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Non-stationary responses in anchovy (*Engraulis encrasicolus*) recruitment to coastal upwelling in the Southern Benguela

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ABSTRACT: Anchovy *Engraulis encrasicolus* is economically important and ecologically critical to the structure and function of the Benguela Current ecosystem, as it transfers energy from plankton to piscivorous fishes, seabirds, and marine mammals. Like other small pelagic fishes, annual recruitment strength varies substantially, but the drivers of these fluctuations are not well understood. To address this issue, we investigated the relationship between 30 yr of anchovy recruitment estimates derived from acoustic survey data and a new coastal upwelling index for the Southern Benguela defined as the monthly sum of offshore Ekman transport over the region 29–36° S. Cumulative December–March upwelling was significantly and positively related to recruitment, and this relationship was improved by integrating the upwelling index over multiple years (i.e. adding autocorrelation). A threshold-generalized additive model further showed that the slope of the linear regression between integrated upwelling and recruitment increased when anchovy spawner biomass on the west coast of South Africa in the preceding year exceeded ~0.74 million tonnes. By combining these 2 simple linear regressions into a single model, we were able to account for 82% of the variability in anchovy recruitment from 1985 to 2014. The biomass threshold in the upwelling–recruitment relationship could relate to the presence of a strong spawner–recruit relationship, or to a shift in the dominant driver of recruitment variability as adult biomass increases, such as effective transport of eggs, larvae retention in coastal habitats, and primary productivity.

KEY WORDS: Anchovy · Recruitment · Benguela · Upwelling · South Africa · Autocorrelation · Generalized additive model · Threshold GAM

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INTRODUCTION

The Benguela ecosystem off southern Africa is one of the 4 major eastern boundary current coastal upwelling zones, which together cover less than 1% of the ocean surface but support as much as 20% of the global wild marine fishery catch (Cushing 1971, Pauly & Christensen 1995). Fish biomass in these systems is dominated by small planktivorous pelagic species, which are critical in transferring energy from primary producers to higher trophic levels (Bakun 2006, 2010). Their population sizes are, however, notoriously variable over time and are characterized by multi-decadal fluctuations from abundance to scarcity (Schwartzlose et al. 1999, Checkley et al. 2017).

In the Southern Benguela, the economically and ecologically important European anchovy *Engraulis encrasicolus* (known locally as Cape anchovy) spawns over the Agulhas Bank off the southwest and south coast of South Africa from September to March, after which eggs and early larvae are transported by a shelf-edge jet current to nursery grounds off the west coast between Cape Columbine and the Orange River (van der Lingen et al. 2001; Fig. 1). As the juveniles grow, they move inshore along the west coast and in late austral winter/spring (August/September) begin a southward return migration to the spawning grounds, reaching the Agulhas Bank as sexually mature fish at an age of approximately 1 yr (Roy et al. 2007, Checkley et al. 2009). The environmental drivers of anchovy recruitment are poorly understood. Previous research into the relationship between coastal upwelling and anchovy recruitment has yielded inconsistent results. Some studies attribute a positive correlation to increased flux of nutrients into the photic zone, which supports primary production and thus the zooplankton upon which clupeoid larvae and pre-recruits feed (Skogen 2005, Garrido & van der Lingen 2014). Other studies suggest a negative correlation in which too much west coast upwelling transports eggs and larvae offshore and away from preferred habitat (Shelton & Hutchings 1982, Boyd et al. 1998, Hutchings et al. 1998, Miller & Field 2002).

In this dynamic system, mechanisms may also vary in relative importance from year to year (van der Lingen & Huggett 2003). For example, close connectivity between spawning and nursery grounds, typical during years in which southerly, upwelling-favorable winds are not too strong to advect larvae offshore, may be particularly beneficial to population growth during periods of low anchovy abundance (Roy et al. 2001, 2007, van der Lingen & Huggett 2003). When anchovy biomass is high, the abundance of eggs and larvae (given high spawner biomass) may compensate for advective losses such that primary productivity associated with upwelling becomes more influential on population growth. This potential 'non-stationarity' could confound attempts to understand climate–biology relationships.

