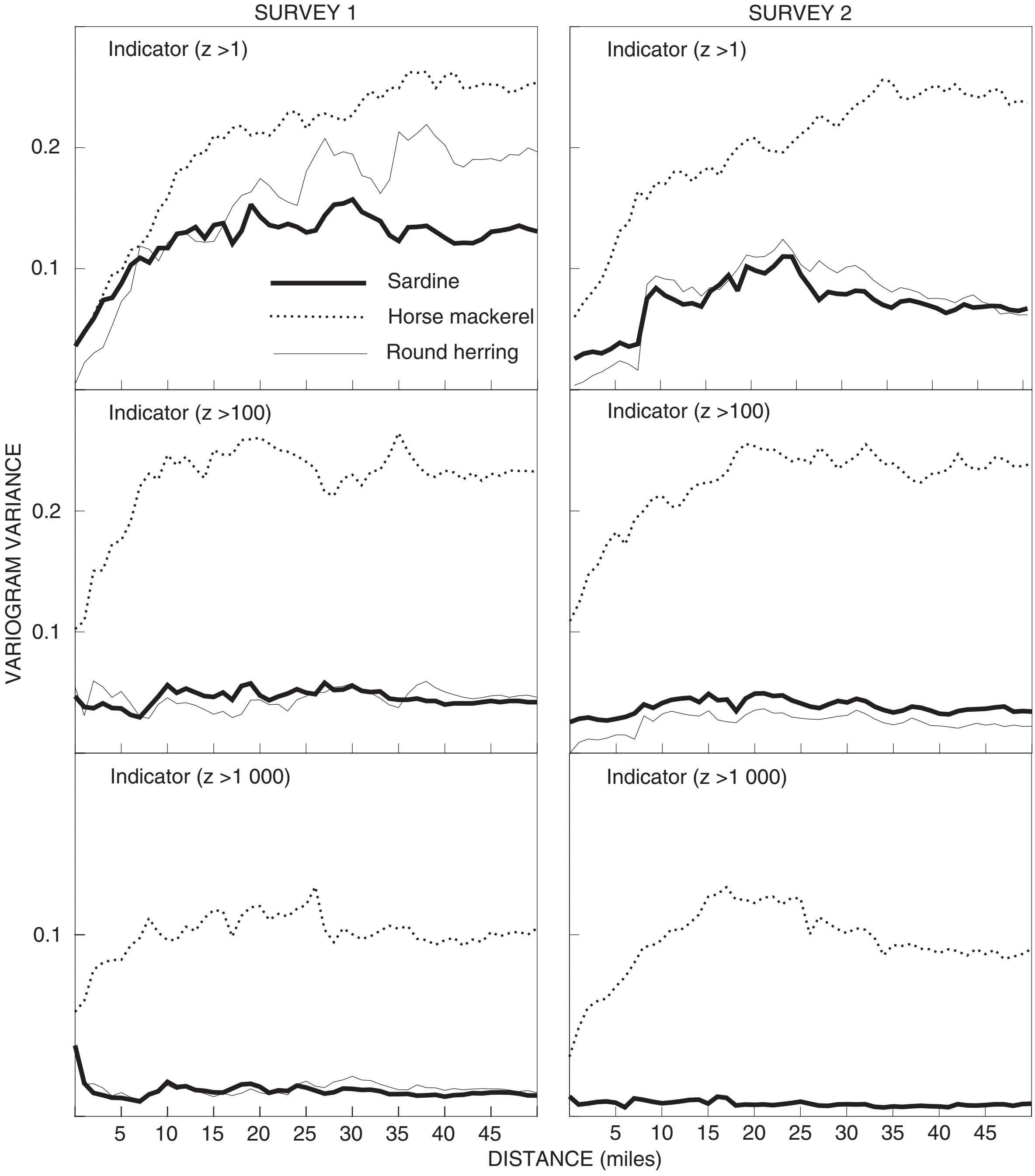

Fig. 5: Comparison of isotropic indicator variograms for cut-off (*z*) >1, >100 and >1 000 for each species for Surveys 1 and 2

