Strategies of space occupation by anchovy and sardine in the southern Benguela: the role of stock size and intra-species competition

Manuel Barange, Janet C. Coetzee, and Nandipha M. Twatwa


Strategies of space occupation by anchovy and sardine populations in the southern Benguela during cruises in 1994 (low biomass) and 2001 (high biomass) are investigated using geostatistical tools. The spatial expansion of anchovy and sardine during the high-density year resulted in an increase in the number and density of hotspots and, in the case of anchovy, a relative increase in the contribution of mid- to high-density intervals to the overall survey biomass. Variogram autocorrelation ranges were larger in the high-biomass year. Otherwise, similarities and differences in the strategies of space occupation between anchovy and sardine are consistent between years of low and high biomass, and are therefore density-independent. Varioimages showing structures for both species and years, with autocorrelation ranges of 30 nautical miles for the smallest indicator (0.1 g m\(^{-2}\)) and 10 miles for the largest (100 g m\(^{-2}\)), reflecting intrinsic spatial structures independent of stock size. The ideal survey inter-transect distance, defined as the autocorrelation range of the highest density indicator, was not influenced by the expanded distribution of both species. Cumulative frequency distributions and cross-variograms revealed differences in space occupancy between both species. Despite the areal expansion, and in contrast to anchovy, a significant portion of the sardine biomass continued to be contributed by a few very high-density areas with little spatial structure, as indicated by large nugget effects in the variograms and lack of transitions in the cross-variograms. Both species were spatially segregated in the low-biomass year, but overlapped extensively in the high-biomass year.

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Introduction

Anchovy, *Engraulis encrasicolus* (until recently referred to as *E. capensis*), and sardine, *Sardinops sagax*, are the main pelagic resources on the South African continental shelf, constituting more than 80% of the total national pelagic purse-seine catch. In the period 1970–2003, anchovy landings fluctuated between 41 000 t and 596 000 t (average 247 000 t) and sardine landings between 16 000 t and 260 000 t (average 81 000 t), including the bycatch associated with the anchovy fishery. The two species have been assessed acoustically since 1984 (Hampton, 1992; Barange *et al.,* 1999), following evidence that catch per unit effort (cpue) was not proportional to abundance, and responding to the need for an independent estimate of stock size. For both species, the spawning biomass is estimated in November/December, and recruitment strength in May/June of each year. Acoustic estimates of adult stock were initially combined with egg-production estimates (Hampton, 1996). Surveys are designed to optimize survey efficiency while estimating the mean density and variance in an unbiased way (Jolly and Hampton, 1990). When more than one species is assessed simultaneously, however, the survey may not be efficient for all species.
Barange and Hampton (1997) conducted analyses of the spatial structure of adult and egg populations of both species, to elucidate patterns and differences in their strategies of space occupation. The goal of that work was to identify ways of improving pre-stratification and effort allocation in surveys, using identified species-specific strategies of occupation of space. They concluded that anchovy formed high-density schools by day and broke up into larger, low-density aggregations at night. Sardine, by contrast, remained in relatively high-density schools throughout the 24-h period. No spatial continuity between low- and high-density areas was observed for sardine, but it was evident for anchovy. Barange and Hampton (1997) indicated that the acoustic survey design was well suited to anchovy, but not to sardine, because of the species’ patchy distribution and variable aggregative behaviour.

The analysis conducted by Barange and Hampton (1997), however, used data for a year when the stock sizes for both anchovy and sardine were low. An important unresolved aspect was whether the structures and patterns observed would apply to situations when the stock size was larger. In this paper we repeat the analyses conducted by Barange and Hampton (1997) with data from a year when stock biomass was high, to ascertain whether the patterns of space occupation by anchovy and sardine are density-dependent or independent.

The analysis uses geostatistical techniques. Spatial structures are inferred from structural characteristics, such as autocorrelation ranges, variogram shapes and variability, and different scales of density. Patterns of covariation were also studied, with particular focus on whether the changes in stock size may drive the species to compete for space. The results should be of interest for a study aimed at understanding differences in the aggregative strategies of co-occurring species.

Material and methods
Survey design and methods
To investigate density-dependent patterns of aggregation, we used data from acoustic surveys conducted in November/December 1994 and 2001 off South Africa, to estimate the biomass and length composition of the stocks (Hampton, 1992). The surveys consist of a series of pre-stratified, randomly spaced parallel transects, designed to obtain unbiased estimates of stock size and sampling variance (Jolly and Hampton, 1990). The strata are pre-defined according to expected anchovy distribution patterns, based on previous surveys. Further information on the survey programme can be found in Hampton (1992) and Barange et al. (1999).

