Environmental conditions, satellite imagery, and clupeoid recruitment in the northern Benguela upwelling system

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ABSTRACT

The relationship between oceanographic conditions and clupeoid (pilchard, *Sardinops sagax,* and anchovy, *Engraulis capensis*) recruitment in the northern Benguela upwelling system was investigated from 1981 to 1987 using a time-series of mean weekly SST images. Two approaches were taken. The first involved correlating recruitment success with the number of weekly coastal 'SST events' above various cut-off temperatures during the main reproductive season. The second involved constructing a multiple regression model of recruitment success with two independent environmental variables: namely, the number of coastal 'SST events' greater than 19°C, and an onshore retention index for the early life-history stages. The retention index was derived from a spatial time-series analysis of the SST images using principal components analysis. In general, pilchard recruitment showed a positive relationship with the 'number of SST events' whilst anchovy recruitment had a negative relationship; 1987 was an outlier year, during which there were exceptionally high levels of both pilchard and anchovy recruitment. The multiple regression R^2 values were high and significant for both species (pilchard $R^2 = 0.88$, anchovy $R^2 = 0.96$). The regression model also accounted for the 1987 outlier according to levels of onshore retention which, despite low inshore SSTs, were particularly high during the 1986/87 reproductive season. Although these results need to be validated with data from a longer time period, they show how satellite data might be used for predicting clupeoid recruitment success in the northern Benguela.

Key words: clupeoids, environment, northern Benguela, recruitment, remote sensing, spatial analysis

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INTRODUCTION

The Benguela upwelling system runs along the southwestern coast of Africa from southern Angola in the north to Cape Agulhas in the south (Fig. 1). Ecologically, it is split into separate northern and southern systems by a zone of intense perennial upwelling activity in the Lüderitz region (26°– 27.5°S). The high levels of offshore transport and wind-driven turbulence associated with this upwelling act as a barrier to the longshore transport of pelagic eggs and larvae (Boyd and Cruickshank, 1983; Agenbag and Shannon, 1988). This, combined with almost no recorded migration of pilchard (*Sardinops sagax*) or anchovy (*Engraulis capensis*) across the Lüderitz upwelling cell (Newman, 1970), indicates that the northern Benguela's clupeoid stocks are largely reproductively isolated from those in the south.

The pilchard, and to a lesser degree anchovy, have formed the basis of an important purse seine fishery off the Namibian coast since the late 1940s (Crawford *et al.*, 1987). However, as with other short-lived pelagic fish stocks, effective management of the northern Benguela's clupeoids has been especially difficult, largely owing to the effects of heavy fishing and environmental variability. In particular, links between environmental conditions and the pilchard and anchovy stocks have been found as regards the following: spawning activity (Parrish *et al.*, 1983; Le Clus, 1990; Le Clus, 1991), larval abundance and distribution (O'Toole, 1977; Badenhorst and Boyd, 1980; Hewitson, 1987; Olivar, 1990), adult distribution (Crawford and Shannon, 1988) and recruitment success (Shannon *et al.*, 1988).

Accurate forecasts of recruitment success would clearly be of great benefit, both to management and to the fishing industry (Cochrane and Starfield, 1992).

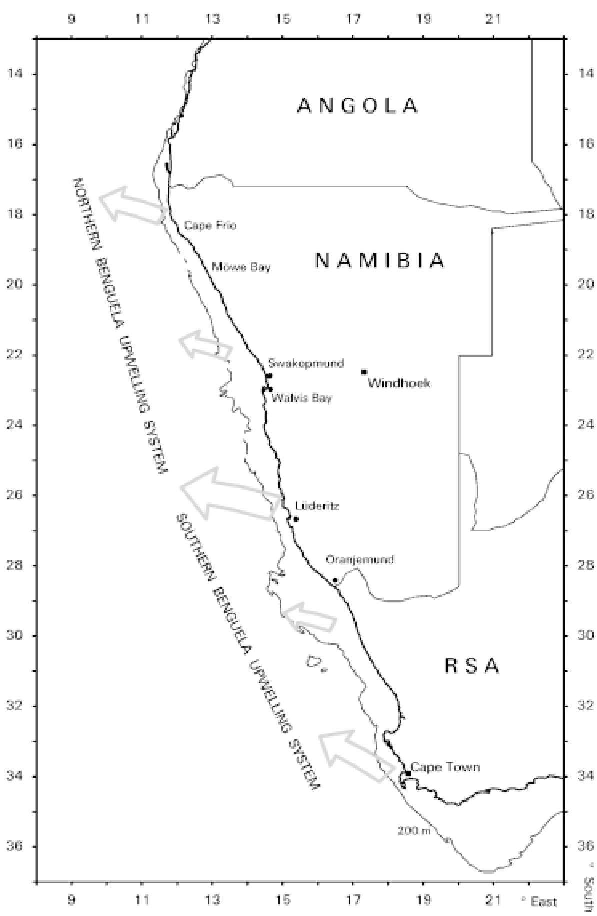


Figure 1. South-west Africa and the Benguela upwelling system. Coastal upwelling is represented by the arrows.

Understanding recruitment with sufficient accuracy to enable reliable predictions remains, however, a central problem in fisheries science. Stock–recruit relationships are typically poor, and it has become widely accepted that environmental conditions play a major role in determining the recruitment success of many marine fisheries, according to their influence on the survival of the planktonic early life-history stages. In spite of the successful testing of various theories concerned with early life-history survival and environmental variability, and the existence of some good general relationships between environmental parameters and recruitment success (Cury and Roy, 1989; Lluch-Belda *et al.*, 1989), there still remains a general failure to predict recruitment success with sufficient accuracy for management purposes.

Theories of how environmental conditions influence recruitment success can be split into 'mechanistic' and 'synthesis' theories (Cole and McGlade, 1998a). Mechanistic theories are concerned with specific causes of larval mortality, such as starvation, predation, or advection into unfavourable habitats (Lasker, 1975; Parrish *et al.*, 1983; Rothschild *et al.*, 1989; Laurence, 1990). Synthesis theories, on the other hand, are a more recent development, and attempt to unite the various mechanistic theories within single unifying frameworks.

The optimal environmental window (OEW) theory (Cury and Roy, 1989) and the triad theory (Bakun, 1996) are the two main synthesis theories. In eastern boundary upwelling regions, such as the Benguela, both are concerned with how the dynamic balance between upwelling activity and calmer conditions affect larval survival. The OEW theory specifies that recruitment success is maximized at intermediate levels of upwelling activity (as reflected by single environmental parameters such as Ekman transport or sea surface temperature) and declines as upwelling activity increases or declines beyond the optimal midpoint. The triad theory specifies that recruitment success will be some function of the trade-off between the differing oceanographic conditions leading to food *enrichment* and *concentration* for the developing fish larvae, and the *retention* of fish eggs and larvae within suitable nursery habitats. Unlike the OEW theory, and despite a large body of anecdotal evidence, it still needs to be empirically tested.