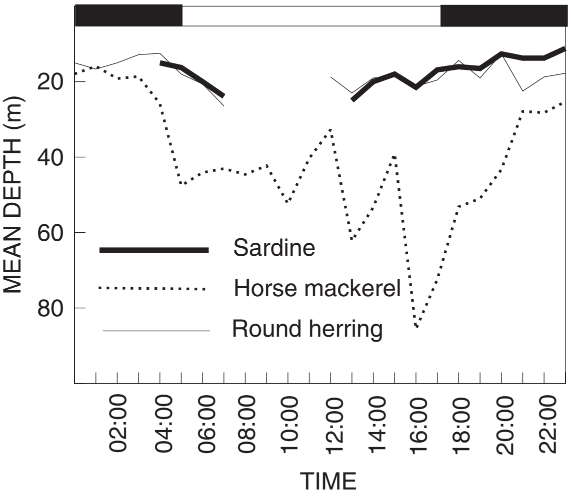

Fig. 6: Mean depth at which each species was recorded throughout both surveys by time of day

they constituted most of the mean and variance. This is particularly evident for sardine and round herring, where <10% of the values contributed to >95% of the variance and >70% of the mean. This is accentuated by the small integration unit (1 mile) used during the study and reflects sampling variance that would normally be high, given the paucity and patchiness of dense sardine and round herring schools. These high values would, however, dominate the variograms constructed from the raw data sets.

The indicator variograms shown in Figure 5 confirm the influence of high-density values on the behaviour of variograms (computed from raw data). They indicate relatively large structures (>15 miles) for all three species at the lowest cut-off level ($z \geq 1$) during the first survey. At higher cut-off levels, the variograms of sardine and round herring showed no spatial structure. This demonstrates that patches of high density are smaller than the integration unit (1 mile) and/or that they were randomly distributed throughout the study area. However, structure was still evident at the highest cut-off level ($z \geq 1\,000$) for horse mackerel. The autocorrelation range decreased for horse mackerel at greater cut-off levels (Table III), but loss of structure was more gradual during the second survey. This implies that the area of influence around each point gets smaller when the value at the point increases. The variograms of sardine and round herring showed little structure, even at the lowest cut-off level ($z > 1$) during the second survey, suggesting either a breakdown of aggregation structure between the surveys or that the core of the aggregations was not sampled during the second survey. The lower density estimates of clupeoids for the second survey (Table I) lend support to the latter theory.

Vertical migrations and diurnal variation in fish density may influence the patterns of spatial structure. If part of the population is not acoustically accessible or equally represented during certain times of the day, then the variograms will not reflect the structure of the entire population (Petitgas and Williamson 1997). Horse mackerel migrated vertically (Fig. 6) from a mean night-time depth of between 20 and 30 m to a daytime depth of between 30 and 80 m. Sardine and round herring did not migrate vertically and remained between 10 and 20 m deep by day and night. Consequently, the populations were within survey limits and analysis of their spatial structure was not affected by diurnal migratory behaviour.

Density estimates were highest during the day for all three species (Fig. 7), when they were likely deepest in the water column (for horse mackerel) and more aggregated. Sardine density peaked at sunrise and round herring at sunset. The large density differences between day and night for all three species suggests changes in their levels of aggregation/dispersal. This indicates that variograms compiled from daylight or night-time data only would be less variable and therefore reflect better the true spatial structure of the population.

DISCUSSION

High spatio-temporal variability in pelagic fish density is a common feature in the Benguela (Coetzee 1997, Boyer *et al.* 2001) and elsewhere (Gerlotto and Petitgas 1991, Marchal and Petitgas 1993, Fréon *et al.* 1996). Such high variances have been attributed to the skewed distributions of acoustic density measurements, the aggregation dynamics of populations and the movement of fish between surveys. However, some studies have shown relatively small variation between replicate surveys. MacLennan and Mackenzie (1988) estimated a precision of 25% for North Sea herring *Clupea harengus* and Strømme and Sætersdal (1987), as cited by Fréon and Misund (1999), observed a variation of only 20% between repeated surveys of pelagic stocks off Senegal and Morocco.