A dramatic and sustained increase in anchovy recruitment since 1999/2000 (Fig. 1) may be associated with altered climate–biology relationships of anchovy, as strong empirical relationships derived

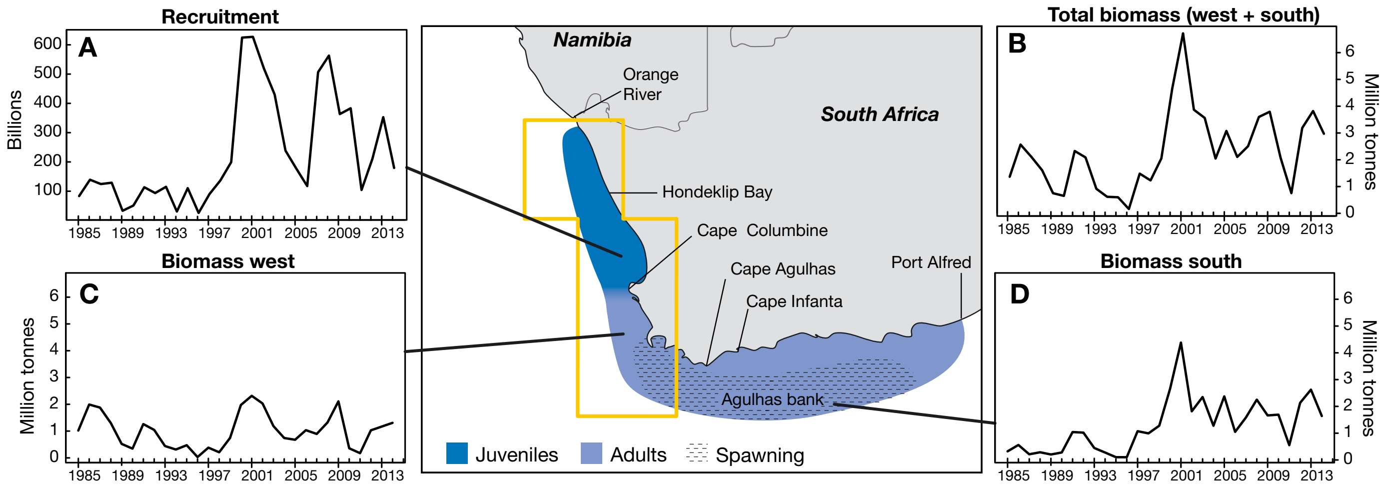

Fig. 1. Distribution of anchovy in South Africa (map based on Checkley et al. 2009) and (A) time-series of anchovy recruitment strength (billions of fish) estimated in autumn/winter (May/June) acoustic surveys covering the area between the Orange River mouth and Cape Infanta, and spawner biomass (Mt) estimated in spring/summer (October/November) acoustic surveys covering the area between Hondeklip Bay and Port Alfred for (B) the entire survey area, and (C) west and (D) south coasts. Yellow squares indicate the 2.5° × 2.5° grid cells used to calculate the upwelling index for the southern Benguela (see details in Lamont et al. 2017)

before this shift failed to explain anchovy recruitment variability in subsequent years (Boyd et al. 1998, Miller & Field 2002, Roy et al. 2002, van der Lingen & Huggett 2003). Here, we tested the hypothesis that non-stationary relationships between upwelling and recruitment explain the shift in anchovy recruitment in the late 1990s/early 2000s. To this end, we exploited 30 yr of acoustic survey data to investigate relationships between anchovy recruitment and upwelling, using a newly published upwelling index for the Southern Benguela defined as the monthly sum of offshore Ekman transport over the region 29–36° S (García-Reyes et al. 2017, Lamont et al. 2017). We modeled recruitment as a function of anchovy abundance and upwelling using a combination of simple linear models, generalized additive models (GAMs), and a non-additive threshold model (TGAM). Given the relatively high levels of autocorrelation in the recruitment time series, we also explored how increasing autocorrelation in the upwelling indices improves explanatory power of the model. We assumed here that anchovy recruitment is affected by upwelling conditions in the current year, as well as by those that the population experienced in prior years, and that the influence of upwelling in earlier years underlies high autocorrelation in the recruitment time series. This study is significant because understanding recruitment and year-class strength in small pelagic fish is essential for management of their fisheries and ecosystems.

MATERIALS AND METHODS

Anchovy and upwelling datasets

Interannual variability in the abundance and distribution of anchovy has been assessed using acoustic surveys conducted since 1983 by South Africa's Department of Agriculture, Forestry and Fisheries. Two major surveys are conducted annually, one in autumn/winter (May–June) to determine the strength (in numbers of recruits) of the year's recruitment and another in spring/summer (October–November) to estimate the biomass of the adult (spawner) stock. Survey design and methods have been thoroughly described by Hampton (1992) and Barange et al. (1999). The area covered by the pelagic surveys extends from the Orange River to Cape Infanta (recruit survey) and from Hondeklip Bay to Port Alfred on the south coast (biomass survey) (Fig. 1). The time series has been revised to take into account changes in survey equipment and an increased understanding of possible sources of error in earlier estimates (Coetzee et al. 2008, de Moor et al. 2008).

We used a newly published coastal upwelling index for southern Africa from 1979 to 2015 (Lamont et al. 2017), calculated along the Namibian and South African coasts (from 29 to 36° S; Fig. 1) and derived from daily averaged NCEP-DOE Reanalysis 2 wind vectors with a spatial resolution of 2.5° (Kanamitsu et al. 2002). Total cumulative upwelling was defined as the sum of daily offshore Ekman transport when Ekman transport was positive, calculated within each month of the time series (Lamont et al. 2017).