Estimates of acoustic backscattering strength for the November 1994 survey were made with a 38-kHz SIMRAD EK400 scientific echosounder, calibrated by the standard sphere method, and interfaced to custom-built echo integrators, as described in Hampton (1987, 1992) and Barange and Hampton (1997). For the November 2001 survey the system was upgraded to the SIMRAD EK500 echosounder, and the signal was integrated using SonarData Echoview® software. Physical inter-calibration of the EK400/500 systems proved them to be similar, except where volume backscattering strengths exceeded −29.9 dB (Barange, 1998), which were underestimated in the EK400 system owing to receiver saturation. In order to compare the 1994 and 2001 data, the recorded EK500 data were re-integrated simulating the performance of the EK400 system (see Barange et al., 1999).

The echosounder was run continuously along and between transects, except for ad hoc breaks to identify scatterers by midwater trawling, and to conduct other sampling (e.g. CTD, plankton sampling). Echo returns exceeding a pre-set threshold were integrated between stations, in intervals of 1 nautical mile. Typical survey speed was 10 knots. Backscattering strengths were apportioned between the different pelagic species (generally anchovy, sardine, and round herring Etrumeus whiteheadi, but also Cape horse mackerel, Trachurus trachurus capensis, and chub mackerel, Scomber japonicus), on the basis of trawl samples. Transformations to fish density were done using a single expression for the backscattering cross-section per kg as a function of length, as explained in Hampton (1987, 1992), and Barange et al. (1999). Density estimates are considered relative rather than absolute.

Trawl samples were pooled to obtain size compositions of the entire populations surveyed. In the process, individual trawl length distributions were weighted according to the acoustically estimated biomass in the vicinity of the trawl. Fish distribution maps were obtained through data interpolation, using standard kriging routines (Barange and Hampton, 1997).

Spatial analysis
Experimental variograms of fish density were computed using Matheron’s (1971) estimator:

\[
\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [Z(X_i + h) - Z(X_i)]^2
\]

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 \(h\) apart. Although omnidirectional, these variograms are dominated by along-track spatial trends, because of the greater number of pairs of points in this direction, particularly for short ranges. Outliers and zeroes were included in the analysis because they are characteristic of the spatial structure of the two species. Kriging algorithms were used to interpolate the data for the plots using SURFER® software, based on the parameters of the exponential fit using grids of 2 × 2 nautical miles (hereafter referred to simply as miles). The use of this model assumes a certain degree of stationarity of
the spatial process, i.e. it must have some homogeneity and should be repeatable in space.

To determine whether the spatial structure depended on density, the raw data were classified into four density classes, separated by cut-offs (z) of 0.1, 1, 10, and 100 g m\(^{-2}\). Each data point was transformed into a binary indicator variable, defined as 1 if \(Z(X_i) \geq z\), and 0 otherwise. Variograms were then computed for the indicator variables using EVA (Petitgas and Prampart, 1993) and MATLAB\(^\text{TM}\) routines. This approach is also known as Multiple Indicator Kriging (Journel, 1983).

Variograms were fitted to the following exponential model using least-squares procedures:

\[ \gamma'(h) = \alpha + \beta \times (1 - e^{-h/\lambda}) \]

where \(\alpha\) is the nugget, \(\alpha + \beta\) the sill, and \(\lambda\) is the autocorrelation range of the variogram.

To examine whether there were transitions between low- and high-density areas, cross-variograms between pairs of indicators needed to be computed. For pairs of points at distance \(h\) apart, the ratio between the cross-variogram of two indicators and the single variogram of the lower cut-off reflects the probability that, when entering the domain of values greater than a cut-off \(z\), a value greater than \(z'\) will be encountered, where \(z < z'\) (Rivoirard, 1993, cited in Petitgas, 1993). The function was estimated from:

\[
\gamma_{Zz}(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} \left\{ I_z(X_i) + I_{z'}(X_i) - I_z(X_i) - I_{z'}(X_i) \right\}
\]

where \(I_z\) and \(I_{z'}\) are the indicator variables for cut-offs \(z\) and \(z'\), respectively (Rossi et al., 1992). The behaviour of the ratio \(\gamma_{Zz}(h)/\gamma_{Zz}(h)\) indicates the presence of transitions (Rivoirard, 1993, cited in Petitgas, 1993). If the ratio is constant with \(h\), then the area determined by the higher cut-off is included inside the area determined by the lower cut-off, and there is also no border effect, so no spatial transition on average. If the ratio increases with \(h\), then border effects exist, and there is a transition between low- and high-density regions (Petitgas, 1993).