The purpose of this study is to investigate the relationship between environmental conditions and clupeoid recruitment in the northern Benguela upwelling system using a time-series of mean weekly sea surface temperature (SST) images from 1981 to 1990. The ultimate aim is to assess whether predictable environmental/recruitment interactions can be identified for pilchard and anchovy. Two approaches were taken in deriving suitable environmental indices from weekly SST images.

The first involved estimating the number of 'environmental events' during the main summer/autumn reproductive period which were likely to influence recruitment success. This was achieved by counting the number of weekly coastal 'SST events' above certain cut-off temperatures. In this way, local and short-term events which may influence recruitment are more likely to be integrated into the index, and not be masked out, as they would be if the data were averaged to produce mean seasonal SSTs. The second approach involved combining the number of 'SST events' with indices of the system's spatial structure from a standardized principal components analysis (PCA) of the SST image time-series. The purpose of this second method was to quantify the three processes encompassed by the triad theory (*enrichment*, *retention*, and *concentration*), so as to investigate how, or whether, different combinations of these three processes were related to different levels of recruitment success.

Details and results of the PCA have already been published (Cole and McGlade, 1998b). It was concluded that the technique could directly quantify oceanographic conditions promoting the *retention of* clupeoid eggs and larvae, from the patterning of SST gradients within the region, and by association, indirectly quantify the *concentration* of food across thermal fronts and thermoclines for the developing larvae. PCA was, however, unable to quantify *enrichment* of the food chain. In this study, it is assumed that the number of 'weekly SST events' above certain cut-off temperatures act as a suitable proxy for *enrichment*, according to the upwelling of cool, nutrient-rich water from below the pycnocline.

An important constraint on any conclusions that can be drawn from the present study is that there is an overlap of only 6 years (1982–1987) between the satellite data and estimates of pilchard and anchovy recruitment strength. This is not long enough to undertake a rigorous testing of theories, and is clearly much shorter than the decadal-scale climate-driven regime shifts thought to be responsible for instigating and maintaining dominance shifts between anchovy and pilchard populations (Lluch-Belda *et al.*, 1989; Sharp and McLain, 1993). Nonetheless, the overlap is adequate for highlighting any clear trends given the wide spread in recruitment success between 1982 and 1987, as illustrated in Fig. 2. Moreover, the small size of the adult populations during this period, as shown by the stock–recruitment plots in Fig. 3, indicates that density-dependent regulation was likely to have been at a minimum, thus allowing the effects of any density-dependent regulation to stand out more prominently.

Figure 2. Recruitment success of pilchard and anchovy from 1982 to 1987, defined as the number of year 0 fish entering the fishable stock $\times 10^9$. Data from Le Clus *et al.* (1988).

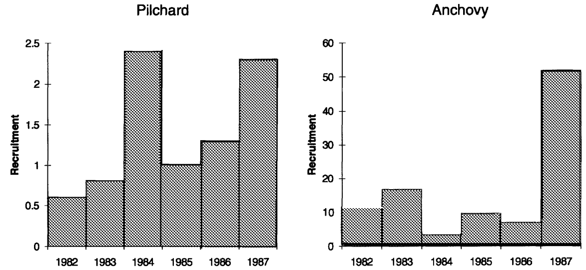
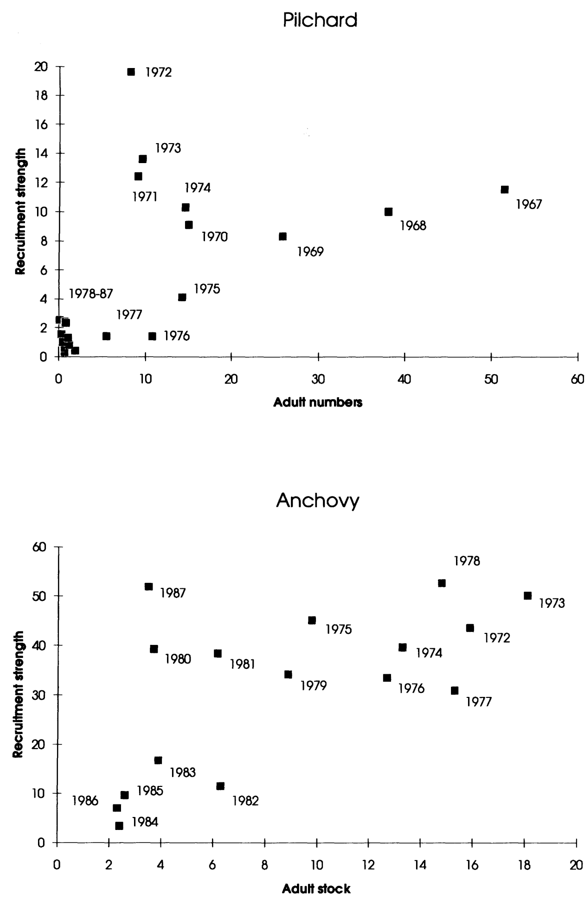


Figure 3. Stock–recruitment plots for pilchard and anchovy in the northern Benguela. Adult stock and recruitment succcess are both in terms of $\times 10^9$ fish. Adult stock for pilchard is defined as the number of fish aged 1 + during the previous year, and for anchovy as the number of fish aged 1 + during the current year. Data from Le Clus *et al.* (1988).



DATA

Recruitment success up to and including 1987 was estimated according to the size of the age 0 year class from a virtual population analysis (VPA) conducted after the end of the 1987 fishing season, as reported in Le Clus *et al.* (1988). Although 'current year' biomass estimates from VPA can be inaccurate, owing to the use of fishing effort as a linear scalar for fishing mortality (Butterworth, 1980), independent evidence for a strong year class (relative to the size of the parent stock) during 1987 (Fig. 2) is provided by there being a high proportion of one-year-old fish in the pilchard and anchovy landings during 1988 (Hewitson *et al.*, 1989).