Although mean densities and variances have been compared here, the data are highly autocorrelated and, given the systematic survey design, means cannot be compared statistically using classic sampling theory because the variances are biased (Jolly and Hampton 1990a). Another important consideration in the present study is the direction of the transects. Because fish

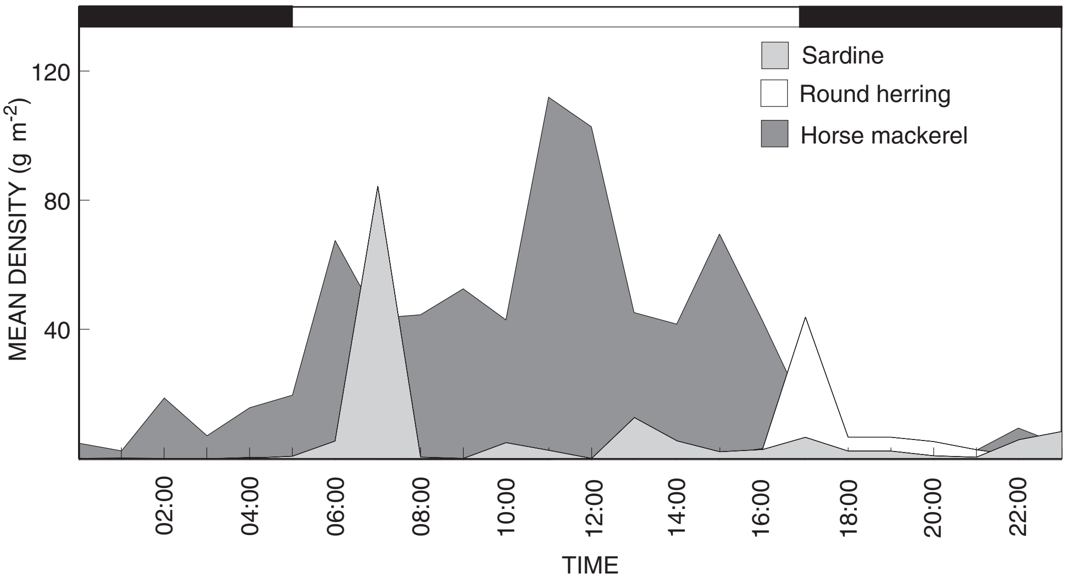

Fig. 7: Mean density estimates for each species with time throughout the surveys

aggregation patterns are often related to both bathymetric and hydrographic features, the maximum density gradient of fish would more likely be across-shelf. Therefore, by sampling longshore (as in the present study), high-density areas would likely be either over- or undersampled (Jolly and Hampton 1990a, MacLennan and Simmonds 1992).

The similar structures and density found for horse

Table III: Model parameters fitted to the indicator variograms

Indicator	Survey 1			Survey 2		
	Range (miles)	Sill	Nugget	Range (miles)	Sill	Nugget
			Sardine			
$S_a > 1$	16	0.105	0.036	–	–	–
$S_a > 100$	–	–	–	–	–	–
$S_a > 1\,000$	–	–	–	–	–	–
			Round herring			
$S_a > 1$	25	0.175	0.0051	–	–	–
$S_a > 100$	–	–	–	–	–	–
$S_a > 1\,000$	–	–	–	–	–	–
			Horse mackerel			
$S_a > 1$	35	0.23	0.04	39	0.19	0.06
$S_a > 100$	16	0.165	0.09	25	0.125	0.12
$S_a > 1\,000$	9	0.055	0.055	20	0.102	0.021

Exponential models best fitted all variograms and are described as follows (Cressie 1993):

$\gamma(h{:}\theta) = 0$ or C_0, when $h = 0$,
$\gamma(h{:}\theta) = C_0 + C_e\,(1-10^{(-|h|/a_e)})$, when $h \neq 0$,

where C_e is the sill attributable to the exponential structure and α_e is the range parameter of the exponential structure mackerel during both surveys indicates that the spatial process has some homogeneity and is repeatable in space, i.e. stationarity. The lack of structure in the clupeoid variograms suggests that, when a concentration is encountered, it would not be possible to predict where the next one may be found (Petitgas 1993). For horse mackerel, the variograms illustrate increasing variance with increase in distance between samples. Also, the decrease in autocorrelation range with increase in cut-off density reflects a gradual transition between areas of low and high density.