Climate–recruitment relationships

We linearly related anchovy recruitment to monthly-averaged estimates of upwelling in the Southern Benguela. In our analyses, a single year runs from July (in the previous year) to June (in the current year). Given the strong correlations between recruitment and upwelling in previous years (Fig. 2A), as well as the much higher level of autocorrelation in the recruitment time series ($\lambda = 0.7$) than in the upwelling indices ($\lambda = 0.4$), we assessed potential carry-over effects from prior years. To this end, we 'reddened' (i.e. added autocorrelation to) the upwelling index. Upwelling (1985–2015) was first normalized, after which we used the following equation to add first-order autocorrelation:

$$\text{RED.upwelling}(t) = \lambda \times \text{RED.upwelling}(t-1) + \text{upwelling}(t) \qquad (1)$$

where 'RED.upwelling' refers to the reddened upwelling index in year t, 'upwelling' refers to the unaltered upwelling index, and λ is the amount of autocorrelation added. The reddened upwelling time series was subsequently normalized. This approach is the same mathematically as the single integration method outlined by Di Lorenzo & Ohman (2013), with λ representing the dampening factor. To explore if there is an optimal λ value for the upwelling–recruitment relationship, we induced autocorrelation using a λ from 0.1 to 1 in steps of 0.1 (Fig. 2C). However, an issue with adding autocorrelation is that statistical assumptions of serial independence are violated, complicating efforts to establish levels of significance for correlations between recruitment and reddened upwelling (Pyper & Peterman 1998). To address this problem, we created 250 000 random (i.e. artificial) data series with the same properties as the upwelling data (same length, mean, standard deviation, and