Mean weekly sea surface temperature (SST) images of the northern Benguela were extracted from the cloud and ocean remote sensing around Africa (CORSA) data set held at the Marine Environment Unit, Space Applications Institute, European Commission Joint Research Centre (JRC). The weekly SST composites were processed from global area coverage (GAC) advanced very high resolution radiometer (AVHRR) data, under a data-sharing agreement with NASA (Nykjaer and Villacastin, pers. comm.). Four weekly composites were produced per month; the first three weekly composites were 7 day averages and the final composite was an average of all the remaining days in the month. Equatorial regions aside, the composites have been successfully validated with data from the COADS (Woodruff *et al.*, 1987; Roy and Mendelssohn, 1998), NASA MCSST, and GOSTA (Global Ocean Surface Temperature Atlas) data sets (Nykjaer and Villacastin, pers. comm.). They have a resolution of 4 km at the Equator and have been georeferenced to a Mercator projection. Examples of the weekly images are shown in Fig. 4.

Indices of the system's spatial structure were derived from the results of a standardized principal components analysis (PCA) performed on the SST images for the period between July 1981 and August 1987. An outline of the technique and the results pertinent to this study are given below. Full details of the analysis and its interpretation are given in Cole and McGlade (1998b).

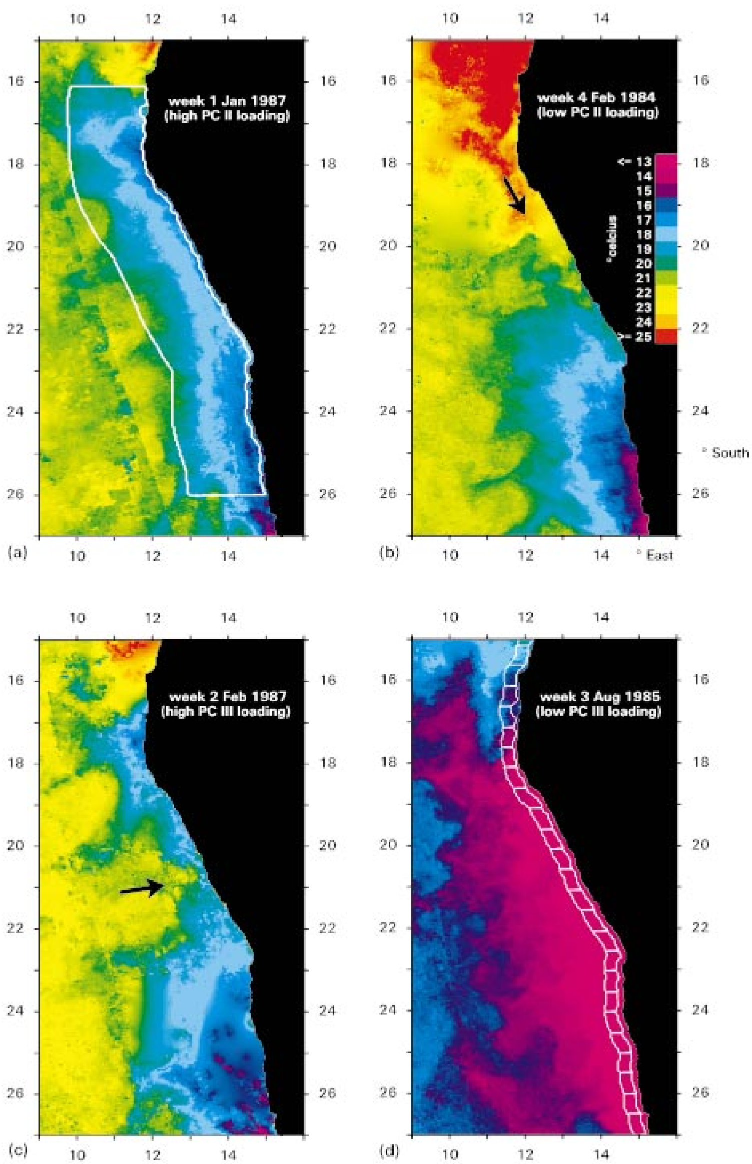


Figure 4. Examples of mean weekly SST composites with high and low loadings on principal components II and III. The white surround in (a) is the area for which PCA was performed, and in (d) the areas from which mean weekly SSTs were extracted for Fig. 6. The black arrows in (b) and (c) indicate advective processes, likely to be associated with these thermal patterns, which could promote the retention of pelagic eggs and larvae.

PCA acts to reduce large multidimensional data sets to a smaller number of uncorrelated principal components. The main advantage of PCA as a method of analysing sequential raster images lies in its ability to provide both spatial and temporal output for as many different features as are detected by the analysis. Principal component I (PC I) represents the spatial pattern which accounts for most of the variability in the image time-series; PC II represents the spatial pattern of most of the residual variability which is uncorrelated with PC I, PC III the spatial pattern of most of the residual variability uncorrelated with PC I or PC II, and so on for successive components.

When each of the input images are standardized by its spatial mean and standard deviation prior to the analysis (i.e. standardized PCA), PC I represents the mean spatial structure of the system and successive components represent time-varying spatial patterns. Associated with each principal component is a set of 'loadings'. These are the temporal output from the analysis, and represent the similarity in spatial pattern between each of the input images and the principal components. General information on PCA, and its application to image time-series analysis, can be found in Eastman and Fulk (1993) and Sharma (1996).

With regards to the PCA of the SST images for the northern Benguela, it was concluded that principal components (PCs) II and III both identified and quantified aspects of the northern Benguela's behaviour which may directly influence the *retention* or otherwise of clupeoid eggs and larvae, and which may indirectly result in the formation of strong thermal fronts and thermoclines across which food may be *concentrated* for the first-feeding larvae.

The 'loadings' on PCs II and III are used as indices of the system's spatial structure. The loadings are shown in Fig. 5, with examples of time steps corresponding to high and low loadings displayed in Fig. 4. The loadings on PC II measured the relative orientation of SST gradients from primarily inshore–offshore gradients (high positive loadings) to primarily longshore gradients (low negative loadings). As such, negative loadings on PC II detect longshore intrusions of warm surface Angolan water from the north, and hence can be used as an index of ***longshore*** *retention* and *concentration*. High positive loadings, on the other hand, indicate more or less uniform conditions throughout the region. As such, the positive loadings on PC II can act as an index of ***onshore*** *retention* and *concentration* when there is a uniform shoreward contraction of the offshore upwelling front along the coast. From a visual inspection of images with high loadings on PC II, it was concluded that this was most likely to be the case when inshore SSTs were greater than 17°C.

The loadings on PC III measured the difference in SSTs off central Namibia (19°S – 23°S) relative to the north and the south. Positive loadings clearly reflected differential warming in the central region owing to locally reduced upwelling and onshore intrusions of oceanic water, as illustrated in Fig. 4. As such, positive loadings on PC III can also act as an index of ***onshore*** *retention* and *concentration*.