Spatial covariation between anchovy and sardine was also computed using Equation (3), replacing the indicator variables by the corresponding anchovy and sardine densities. In this case, trends in \(\gamma_{ZZ}\) indicate positive or negative covariation, providing a tool to investigate the degree of covariation between both species.

Results

The 1984–2002 time-series of anchovy and sardine spawning biomass is presented in Figure 1. Anchovy biomass in 2001 was 4.3 million tonnes, about nine times higher than in 1994. Sardine biomass in 2001 was almost three times higher than in 1994, some 1.6 million tonnes.

The change in biomass has also been reflected in the size frequency of the populations (Figure 2). The low anchovy and sardine biomasses in 1994 were largely attributable to poor recruitment (Barange et al., 1999), so older fish dominated the population. The good recruitment of 2001 is reflected in a decreased contribution from older fish. The average caudal length in 2001 was 9.2 cm for anchovy and 12.9 cm for sardine, down from 11.0 and 17.4 cm, respectively, in 1994.

Cumulative frequency distributions and biomass-per-interval plots for both species and years are presented in Figure 3 and Table 1. In 1994, <10% of the data contributed to >90% of the biomass of both species. In 2001, the increase in anchovy biomass influenced the shape of the frequency distribution: some 25% of the data contributed to an equivalent 90% of the biomass, thus making the distribution less skewed. Significantly, the curve for sardine in 2001 was largely unchanged from that in 1994, despite the increase in biomass, indicating that most of the increase was contributed by relatively few data points. The distribution of the biomass-by-biomass intervals (Figure 3b) shows that the increase in biomass in 2001

![Figure 1. Acoustic time-series of spawner stock biomass for anchovy and sardine. Arrows indicate the years selected for the analysis.](image)

![Figure 2. Normalized size frequencies of anchovy and sardine for 2001 (bars) and 1994 (lines), obtained from survey catches.](image)
resulted in a significant increase in the number of high-density intervals for both species. This was particularly evident for sardine, where almost 10% of the biomass came from intervals of mean density \( \gtrsim 1 \text{ kg m}^{-2} \).

The distribution maps (Figure 4) show that both species expanded their area of distribution with increased stock biomass, as expected. In 2001, anchovy occupied the entire shelf (Figure 4c), whereas sardine were distributed mainly inshore of anchovy over the western Agulhas Bank (18°–20°E) and offshore along the Mossel Bay ridge (21°–23°E; Figure 4d). There were also a few isolated patches of sardine on the shelf. In comparison, a distinct cross-shelf separation between species was visible in 1994 (Figure 4a, b).

Normalized isotropic variograms of anchovy and sardine for both years are presented in Figure 5. Exponential models fitted to these (Table 2) highlight the main differences. In 1994, both anchovy and sardine displayed autocorrelation ranges of approximately 10 miles. In addition, sardine variograms displayed marked irregularities and nugget effects at the scales studied, indicating less spatial structure at a population level than anchovy. The sardine variogram for 2001 is also weakly structured (Figure 5b), and the large nugget effect suggests that most of the variability is unresolved. Nevertheless, the range of autocorrelation was larger in 2001 (about six times that in 1994), probably influenced by the large patch of sardine encountered between 21 and 23°E (Figure 4). In contrast to sardine, the 2001 anchovy variogram is more structured. The autocorrelation range was about three times larger than in 1994, as a result of the larger area occupied (Figure 4a).

To remove density-dependent structures from the spatial analysis, a structural analysis was conducted using indicator variables, as defined above. Figure 6 shows indicator variograms for both years and species, and the parameters of the exponential models fitted are given in Table 3. As expected, autocorrelation ranges generally decrease with increasing cut-off density of the indicator, for both 1994 and 2001, reflecting the smaller area of influence of high-density spots. Interestingly, autocorrelation ranges for the smallest (\( z \approx 0.1 \text{ g m}^{-2} \)) and largest (\( z \approx 100 \text{ g m}^{-2} \)) indicators are approximately 30 miles and 10 miles, respectively, for both species and years. Only the indicators of medium densities (\( z \approx 1 \) and \( 10 \text{ g m}^{-2} \)) depicted larger ranges in 2001 than in 1994 (Table 3). This suggests that the increase in population biomass in 2001 is reflected in the size of medium density patches, but not the overall spatial structure of the populations. Nugget effects, however, were larger in 2001, suggesting that the proportion of small-scale (<1 mile) variability was significantly larger than in 1994. This may reflect the randomness of particularly high-density spots.