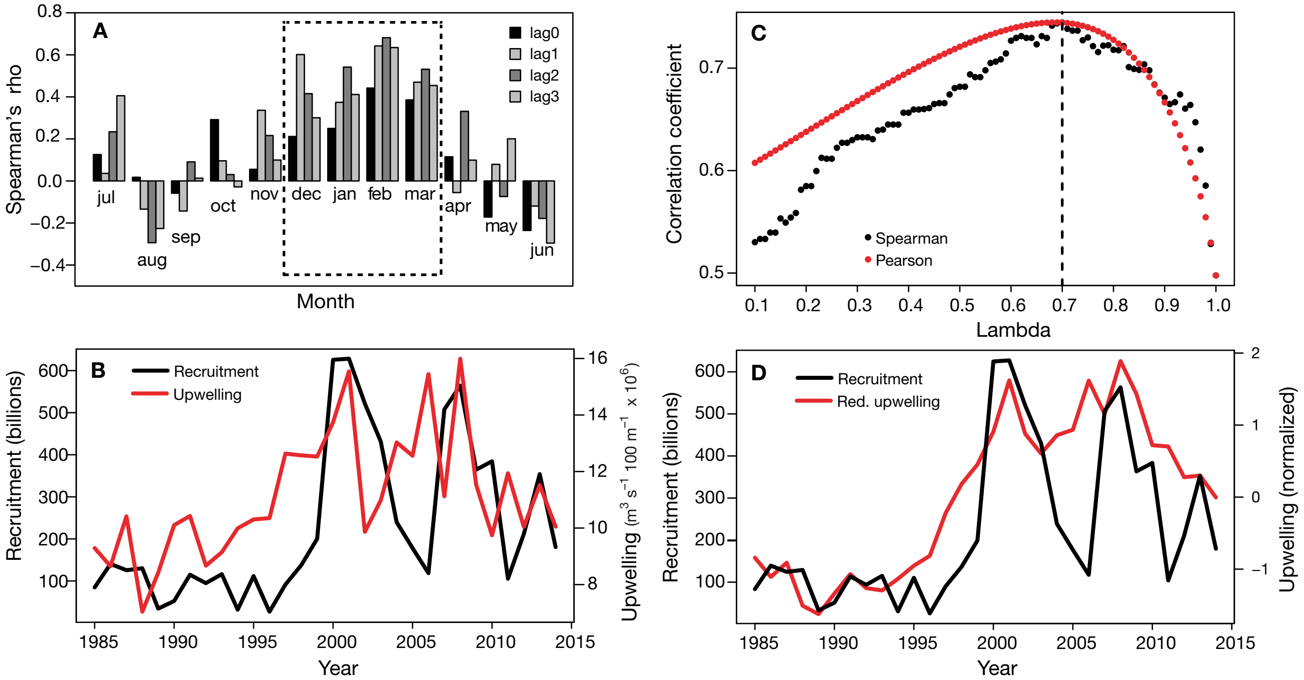

Fig. 2. (A) Spearman's rho values for linear correlations between Cape anchovy recruitment (in billions of individuals) and monthly coastal upwelling (total cumulative upwelling, in m^3 s^{-1} 100 m^{-1} × 10^6) from 1985 to 2014. In our analyses, the years run from July (previous year) to June (current year). Recruitment was correlated to monthly upwelling without a lag (lag0) as well as with a lag of 1 to 3 yr. (B) Anchovy recruitment and cumulative coastal upwelling from December to March at lag0 (R^2 = 0.24). These are the months of the year (in A) when correlations between anchovy recruitment and coastal upwelling peaks. (C) Spearman and Pearson correlation values for anchovy recruitment and reddened upwelling (using a λ of 0.1 to 1). (D) As in B, but using reddened upwelling (λ = 0.7) from December to March (R^2 = 0.55)

autocorrelation) and correlated each to the anchovy recruitment data. Those random upwelling series that correlated as strongly to anchovy recruitment as the original 'real' upwelling data were retained. These retained random upwelling series were reddened (adding $\lambda = 0.7$), and we recorded the extent to which the correlation with recruitment changed by adding extra autocorrelation. We choose this sub-setting because, logically, most of the 250 000 random series correlated only very weakly with anchovy recruitment, having a correlation coefficient close to zero. Adding autocorrelation (i.e. increasing low-frequency variability) can strongly increase their correlation with recruitment, but that is only because the initial correlation coefficient is low. Therefore, to properly differentiate between increased causality and method artifacts, we used only those random upwelling series that had an initial correlation coefficient similar to the 'real' upwelling index, and assessed how reddening affected their relationship with anchovy recruitment. If the increase in correlation that reddening provided is high (>95th percentile) in the observed upwelling data relative to that in the ensemble of simulated upwelling data, this would suggest that any increase in correlation in the observed upwelling data was not merely an artifact of the reddening procedure.

Lastly, the relationship between anchovy recruitment and upwelling is hypothesized to be nonstationary. To this end we used GAMs to examine whether relationships between upwelling and recruitment were better explained by linear or nonlinear equations, and tested for non-stationarity by comparing the results of a GAM to that of a nonadditive threshold model (TGAM; Ciannelli et al. 2004, Litzow & Ciannelli 2007). TGAMs assess whether the relationship between upwelling and recruitment changes at some level of a third 'threshold' variable; those tested here were calendar year and anchovy spawner biomass on the west coast (i.e. west of Cape Agulhas), south coast or total spawner biomass (west+south coast). The model can be formulated as:

$$\text{Recruitment}_t = \begin{cases} b_1 + f_1\,(\text{upwelling}_t) + \varepsilon_t & \text{if SSB}_{t-1} \leq th \\ b_2 + f_2\,(\text{upwelling}_t) + \varepsilon_t & \text{otherwise} \end{cases} \qquad (2)$$

where th is a threshold (here for spawner biomass, SSB) across which the upwelling function switches from f_1 to f_2 (with f as a nonparametric, smoothing function), with possible changes in the intercept as well (from b_1 to b_2);

ε is the error term (Ciannelli et al. 2004, Litzow & Ciannelli 2007). The TGAMs were run using unaltered upwelling and using reddened upwelling values. In the models, upwelling and recruitment data were sorted with respect to the threshold variable (spawner biomass or calendar year). One GAM was fit to the upwelling–recruitment relationship for all values below a given threshold value, and a second GAM was fit to the upwelling–recruitment relationship for all values above the given threshold value. This step was repeated for all threshold values between the lower 0.1 and the upper 0.9 quantiles of spawner biomass (in each region) and for each calendar year. The threshold value that minimized the generalized cross validation (GCV) of the whole model was selected. The GCV of a model is a proxy for the out-of-sample predictive mean squared error, where a model with lower GCV has more explanatory power and hence is preferred to a model with higher GCV. For all GAM and TGAM models, the probability distribution was 'Gaussian' and the link function was 'identity'.

Akaike's information criterion (AIC) and GCV are commonly used to select the best GAMs or TGAMs, but these metrics cannot be used to compare GAMs to TGAMS, as there is no obvious way to penalize for the extra threshold parameter. To compare the TGAM and GAM, we calculated the genuine cross-validatory squared prediction error (gCV) following Ciannelli et al. (2004). In this procedure, 1 data point was deleted and its value then predicted using a model (GAM or TGAM) fitted to all remaining data points. A square prediction error was then calculated between observed and predicted values, and the same routine was repeated sequentially for all data points. The mean of all squared prediction errors was the gCV. Thus, we first used the GCV to select the best GAM and TGAM, and then used the gCV for their comparison.