METHODS

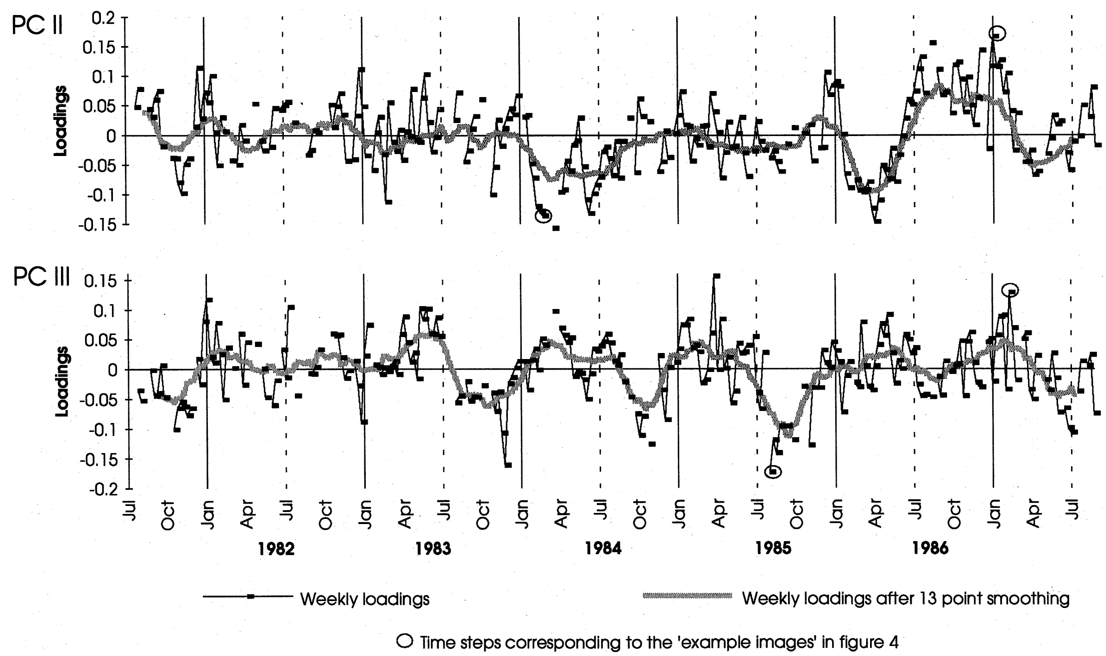
The methodology can be separated into three main stages: first, the construction of time- and latitude-specific SST time-series from the satellite image composites; second, counting the number of 'SST events' above certain cut-off temperatures over the course of the reproductive season and examining how they relate to clupeoid recruitment; and third, the construction and testing of a model of clupeoid recruitment which combines data on 'SST events' and spatial structure.

For the purposes of this study, November to May has been defined as the main reproductive season. Pilchard and anchovy in the northern Benguela are serial spawners (Le Clus, 1990), and although they maintain some level of reproductive activity throughout the year, most of the spawning activity and larval development occurs during these seven months between 17° and 24°S (O'Toole, 1977; Badenhorst and Boyd, 1980; Hewitson, 1987; Le Clus, 1990; Le Clus, 1991). It should be noted, however, that prior to the collapse of the pilchard stock in the mid 1970s, elevated levels of pilchard spawning activity also occurred around September and October off Walvis Bay (Crawford *et al.*, 1987).

Time- and latitude-specific SST time series

The time- and latitude-specific SST time-series were constructed as follows. Mean weekly SSTs between 20 and 50 km offshore from 0.5° latitudinal intervals between 14°S and 28°S were extracted from each of the weekly composites in the CORSA data set. The areas from which the mean SSTs were taken are shown in Fig. 4(d), and the entire set of 0.5° latitude time-series are presented as a colour chart in Fig. 6. Missing SST values owing to total cloud contamination within the 0.5° latitudinal areas accounted for less than 5% of all the values extracted; these missing values were interpolated as the average SST of the surrounding eight cells.

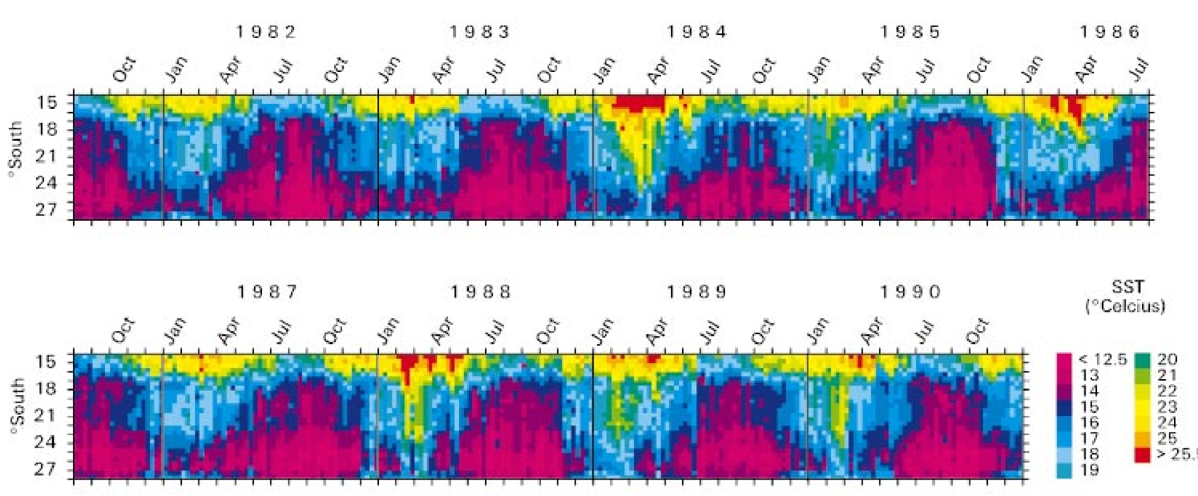
Figure 5. Weekly and 13 point smoothed loadings on principal components II and III. Missing data points are because weekly SST composites were excluded from the PCA owing to a high proportion of cloud cover. See Cole and McGlade (1998b) for more details.



SST events

The number of 'SST events' over the course of the reproductive season for each year was estimated by counting the number of weekly 0.5° latitudinal blocks in Fig. 6, between 17°S and 24°S, which exceeded a certain temperature from November to May. Five cut-off temperatures were used: 17, 18, 19, 20, and 21°C. The strength of any relationship between recruitment success and the number of 'reproductively important environmental events' was then assessed by fitting linear regressions.

Figure 6. Average weekly SSTs between 20 and 50 km offshore and per 0.5° latitude, as extracted from the areas illustrated in Fig. 4(d).