In order to investigate transitions between low- and high-density areas, ratios of cross- and simple variograms of the indicator variables were computed, and a selection is presented (Figure 7). Anchovy ratios for both years show...
significant and comparable structures, indicating a smooth transition between low- and high-density spots. Conversely, sardine ratios suggest sharp transitions between low- and high-density areas, reinforcing the observation of patchiness in the distribution of sardine. This pattern is particularly evident in 1994 for both low- and high-density thresholds (Figure 7a), but also in 2001 for high-density thresholds (Figure 7b). Clearly, sardine cross-variograms are less structured than those of anchovy.

On the basis of acoustic survey data from 1984 to 1998, Barange et al. (1999) concluded that anchovy off South Africa occupy the offshore part of the continental shelf, while sardine are more abundant inshore of the anchovy shoals. This perception has changed as sardine abundance increased and the distribution expanded to cover both the inshore area and the outer shelf in the central survey region (Figure 4d). To ascertain how the two species occupy the available shelf, perhaps avoiding competition for resources,
cross-variograms were computed between both species. The analysis was conducted both with the raw density data and with indicator variables, and for several sectors of the coastline, but as the results were consistent, only isotropic cross-variograms for the indicator variable $z \geq 0.1 \text{g m}^{-2}$ are presented (Figure 8). For 2001, both indicator variables co-vary in space up to about 30–40 miles, roughly agreeing with the species autocorrelation ranges for the same threshold (Table 3). For 1994, however, the cross-variogram has three different behaviours. At distances $< 15–20$ miles, the cross-variogram has a negative trend. It then increases sharply up to a distance of about 40 miles, then flattens. This indicates that anchovy and sardine patches (patches being defined here by areas where the fish density exceeds $0.1 \text{g m}^{-2}$) in 1994 tended to be separated at an average of 15–20 miles, but otherwise were correlated at larger scales. This separation between the patches of both species in 1994 can be confirmed visually by computing an index of relative species abundance (Figure 9). The niche separation between anchovy and sardine in 1994, following two parallel bands of abundance along the continental shelf, is clear. In 2001, on the other hand, sardine were distributed inside an area of largely anchovy dominance, except for a single monospecific sardine area towards the south. This supports the idea that anchovy and sardine occupy different sections of the shelf during low-density situations, but share space and resources when abundant.

**Table 2. Parameters obtained by fitting an exponential model to the isotropic density variograms computed from the 1994 and 2001 data, according to a least-squares procedure (all significant, $p < 0.001$).**

<table>
<thead>
<tr>
<th>Species and year</th>
<th>Nugget</th>
<th>Sill</th>
<th>Range (nautical miles)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anchovy, 1994</td>
<td>0</td>
<td>1.45</td>
<td>9.7</td>
</tr>
<tr>
<td>Sardine, 1994</td>
<td>0.19</td>
<td>0.84</td>
<td>6.1</td>
</tr>
<tr>
<td>Anchovy, 2001</td>
<td>0.38</td>
<td>0.83</td>
<td>30.5</td>
</tr>
<tr>
<td>Sardine, 2001</td>
<td>0.67</td>
<td>0.55</td>
<td>36.6</td>
</tr>
</tbody>
</table>

**Discussion**

The analysis conducted has been based on the expectation that fish distributions have spatial structures that can be quantified and characterized using geostatistical techniques. The maximum resolution of the study is driven by the minimum sample size of 1 mile. We therefore expected to resolve mesoscale structures larger than school size. The main structural tools were variograms and cross-variograms, using both raw density data and indicator variables. The latter are designed to minimize the distorting effect of extreme values. No outliers were eliminated because they are typical of the aggregative strategies of pelagic fish, but variograms were also computed after removing zero densities (data not shown), confirming that the window of observation did not have an influence in the identified spatial structures.

The main objective of the analysis was to compare the spatial structures of anchovy and sardine during periods of high and low stock size, with the intention of determining whether such structures were density-dependent or -independent. This assumes that the spatial structures observed in the two study years reflect general patterns of space occupancy rather than singular situations. As the surveys are the main assessment tool for a fishery that has targeted anchovy and sardine at different periods, it is important that their design addresses the behavioural differences in each species that are reflected in their space occupation. Barange and Hampton (1997) concluded that the survey design behind assessment cruises was well adapted to aggregative behaviour of anchovy but not to sardine strategies of occupation of space, because of the high degree of patchiness in distribution of the latter species. Spatial analyses conducted during years of both high and low stock sizes would determine whether the conclusions reached by Barange and Hampton (1997) described general principles in the spatial strategies of the species, or were biased by the low stock sizes in the year of their analysis.