To assess if upwelling–recruitment correlations are driven by specific conditions in a few years, we estimated the relative importance of each data point in the correlation by calculating the 'difference in fits' (DFFITS; Belsley et al. 1980). In this calculation, 1 data point (calendar year) was dropped from the full dataset, and the change in correlation was calculated; the procedure was repeated for each data point (calendar year) in the time series, first for the unaltered upwelling data and then repeated for the reddened upwelling data. All analyses were performed in R (version 3.3.0; R Development Core Team 2008), using the mgcv package (Wood 2001) for the GAMs; the R-code for the TGAM and gCV was personally provided by L. Ciannelli.

RESULTS AND DISCUSSION

Anchovy recruitment and upwelling

The upwelling indices used here are calculations of monthly cumulative (positive) offshore Ekman transport (Lamont et al. 2017) and serve as a proxy for the amount of upwelled water lifted into the euphotic zone. Correlations between recruitment and monthly upwelling indices were significant ($p < 0.05$) and positive for the months February and March. These results are consistent with previous findings that the individual weight of anchovy recruits was positively correlated with January upwelling intensity off the west coast of South Africa (Skogen 2005). However, we also found strong correlations between current-year recruitment and upwelling in the previous year(s) over the period December to March (Fig. 2A). This suggests that recruitment may be affected by upwelling strength in the present as well as prior year(s). Corroborating this finding is the higher autocorrelation in the recruitment time series ($\lambda = 0.7$) than in the upwelling time series ($\lambda = 0.4$ for cumulative upwelling from December to March). Although anchovy have a near annual life cycle, our λ value would correspond to a life span (τ_{bio}) of 3.33 yr (Di Lorenzo & Ohman 2013). It is unclear as to which processes explain effects of prior upwelling on recruitment, although it is highly likely that feedbacks exist between recruitment in one year and that in the next via spawner biomass (i.e. a stock–recruitment relationship). For example, changes in the prey biomass available to parents or changes in the condition of spawners will determine the energy available to produce eggs and/or the amount of energy available per egg, which in turn may affect recruitment and adult biomass in the next year. These potential linkages are statistically evident: anchovy recruitment (measured in May–June) is closely related to total spawner biomass measured 6 mo later in October–November (Pearson's $r = 0.83$, $p < 0.001$ from 1985–2014), and adult biomass affects recruitment in the next year (Pearson's $r = 0.64$, $p < 0.001$). Thus, part of the anchovy population dynamics will likely be carried over from year to year, which may account for the effect of upwelling in prior years. This may be especially true for highly abnormal environmental (i.e. upwelling) conditions, which could have a legacy over several subsequent years.

To take the effects of upwelling in prior years into account, we induced autocorrelation in the upwelling index (for the months December to March). We found a peak in the strength of the upwelling–recruitment relationship when adding $\lambda = 0.7$ (Fig. 2C), with the correlation increasing from r = 0.49 (for unaltered upwelling) to r = 0.74 (for reddened upwelling). The reddening procedure acts to phase-shift the timing of the increase in upwelling to better match the increase observed in the anchovy recruitment record (Fig. 2B versus 2D). In fact, a reddened response of anchovy to environmental conditions appears to underlie the abrupt increase in recruitment at the start of the 2000s.

A better fit between reddened upwelling and recruitment (compare Fig. 2B and 2D) was most likely not an artifact of adding autocorrelation. Of the 250 000 randomly simulated upwelling time series, 5841 correlated similarly to anchovy recruitment as did the 'real' December–March upwelling index (r = 0.49; we selected those with r of 0.49 ± 0.05). An increase in r equal to or greater than that in the observed data (≥0.25) was only found in 184 of the 5841 random data series, giving an estimated probability of 0.03.

Threshold models

Although reddening the upwelling index improved the correlation with recruitment, 45 % of the variance in the relationship remained unexplained, part of which may be due to changes in the upwelling–recruitment relationship over time. For example, Boyd et al. (1998) found a strong inverse relationship between anchovy recruitment and average October–March southeasterly (SE) wind anomalies over 1985–1994, in contrast to the positive relationship suggested by the present study, and other global studies on anchovy (reviewed by Checkley et al. 2017). The negative relationship was thought to reflect an offshore displacement of the jet current by strong winds, which increased advective loss of anchovy eggs and larvae. However, these climate relationships did not persist over time: strong SE wind anomalies in 2000 and 2001 were associated with exceptionally high anchovy recruitment (van der Lingen & Huggett 2003). In a newer hypothesis, Roy et al. (2001) proposed that a succession of weak and intense upwelling periods appropriately timed within the anchovy life cycle maximizes anchovy recruitment success. That model reconciled previous findings, but cannot explain the high recruitment recorded for most years since 2000. Ultimately, the shift in such empirical relationships may be a consequence of variations in what are likely to be several factors affecting anchovy recruitment in the Benguela (van der Lingen & Huggett 2003).