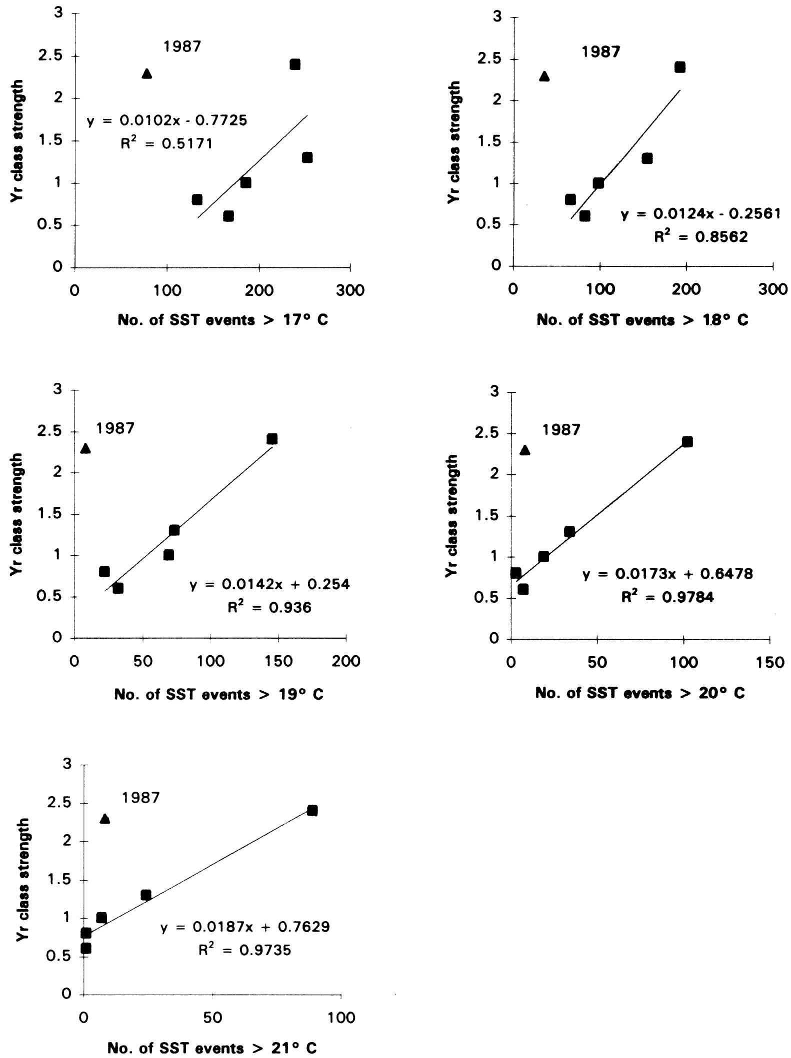


Figure 7. Relationship between the number of coastal SST events above various cut-off temperatures and pilchard recruitment success (0 group number × 10^9) from 1982 to 1987. The year 1987 was treated as an outlier and excluded from the regressions; see text for more details.

Recruitment model

The model was constructed by first calculating an inshore retention index for each year's reproductive season, secondly plotting this index against the corresponding number of 'SST events' greater than 19°C, and then identifying whether different domains in the relationship between these two variables corresponded to high, intermediate or low levels of recruitment success. Calculation of the inshore–offshore retention index is outlined below. A cut-off temperature of 19°C was selected as suitable given that the R^2 values from the regressions of recruitment success against number of SST events (see Figs 7 and 8) were high for both species at this temperature.

The inshore–offshore retention index was calculated from the sum of positive loadings on principal component III (PC III) and the temperature-weighted sum of positive loadings on PC II. Positive loadings on PC II were included in the retention index if the inshore temperatures from Fig. 6 were over 17°C (see below for the weighting procedure), so as to include conditions when there was a fairly uniform contraction of the offshore upwelling front and onshore flow of surface water throughout the region. In terms of spawning activity, 17°C was also a suitable temperature for weighting the positive loadings on PC II, given that peak anchovy and pilchard spawning tends to occur when coastal surface water is greater than or equal to 17°C (Cole, 1997).

Calculation of a longshore retention index using negative loadings on PC II was not considered necessary because strong longshore intrusions of warm water from the north are associated with a high number of coastal SST events above 19°C. It should be added that the inshore–offshore retention index

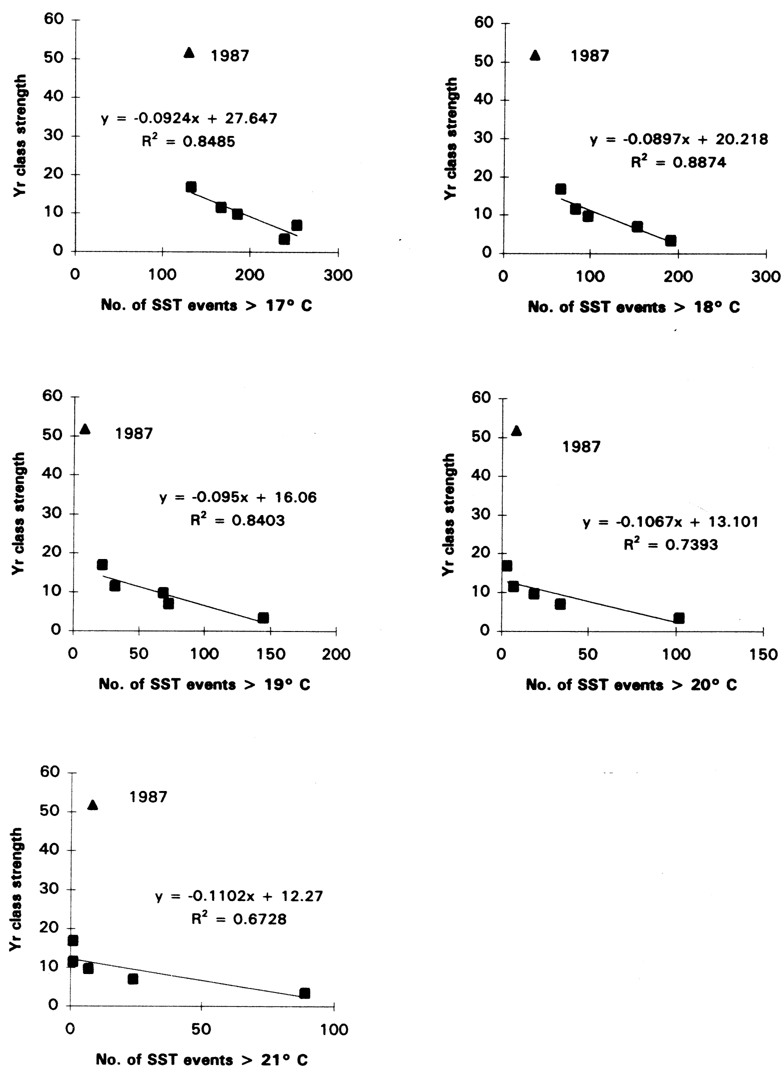


Figure 8. Relationship between the number of coastal SST events above various cut-off temperatures and anchovy recruitment success (0 group number $\times 10^9$) from 1982 to 1987. The year 1987 was treated as an outlier and excluded from the regressions; see text for more details.

may also indirectly act as a concentration index, given that onshore movements of surface water will be associated with the onshore movement of the offshore upwelling front and the formation of thermoclines (Boyd, 1987).