The lack of structure for sardine and round herring during the second survey is probably a consequence of the scale of the patchy distributions being smaller than the sampling resolution, i.e. the nugget effect. Similar structural analysis carried out by Barange and Hampton (1997) and Coetzee (1997) on South African sardine, Porteiro *et al.* (1995) on Atlantic sardine *Sardina pilchardus* and Maravelias and Haralabous (1995) on North Sea herring indicated autocorrelation distances of 10 miles or less. The probability of sampling high-density patches would be higher and the sampling distribution of the mean would tend to be more normal if the maximum inter-transect distance is similar to the autocorrelation range. A transect spacing of <10 miles is therefore required to sample local sardine distributions adequately.

Diurnal density differences may have influenced the structural analysis of the horse mackerel population. However, sardine and round herring variograms were not markedly affected because of the small diurnal changes in their densities, except at sunrise and sunset. Diurnal changes in spatial structure and density have been reported for many pelagic fish species (e.g. Fréon *et al.* 1993, Barange and Hampton 1997, Coetzee 1997, Petitgas and Williamson 1997). Such changes result from schools being less structured or more dispersed at night. Generally, night-time variograms are characterized by lower nugget effects, lower sills (maximum structural variability) and larger autocorrelation ranges than daytime variograms. Theoretically, it should be possible to sample the same fish population with reduced effort at night. However, because the current dataset was too small to compute variograms effectively and separately for day and night, this hypothesis could not be tested.

The lack of diurnal changes in densities of sardine and round herring may be a result of the large number of zero values recorded. Artifacts caused by avoidance and diurnal differences in the acoustic target strength of fish could also have been responsible for these changes, as has been observed in other species (Huse *et al.* 1998). Sardine may, for instance, have avoided the research vessel during the second survey. In this regard, it is of note that sardine were caught by purse-seiners in the vicinity of the survey area while the schools were not being recorded by the research vessel. Because part of the sardine population was not recorded, it is possible that the underlying structure of the population or diurnal density effects were not accurately reflected. However, paucity of data precludes supportive evidence for this theory.

Because horse mackerel were more dispersed than the clupeoids, there was a greater probability of encountering the former. Also biomass estimates of horse mackerel were similar between the two surveys. Therefore, more accurate estimates of horse mackerel could be obtained with less sampling effort and a simpler survey design than for sardine or round herring.

Because of the skewness of the clupeoid density distributions, the present survey estimates of density and variance were strongly influenced by a few extremely high values. For the first survey, removal of only one high value for sardine reduced the biomass estimate by approximately 45% and the variance by 90%. It is therefore clear that adequate sampling effort and well-designed surveys are essential to ensuring that these scarce, but high-density, schools are sampled in an unbiased and efficient manner. It should, however, be noted that the data analysed here are highly correlated, so the survey means cannot be statistically tested using conventional statistics. The present *CV* estimates are likely to be higher than those computed for surveys designed according to random sampling theory (Jolly and Hampton 1990b), in which densities are averaged along the transects surveyed.

The short autocorrelation ranges of the sardine and round herring variograms shown here, even for low densities, suggest that, if a stratified systematic or random sampling is used in future pelagic fish surveys, a small average inter-transect distance should be maintained (Barange and Hampton 1997). This would ensure more precise sampling especially in high-density areas, and a more accurate estimate of mean stock size. Care should also be taken to ensure an unbiased estimate of both mean and variance (Thompson 1992).

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