We used TGAMs to include a single threshold parameter and address this issue of non-stationarity in the relationship between upwelling and recruitment (Ciannelli et al. 2004, Litzow & Ciannelli 2007). This analysis, however, did not provide any evidence that the nature of the upwelling–recruitment relationship had changed as a function of calendar year in the late 1990s, or at any other calendar year in the dataset (Table 1). Beyond calendar year, it is also possible that shifts in the upwelling–recruitment relationship, if present, are more closely related to anchovy spawner biomass. Thus, in a subsequent analysis, we tested for changes in the upwelling–recruitment relationship with respect to anchovy spawner biomass (of the previous year) on the west coast only, south coast only, and total biomass (west and south coasts combined). When using unaltered upwelling and anchovy recruitment, we did not find any evidence for threshold shifts (Table 1A). However, a clear threshold shift was identified when reddened upwelling was used, with recruitment being more sensitive to upwelling when biomass on the west coast reaches ~0.74 million t (Table 1B). Above and below this threshold the upwelling–recruitment relationships are still positive and linear (estimated df = 1; Table 1B), but have different slopes (Fig. 3A). By combining 2 simple linear relations into a single model, we were able to account for 82 % of the variability in anchovy recruitment from 1985 to 2014 (Fig. 3B).

Mechanisms for non-stationary relationships

We found a clear threshold shift in the upwelling–recruitment relationship with respect to anchovy spawning biomass on the west coast, but not with respect to south coast or total spawning biomass (Table 1). These findings are consistent with an individual-based model study (Huggett et al. 2003) showing that eggs spawned on the western Agulhas Bank (west of Cape Agulhas) are more successfully transported to the west coast nursery grounds (~30 % success) relative to spawning on the central Agulhas Bank or eastern Agulhas Bank (~10 and <5 % success, respectively). This is similar for sardine *Sardinops sagax*, in which 40 % of eggs spawned on the western Agulhas Bank were transported to the west coast nursery ground compared to <5 % for eggs spawned on the eastern Agulhas Bank (Miller et al. 2006). Thus, the present study further corroborates the importance of the west coast biomass to recruitment. Hence, a potential reason for a threshold in the

Table 1. Relationship between anchovy recruitment and (A) cumulative and (B) reddened upwelling from December to March. Non-additive threshold model (TGAM) analyses included thresholds for previous year spawning biomass (*th*, in million t) on the west coast, south coast, total biomass (west+south), or calendar year (1985–2014). GAM: generalized additive model; R^2: proportion of variance explained; gCV: genuine cross-validatory squared prediction error; AR: autocorrelation in model residuals, with 0 indicating its absence; SW: p-value of a Shapiro-Wilk normality test on model residuals; edf: estimated degrees of freedom, as a proxy for the shape of the relationship (edf = 1 for linear relationships and increasing values for progressively more nonlinear relationships); n: number of observations. The model with the lowest gCV is indicated by bold-face

Threshold variable	Model	*th*	R^2	gCV	AR	SW	Predictor	*F*	edf	p	n
(A) Anchovy recruitment ~ upwelling (December–March)											
None	**GAM**	**–**	**0.22**	**39199**	**0.37**	**0.15**	**Upwelling**	**8.987**	**1**	**0.006**	**30**
Biomass west	TGAM	1.88	0.81	101625	0	0.55	Upwelling ≤ *th*	8.820	8.55	<0.001	25
							Upwelling > *th*	3.905	3.78	0.017	5
Biomass south	TGAM	2.39	0.77	3762217	0	0.16	Upwelling ≤ *th*	8.561	7.69	<0.001	26
							Upwelling > *th*	3.970	2.85	0.0261	4
Biomass total	TGAM	3.60	0.83	846504	0	0.12	Upwelling ≤ *th*	10.71	8.62	<0.001	25
							Upwelling > *th*	3.236	3.84	0.039	5
Calendar year	TGAM	2001	0.97	62240	−0.28	0.007	Upwelling ≤ *th*	56.73	7.90	<0.001	17
							Upwelling > *th*	29.35	8.87	<0.001	13
(B) Anchovy recruitment ~ reddened upwelling (December–March)											
None	GAM	–	0.53	19348	0.29	0.99	Upwelling	33.91	1	<0.001	30
Biomass west	**TGAM**	**0.74**	**0.82**	**11249**	**0**	**0.38**	**Upwelling ≤ *th***	**7.65**	**1**	**0.01**	**15**
							Upwelling > *th*	**78.5**	**1**	**<0.001**	**15**
Biomass south	TGAM	2.41	0.57	$>10^8$	0	0.87	Upwelling ≤ *th*	24.0	1	<0.001	27
							Upwelling > *th*	6.84	1	0.01	3
Biomass total	TGAM	3.60	0.62	27001	0	0.20	Upwelling ≤ *th*	24.0	1	<0.001	25
							Upwelling > *th*	7.66	1	0.01	5
Calendar year	TGAM	2003	0.69	42529	0	0.54	Upwelling ≤ *th*	13.63	3.614	<0.001	19
							Upwelling > *th*	3.68	1	0.067	11