Mathematically, the weighting and summation procedure for calculating the annual inshore–offshore retention index are expressed as follows:

$$r_t = \sum_{i=1}^{i=28} (a_i + |a_i|)/2 \cdot (p_i/14) + \sum_{i=1}^{i=28} (b_i + |b_i|)/2 \quad (1)$$

where r_t denotes the annual inshore–offshore retention index for year t, i represents the week (28 weeks between the beginning of November and the end of May), a_i is the loading on PC II during week i, $|a_i|$ is the absolute size of the loading on PC II during week i, p_i is the number of coastal 0.5° latitude blocks between 17°S and 24°S with SSTs greater than 17°C during week i (fourteen 0.5° blocks in total), and b_i is the loading on PC III during week i.

The terms $(a_i + |a_i|) / 2$ and $(b_i + |b_i|) / 2$ ensure that only positive PC II and PC III values are included for weighting and summation. If there was a gap in the loadings because of cloud cover, the mean of the two values either side of the gap was used.

Testing the recruitment model

The strength and significance of any relationships between onshore retention, SST events and recruitment strength was tested by performing a nonlinear multiple regression for both anchovy and pilchard. The same alternating conditional expectation (ACE) algorithm used by Cury and Roy (1989) to test their optimal environmental window theory was used here to uncover the nature of any underlying nonlinear relationships between the variables. Essentially, the algorithm finds the optimal transformation of the input data so as to maximize the R^2 value of a multiple regression.

In the present study, using two independent variables, onshore retention and SST events, the multiple regression is of the following form:

$$T_y = T_s + T_r \qquad (2)$$

where T_y denotes the optimal transformation of annual year-class strength (i.e. recruitment success) in terms of the number of year 0 fish $\times\ 10^9$ (constrained to be linear), T_s is the optimum transformation of number of SST events, and T_r is the optimum transformation of the onshore retention index.

The functional nature of the relationship between the two independent variables and recruitment is deduced by plotting the transformed values of the variables against their original values. The statistical significance of any relationship between these variables was tested by performing a standard linear multiple regression on the transformed values.

RESULTS

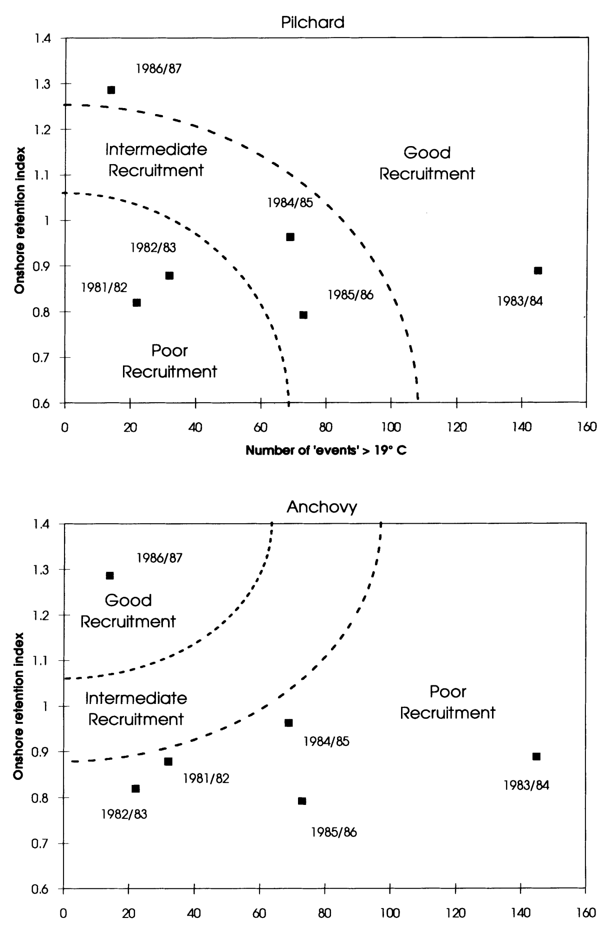
The relationship between the number of coastal SST events above a minimum cut-off value and recruitment success for both species is presented in Figs 7 and 8. In all cases, 1987 was identified as an outlier, and was omitted when fitting the regressions. This omission is justified on the grounds that strong recruitment during 1987 may have been at least partially fuelled by the northward advection of clupeoid eggs and larvae from the southern Benguela during an anomalous intrusion of Agulhas Current water into the northern Benguela during the latter part of 1986 (Hewitson, 1987; Shannon and Agenbag, 1987; Le Clus *et al.*, 1988). Normally these Agulhas intrusions do not have any coastal effects north of 33°S (Shannon, 1985). But 1986 was different, in so far as the warm intrusion extended as far north as the Lüderitz region, where it suppressed the normally vigorous late winter/spring upwelling activity (Shannon and Agenbag, 1987).

Outliers apart, pilchard and anchovy both had highly significant relationships between recruitment strength and the number of coastal SST events above certain temperatures from 1982 to 1986. For pilchard, the relationship is positive and is strongest for cut-off SSTs of 19, 20 and 21°C, whilst for anchovy the relationship is negative and strongest for cut-off SSTs of 17, 18 and 19°C.

The combined spatial structure and SST models of pilchard and anchovy recruitment are presented in Fig. 9. Domains in which one might expect to find good, intermediate, and poor recruitment success have been identified by eye, based on the levels of recruitment success resulting from each of the plotted reproductive seasons (see Fig. 2). For pilchard, recruitment success during 1984 and 1987 was classified as 'good', during 1985 and 1986 as 'intermediate', and during 1982 and 1983 as 'poor'. For anchovy, recruitment success from 1982 to 1986 was 'poor', and for 1987 it was 'good'.