The indicator variograms for both species suggested progressive “destruction”, and decreasing radius of...
influence with increasing density, as expected by theory, and as observed with the 1994 data. The results of the variograms indicate that the autocorrelation ranges are similar in both years, even though the anchovy and sardine stocks were much larger in 2001. This confirms that the variograms reflect intrinsic structures of fish distribution, i.e. properties independent of the spatial window used to estimate them, and therefore independent of the geographical range of the populations. This geographical range

Table 3. Parameters obtained by fitting an exponential model to the indicator variograms computed from the 1994 and 2001 data, according to a least-squares procedure (all significant, p < 0.001).

<table>
<thead>
<tr>
<th>Species and year</th>
<th>Variable (g m⁻²)</th>
<th>Nugget</th>
<th>Sill</th>
<th>Range (nautical miles)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anchovy, 1994</td>
<td>I ≥ 0.1</td>
<td>0.11</td>
<td>0.85</td>
<td>31.0</td>
</tr>
<tr>
<td></td>
<td>I ≥ 1</td>
<td>0.00</td>
<td>1.06</td>
<td>22.9</td>
</tr>
<tr>
<td></td>
<td>I ≥ 10</td>
<td>0.00</td>
<td>1.25</td>
<td>17.8</td>
</tr>
<tr>
<td></td>
<td>I ≥ 100</td>
<td>0.10</td>
<td>1.30</td>
<td>13.5</td>
</tr>
<tr>
<td>Sardine, 1994</td>
<td>I ≥ 0.1</td>
<td>0.28</td>
<td>0.53</td>
<td>31.5</td>
</tr>
<tr>
<td></td>
<td>I ≥ 1</td>
<td>0.34</td>
<td>0.50</td>
<td>24.0</td>
</tr>
<tr>
<td></td>
<td>I ≥ 10</td>
<td>0.25</td>
<td>0.53</td>
<td>16.5</td>
</tr>
<tr>
<td></td>
<td>I ≥ 100</td>
<td>0.40</td>
<td>0.30</td>
<td>9.0</td>
</tr>
<tr>
<td>Anchovy, 2001</td>
<td>I ≥ 0.1</td>
<td>0.38</td>
<td>0.48</td>
<td>31.0</td>
</tr>
<tr>
<td></td>
<td>I ≥ 1</td>
<td>0.41</td>
<td>0.51</td>
<td>38.8</td>
</tr>
<tr>
<td></td>
<td>I ≥ 10</td>
<td>0.43</td>
<td>0.58</td>
<td>27.5</td>
</tr>
<tr>
<td></td>
<td>I ≥ 100</td>
<td>0.35</td>
<td>0.79</td>
<td>10.0</td>
</tr>
<tr>
<td>Sardine, 2001</td>
<td>I ≥ 0.1</td>
<td>0.42</td>
<td>0.53</td>
<td>31.0</td>
</tr>
<tr>
<td></td>
<td>I ≥ 1</td>
<td>0.35</td>
<td>0.76</td>
<td>39.1</td>
</tr>
<tr>
<td></td>
<td>I ≥ 10</td>
<td>0.40</td>
<td>0.74</td>
<td>26.0</td>
</tr>
<tr>
<td></td>
<td>I ≥ 100</td>
<td>0.53</td>
<td>0.62</td>
<td>12.4</td>
</tr>
</tbody>
</table>

Figure 6. Normalized isotropic variograms of anchovy and sardine indicators for (a) $z \geq 0.1$, (b) $z \geq 1$, (c) $z \geq 10$, and (d) $z \geq 100$ g m⁻², for the 1994 and 2001 surveys.

Figure 7. Cross-variograms between pairs of indicators (a) $I_1 = 0.1$ g m⁻² and $I_2 = 1.0$ g m⁻², and (b) $I_1 = 0.1$ g m⁻² and $I_3 = 10$ g m⁻², normalized to the smallest indicator, for anchovy and sardine in 1994 and 2001.
has in fact increased as a result of the boost in stock sizes, consistent with MacCall’s (1990) hypothesis that populations expand their geographical range with increased abundance, as observed using the 1984—1999 time-series of South African anchovy stock estimates (Barange et al., 1999).