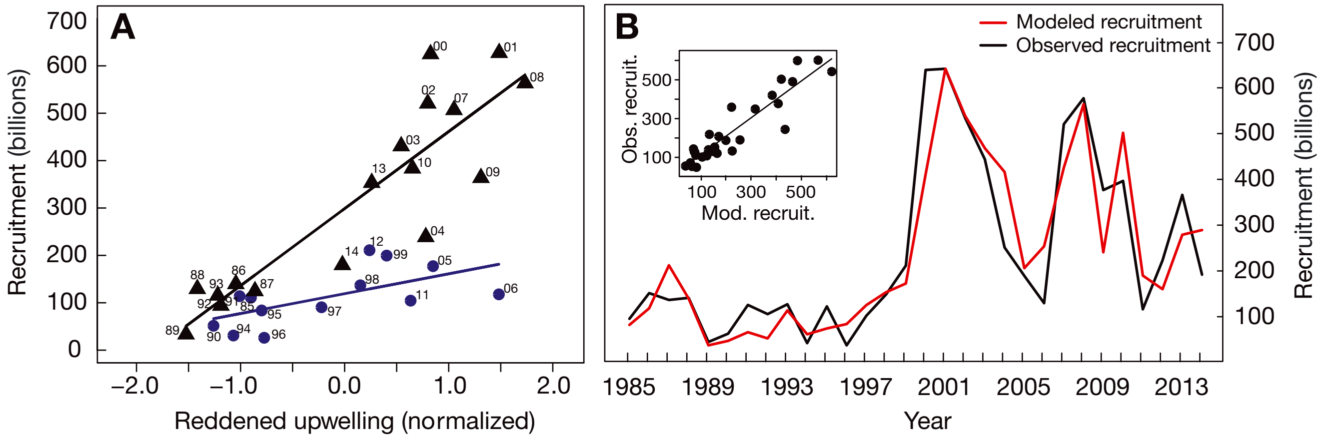

Fig. 3. (A) Two linear upwelling–recruitment relationships identified in the non-additive threshold model (TGAM) with the lowest genuine cross-validatory squared prediction error (gCV). The calendar year of each recruitment data point is labeled. The threshold at which the relationship between upwelling and anchovy recruitment changes function is when spawner biomass on the west coast in the preceding year reaches ~0.74 million t (circles indicate data points below threshold; triangles those above threshold). Note that reddened upwelling was normalized once before the analysis (i.e. upwelling is on the same scale below and above the threshold). (B) The 2 relationships identified in the TGAM (in panel A) were combined in a single model (red line), which accounts for 82% of the variability in the observed recruitment (black line). Inset shows correlation between modeled and observed anchovy recruitment

upwelling–recruitment relationship is that high west coast anchovy biomass means more eggs are spawned in a location with relatively effective transport to nursery habitats, leading to greater recruitment the following year. In contrast, relatively few eggs are spawned by this portion of the stock in low biomass years, leading to relatively low recruitment. Thus, over a given range of upwelling intensity, there is greater recruitment when spawning biomass west of Cape Agulhas is high, as has been identified by 2 independent models (Fig. 3A). This threshold effect is likely accentuated by a series of very low and then very high biomass events characteristic of this time series, as well as the general absence of 'average' biomass years.

Previous studies have hypothesized a 'regime' shift in anchovy recruitment beginning in the late 1990s (Cury & Shannon 2004, van der Lingen et al. 2006). Indeed, a transition from relatively low mean and variance in recruitment to relatively high mean and variance in recruitment appears to have occurred around the year 2000 (Figs. 1–3). Although our TGAM analysis did not identify a change in the nature of the upwelling–recruitment relationship with respect to calendar year (Table 1), it did indicate a transition, with the explanatory power of our recruitment model lower pre-2000 (R^2 = 0.47) than post-2000 (R^2 = 0.69) (Fig. 4). A possible reason could be that the efficiency of transport from spawning to nursery areas was much more important to recruitment strength prior to 2000 (as found in previous studies), after which upwelling intensity and primary productivity became more important. However, the difference in explanatory power could also be an artifact of the low variance prior to the year 2000 and that leverage in the extremes drive the relationship between observed and modeled recruitment (Fig. 4). Yet the dramatic difference in the ability of upwelling to predict recruitment prior to 2000 suggests that a regime shift in the late 1990s may be affecting recruitment in addition to the thresholds identified in west coast biomass.