The optimal nonlinear transformed values of the independent variables are shown plotted against their original values in Figs 10 and 11. In effect, these confirm the relationships shown in Fig. 9, namely, that pilchard recruitment success has a positive relationship

Figure 9. Models of pilchard and anchovy recruitment success according to SST conditions and an onshore retention index. The boundaries between differing levels of recruitment success were estimated by eye; see text for more details.



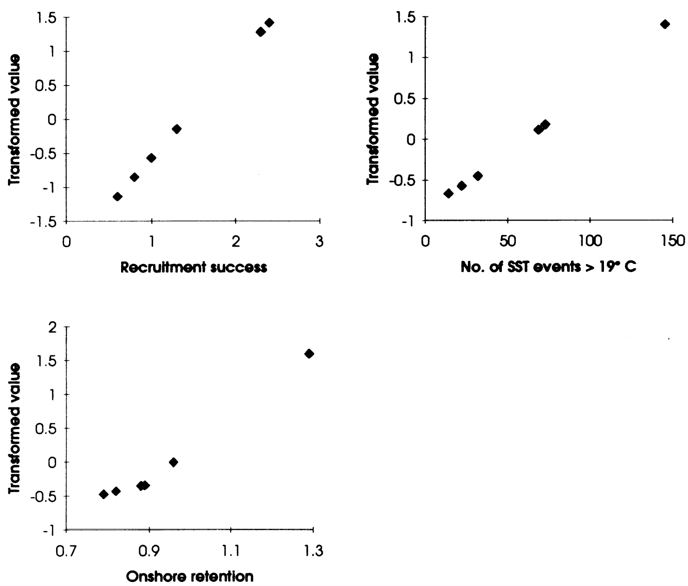


Figure 10. Optimal tranformation plots for pilchard recruitment (constrained to be linear), the number of SST events > 19°C and the onshore retention index; see text for more details.

with both onshore retention and 'SST events', whilst anchovy recruitment has a positive relationship with onshore retention only, and a negative relationship with the number of SST events.

The results from the multiple regressions of the transformed values are displayed in Tables 1 and 2. The R^2 values are high for both anchovy and pilchard, with SST events and onshore retention together explaining 88% of the variation in pilchard recruitment, and 96% of the variation in anchovy recruitment. The relationship between recruitment success and the two environmental parameters is weakly significant ($P < 0.05$) for pilchard and strongly significant ($P < 0.01$) for anchovy.

DISCUSSION

Recruitment and SST

Figures 7 and 8 show that between 1982 and 1987, anchovy and pilchard recruitment had very different relationships with inshore SST conditions in the northern Benguela, and that both stocks appear to conform to the same trend that has been observed in

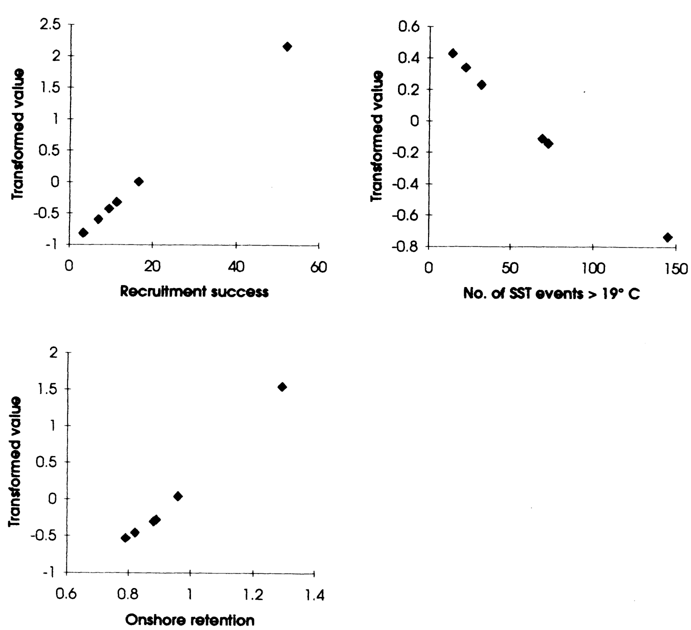


Figure 11. Optimal tranformation plots for anchovy recruitment (constrained to be linear), the number of SST events > 19°C and the onshore retention index; see text for more details.

Table 1. Multiple regression analysis of pilchard recruitment (dependent variable) vs. the number of SST events > 19°C and onshore retention (independent variables) from 1982 to 1987. The transformed values illustrated in Fig. 10 were used in the analysis. Statistical significance is represented by an asterix (*).

Regression statistics					
Multiple R	0.937				
R^2	0.878				
Adjusted R^2	0.797				
Standard error	0.494				
Observations	6				
Analysis of variance	d.f.	SS	MS	F value	P
Regression	2	5.269	2.634	10.811	< 0.05*
Residual	3	0.731	0.244		
Total	5	6.000			
	Coefficient	SE	t value	P	
Intercept	0.00000	0.201	0.000	1.000	
SST events (transformed values)	1.17774	0.311	3.784	< 0.01*	
Retention index (transformed values)	1.19852	0.301	3.984	< 0.01*	

the eastern Pacific and the eastern North Atlantic: namely, that both pilchard and sardine stocks tend to flourish under warmer conditions, and that anchovy populations flourish during cooler conditions (Sharp and McLain, 1993; Cushing, 1996).

It is possible that this difference between the two species is linked to larval feeding preferences, in terms of prey type and prey size. It is well established that different levels of upwelling activity are associated with differences in abundance, species composition and size distribution of phytoplankton and zooplankton (Hutchings *et al.*, 1995). During cool upwelling conditions, productivity levels are high, phytoplankton production is dominated by large diatoms, and zooplankton production is dominated by macrozooplankton. During warm, stable conditions, productivity

Table 2. Multiple regression analysis of anchovy recruitment (dependent variable) vs. the number of SST events > 19°C and onshore retention (independent variables) from 1982 to 1987. The transformed values illustrated in Fig. 11 were used in the analysis. Statistical significance is represented by an asterix (*).

Regression statistics					
Multiple R	0.978				
R^2	0.956				
Adjusted R^2	0.927				
Standard error	0.296				
Observations	6				
Analysis of variance	d.f.	SS	MS	F value	P
Regression	2	5.738	2.870	32.747	< 0.01*
Residual	3	0.263	0.088		
Total	5	6.000			
	Coefficient	SE	t value	P	
Intercept	− 0.0035	0.121	− 0.003	0.998	
SST events (transformed values)	0.87295	0.340	2.565	0.050*	
Retention index (transformed values)	1.09867	0.188	5.858	< 0.05*	

is lower, the phytoplankton become dominated by micro- and dinoflagellates, and smaller zooplankton become relatively more abundant.