Barange and Hampton (1997) suggested that the ideal inter-transect distance would be driven by the range of the highest density indicator for sardine, approximately 10 miles in 1994. The expansion in the distribution of both species in 2001 did not change that ideal inter-transect distance. Furthermore, indicator variograms suggested larger nugget effects in 2001, which indicate significantly larger small-scale (<1 mile) variability than in 1994. An increase in biomass and area of distribution, therefore, did not eliminate a large degree of randomness in the distribution of high-density spots, nor did it indicate that a reduction in survey effort (e.g. by increasing the inter-transect distance) would be advisable. The reason for this small-scale variability resides in the increased number of high-density spots in both species, but particularly sardine (see Figure 3). The concerns over whether the anchovy-based survey design was as effective for estimating sardine (Barange and Hampton, 1997) as it is for anchovy, are independent of the size of the stocks. Sardine remain a difficult species to survey adequately by acoustic means, because of their tendency to form isolated aggregations of very high density.

The relative differences in the spatial structures between anchovy and sardine previously noted by Barange and Hampton (1997) were also observed in this study, suggesting that they are caused by a combination of intrinsic behavioural aspects as well as by changes in population density (Petitgas, 1998). Cumulative frequency plots (Figure 3) revealed that despite the almost threefold increase in sardine biomass, 90% of it was still contributed

![Variogram ratio 2001](image)

**Figure 8.** Cross-variograms between anchovy and sardine indicators (cut-off = 1 g m$^{-2}$) in 1994 and 2001.

![Spatial distribution of relative dominance](image)

**Figure 9.** Spatial distribution of relative dominance between anchovy and sardine in the survey area in (a) 1994, and (b) 2001. The index of dominance varies between 1 (full anchovy dominance) and -1 (full sardine dominance). Densities <1 g m$^{-2}$ are considered as zero to avoid distortion of the patterns.
by <10% of the data. The conclusion is that the increase in sardine biomass is mostly driven by an increase in the number and density of very high-density “hotspots”, rather than a general increase in the number of positive stations. Conversely, the increase in anchovy stock size resulted in a relatively large number of stations contributing to the overall abundance, as well as a general increase in the mean density of positive intervals (see Figure 3). Cross-variograms further support this view (Figure 7). The smoothly structured transition between pairs of anchovy indicators reflects that before reaching a high-density area for anchovy, we must cross through areas of lower density. The much reduced or absence of structure in sardine indicator cross-variograms suggests that once a high-density area has been encountered, it is not possible to predict whether the density in the vicinity is likely to exceed a specific level (Petitgas, 1993). This is proof of a high degree of density-independent patchiness in sardine, in agreement with results from other sardine stocks (Scalabrin and Massé, 1993). This difference in the occupation of space is consistent with the feeding ecology of both species. Van der Lingen (1994) showed that sardine are mainly filter-feeders in the southern Benguela, whereas anchovy are particle-feeders. The latter strategy requires that a minimum distance be maintained between individual fish, while the former strategy does not benefit energetically from maintaining a constant school density. It is worth noting here that sardine schools in the Benguela are on average much denser than anchovy schools (Lawson et al., 2001).

The cross-variograms between anchovy and sardine confirmed that, in 1994, anchovy and sardine occupied distinctly separate niches of the continental shelf, sardine inshore and anchovy offshore, as reported elsewhere (Hampton, 1992; Barange and Hampton, 1997; Barange et al., 1999). The cross-variogram (Figures 8 and 9) can be interpreted as reflecting both species occupying parallel bands along the continental shelf, separated by some 15–20 miles. Conversely, the analysis with the 2001 data revealed a well-structured cross-variogram (Figure 8), indicating that both species are correlated and occupy similar spatial areas. The ecological interpretation is that the increase in stock size and the subsequent expansion of the populations have brought both species together, having to face competition for resources. Perhaps their differences in feeding strategy (Van der Lingen, 1994) can minimize such competition, but further research on this topic needs to be conducted.

Finally, the continuous growth of both anchovy and sardine stocks off South Africa over the last 7–8 years may challenge the concept of replacement between populations of anchovy and sardine (Schwartzlose et al., 1999). As the size of anchovy spawner stock is driven by short-term recruitment, while that of sardine is driven by the previous year’s spawning stock (Barange et al., 1999), it can be concluded that present conditions have benefited both recruitment and adult survival, an unlikely scenario during species replacements. However, a longer time-series may be required to ascertain whether replacement is taking place, and if not whether it is caused by differences in their specific life history strategies.

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References