Management implications

The results of this analysis have potential utility for incorporation into management of South Africa's anchovy fishery since they potentially provide early insight into expected anchovy recruitment strength. The anchovy fishery primarily harvests anchovy recruits between April and September, but survey estimates of recruitment strength only become available in June–July of that year, which is too late for the fishery to take full advantage of the availability of anchovy recruits on the west coast. Therefore, in the absence of further information at the start of the season (January), an initial total allowable catch (TAC) for anchovy is calculated based on a fixed proportion of the observed anchovy total biomass in the preceding year and assuming average recruitment will occur. To guard against possible poor recruitment, this initial TAC is scaled down by a factor of 0.85 (de Moor et al. 2011). The initial TAC is then revised to a final TAC mid-year (July) using estimates of recruitment as observed during the annual pelagic recruitment survey (May–June).

A survey observation of anchovy biomass west of Cape Agulhas in the preceding year that is above/below the 0.74 million t threshold level could allow for a less/more conservative scale-down factor when setting the initial TACs. In addition, calculating the

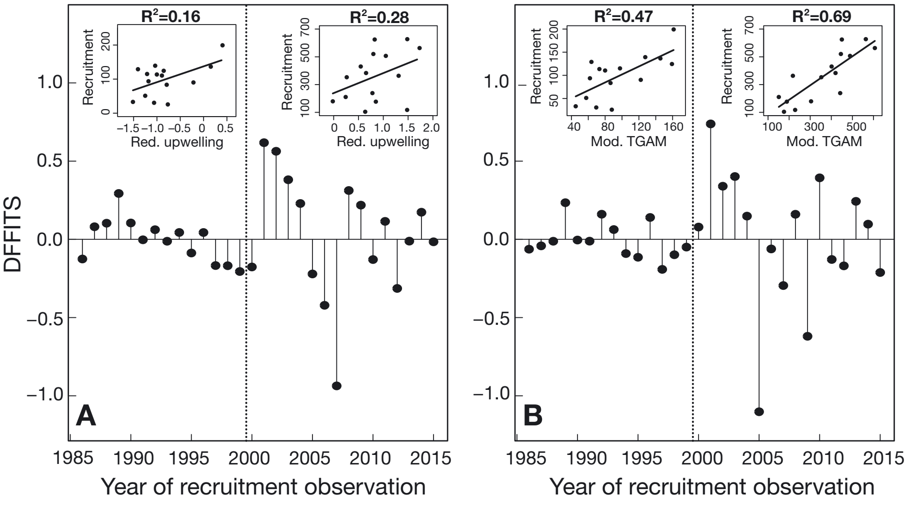

Fig. 4. Difference in fits (DFFITS) values were calculated to illustrate the influence of each point (calendar year) in the relationship between (A) anchovy recruitment and reddened upwelling and (B) anchovy recruitment and the model based on the TGAM with a threshold based on anchovy spawner biomass along the west coast in the previous year (Fig. 3, Table 1B). Low absolute values indicate small leverage, whereas high values indicate high leverage and influence. Insets show correlation plots for the relationship examined before (1985–1999) and after (2000–2014) the increase in mean and variance of anchovy recruitment

cumulative upwelling during December to March and using the relationships described in this study could allow for a prediction of forthcoming recruitment in early April already, 2 to 3 mo before the final TAC is routinely set. This could increase average annual catch, possibly substantially, without increasing risk (Cochrane & Starfield 1992). De Oliveira & Butterworth (2005) used simulations to investigate the benefits of using environmental indicators to set appropriate TACs for anchovy, and suggested that such indices needed to explain 50% or more of the total variation in anchovy recruitment in order to show benefit in terms of risk and/or average catch for management procedures then in use. Our analyses satisfy this level of explanatory power by some margin, and whereas the management procedures now used for anchovy have changed (albeit to no great degree) over the past decade, we suggest that the approach outlined could be beneficial if incorporated into management. This is particularly relevant given that one of the factors contributing to a substantial under-catch of the South African anchovy TAC in recent years has been a large difference in initial and final TACs and the inability of the fishery to catch this whilst anchovy recruits are still available off the west coast (Department of Agriculture Forestry and Fisheries 2014).

In summary, considering the effects of upwelling over multiple spawning seasons strengthens the upwelling–recruitment relationship. The novel significance test we developed showed that this strengthening was above levels that could be considered an artifact of adding autocorrelation. Furthermore, only when accounting for upwelling over multiple spawning seasons were we able to identify a clear threshold in the upwelling–recruitment relationship, which increased model explanatory power to 82% and suggested that drivers of recruitment may be non-stationary. This non-stationarity in the upwelling–recruitment relationship could relate to changes in the number of eggs spawned or to alterations in survival of larvae. The power to test these potential mechanisms is limited. Yet, this potential non-stationarity, as well as the effects of upwelling in prior years deserve future research attention as it could have important implications for the management of anchovy in South Africa.

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