Whilst no information on clupeoid larval feeding is available for either the northern or southern Benguela, studies in the Californian system on *Engraulis mordax* and *Sardinops sagax* larvae (Arthur, 1976) and in the Peruvian system on *E. ringens* and *S. sagax* (Muck *et al.*, 1989) both indicate that at lengths greater than about 9 mm the anchovy/anchoveta larvae start to prefer larger prey than sardine larvae.

If these trends also hold for the northern Benguela, then after the larvae have grown to about 9 mm in length, the feeding success and survival of anchovy larvae would be maximized by cooler upwelling conditions, when larger prey would be relatively more prevalent, and pilchard larvae by warmer conditions, when smaller prey would be relatively more prevalent. Hence, one might expect to find a negative relationship with SST conditions for anchovy recruitment and the positive one for pilchard. Moreover, if this is indeed the case, it is also consistent with the increasingly held view, as reported in Cushing (1996), that if there is a critical larval period influencing eventual recruitment success, it occurs at larger larval sizes (i.e. $> \approx 9$ mm) rather than at the first-feeding stages as originally suggested by Hjort (1914).

Recruitment and SST: comparison with previous studies

Shannon *et al.* (1988) is the only previously published work to examine the relationship between clupeoid recruitment and SSTs in the northern Benguela. In contrast to the present study, they found a negative relationship between mean SST conditions and pilchard recruitment, and a positive one for anchovy. Possible reasons why their findings were different are discussed below, but essentially they fall into one of two categories: the years for which the studies were conducted, and the intra-annual period used to define the reproductive season.

Shannon *et al.* (1988) examined pilchard recruitment from 1954 to 1984 and anchovy recruitment from 1972 to 1983. Cole (1997), using COADS data, showed that on balance, the 1960s and 1970s were both cooler than the 1980s in the northern Benguela upwelling system. This is particularly relevant to anchovy, because Shannon *et al.*'s (1988) positive correlation occurred over a predominantly cool period, whilst the negative relationship in Fig. 8 occurred over a predominantly warm period. As a consequence, the optimal environmental window (OEW) model (Cury and Roy, 1989) has been shown to be able to account for these different correlations (Cole, 1997), with recruitment success being maximized at intermediate SSTs and tailing off as SST conditions deviate from the 'optimum' mid-point. The OEW model cannot, however, account for the different results between the two studies for pilchard – except in the unlikely event that a U-shaped relationship exists, with recruitment being *minimized* at intermediate SSTs.

For pilchard, the different results between the present study and that of Shannon *et al.* (1988) may be more adequately explained by the very different periods used in each study to define the 'reproductive season'. Shannon *et al.* compared the previous year's summed monthly SST anomalies with the 'current year' pilchard recruitment. For example, they would have matched 1982 pilchard recruitment with the summed monthly SST anomalies from January 1981 to December 1981, whilst the present study used SST conditions from November 1981 to May 1982.

In both the eastern Pacific and eastern Atlantic, warm events tend to be preceded by especially cold years (Hisard, 1986; Sharp and McLain, 1993), during which there is enhanced cold water upwelling. For example, Fig. 6 illustrates how both the 1984 and 1988 warm events in the northern Benguela were preceded by cool years. The implication, therefore, is that positive correlations between SSTs and recruitment success, when one uses SST data from the main reproductive season, may turn into negative correlations if one uses SST data from the previous year.

Incorporating spatial structure: towards recruitment prediction?

Figures 7 and 8 illustrate a classic problem with environment/recruitment studies. Although there may be a good relationship between recruitment success and a single environmental index for most of the years in a time-series, the relationship does not hold consistently. Hence although 'SST events' usually act as a good proxy of conditions which determine recruitment success, this was not the case during 1987. However, by taking the spatial structure of the system into consideration and identifying patterns that are likely to lead to the successful retention of eggs and larvae, and (by association) the concentration of suitable food across thermal fronts and thermoclines, the models in Fig. 9 illustrate how years with unusual conditions such as 1987 may be taken into account.

Whether or not the high levels of recruitment during 1987 resulted from the northward advection of eggs and larvae into the northern Benguela during the 1986/87 reproductive season, as proposed by Shannon and Agenbag (1987), has not been resolved. Some support was offered by the finding of a few anchovy larvae off Lüderitz during the January and February egg and larval cruises during 1987 (Hewitson, 1987). Nonetheless, back-calculation of anchovy birth dates from the 1987 fishing season indicated that most of the strong 1987 anchovy recruitment was from eggs that had been spawned earlier than usual, and that the larvae found off Lüderitz were in fact too small to have belonged to the main recruiting cohorts (Le Clus *et al.*, 1988).

The results in Fig. 9 indicate that one need not look outside the system to account for the high levels of recruitment success in both species during this year. Indeed, according to the triad theory, conditions during 1986/87 would have been excellent for recruitment success given that not only were oceanographic conditions good for the onshore *retention* of eggs and larvae, but also that levels of nutrient *enrichment* were high, as indicated by the low coastal SSTs. Moreover, the combination of good levels of enrichment combined with the onshore movement of oceanic water would most likely have resulted in good levels of food *concentration* across thermal fronts and thermoclines.

Without information on the system's spatial structure, it would have been more difficult to identify this, in so far as we would usually assume that low inshore SSTs meant high levels of upwelling activity, high levels of offshore transport, and thus low levels of onshore retention. Why levels of enrichment and onshore transport were both high during the 1986/87 reproductive season is a separate question, but is likely to be related to dynamic forces resulting from the strong intrusion of Agulhas water into the Benguela system during the latter half of 1986.

Figure 9 also demonstrates how the incorporation of information on spatial dynamics with SST data might provide a robust basis for making year-to-year forecasts of recruitment success for management purposes. Nonetheless, although the six years covered by this study include a wide range of environmental conditions, including a Benguela Niño warm event in 1984 (Boyd *et al.*, 1985), and a strong intrusion of Agulhas Current water in 1986, the fact that they cover only six years is in itself sufficient reason for caution. The relationships found here clearly need to be tested with more years of data. Furthermore, if the stocks recover to anything like their pre-1980s levels, then density dependence would need to be taken into consideration, and for pilchard the tendency for older fish to display elevated levels of spawning during September and October might also require a re-definition of the 'main reproductive season'.

Despite these reservations, the fact that the relationships between recruitment success, SST events and onshore retention had high R^2 values and were significant for both pilchard and anchovy is particularly encouraging (Tables 1 and 2), and represents a first step in empirically testing the triad theory in the northern Benguela. The methods used herein should thus serve as a useful prototype for future environment recruitment studies in this system, and perhaps other eastern boundary systems also.

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