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REGIME SHIFTS IN THE WESTERN AND CENTRAL PACIFIC OCEAN

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Oceanographic regime shifts and tuna recruitment in the western and central Pacific Ocean

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ABSTRACT: This analysis aims to establish whether the ‘regime shifts’ documented for the north Pacific Ocean are seen in the western and central Pacific Ocean (WCPO) and are relevant to recruitment variation for tropical tunas. Quantitative indicators of oceanographic state are derived by multivariate analysis of physical and biological variables output from an ocean general circulation and biogeochemical model. Tests are applied to determine the existence of statistically significant regime shifts in time series of both ecosystem indicators and tuna recruitment estimates. Shifts are found at times that are broadly consistent with other studies for the north Pacific (1976, 1989, 1998) although earlier shifts (ca. 1964) appear to be just as significant. The methods are sound for the purposes of oceanographic monitoring and analysis but are inadequate to build causal or predictive relationships between the ocean environment and tuna recruitment. Other statistical models have proved useful in that regard and the best single indicator for monitoring the effect of long-term environmental variability on yellowfin tuna recruitment appears to be the area of the western Pacific warm pool.

Kirby et al.: Regime shifts and recruitment

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1. INTRODUCTION

The literature on regime shifts is dominated by studies on the North Pacific, with changes in the phase of the Pacific Decadal Oscillation (PDO) – the leading principal component of monthly sea surface temperature (Mantua et al. 1997) – being related to various marine populations (Mantua et al. 1997, Francis et al. 1998, Anderson & Piatt 1999, Beamish et al. 1999, Hare & Mantua 2000, Benson & Trites 2002, Mantua & Hare 2002). In the Western and Central Pacific Ocean (WCPO) El Niño Southern Oscillation (ENSO) events on inter-annual scales are the dominant mode of variability. ENSO affects WCPO tuna fisheries by eastward expansion of the western Pacific warm pool during El Niño and contraction, generally westwards, during La Niña (Picaut et al. 1996). The zonal distribution of tropical tuna fisheries also follows this pattern (Lehodey et al. 1997).

While ENSO and PDO patterns are clearly related (see Fig. 4), PDO phases seem to last for 20–30 yr, with some interannual variability, while ENSO events tend to last for only 6–18 mo, with high monthly variability in indicators such as Southern Oscillation Index (SOI). ENSO effects, in terms of sea-surface temperature variability, are greatest across the tropical/sub-tropical Pacific; the PDO is greatest in the North Pacific, has only a weak signal in the western tropical Pacific, but is also strong in the subtropical south Pacific and in the central and eastern tropical Pacific (Mantua & Hare 2002).

The ‘regime shift’ concept has been well discussed (Cushing 1982, Steele 1996, 1998, Beamish et al. 1999, Harris & Steele 2004) although the term has had no agreed definition. deYoung et al. (2004) defined a regime shift as ‘...an abrupt change from a quantifiable ecosystem state’ with the qualification that ‘The determination of ecosystem state remains an unresolved, and imprecise, oceanographic problem’. The emerging consensus is to clearly define the context, e.g. climate/ecosystem/recruitment regime shift (Overland et al. 2006). This paper is therefore concerned with oceanographic regime shifts as they relate to shifts in tuna recruitment and climate indices.

The motivation for the study came from uncertainty in the interpretation of stock assessment results, which showed apparent shifts in recruitment estimates that could be due either to real oceanographic change impacting on survival of pre-recruits, or to the assessment model misinterpreting catches of small fish in purse seine fisheries that started during the assessment period. This paper therefore analyses the inputs to and output from a generalised linear model (GLM) developed to predict tuna recruitment variation in response to oceanographic variables.

There are a number of methods available for the detection of long-term variability and shifts in time series characteristic of ocean ecosystems (see Mantua 2004). Multivariate methods may be useful for considering ecosystems as a whole, as they can allow the integration of many variables into a reduced set of dimensions. These can function as indicators of ecosystem state, which in turn may be analysed by univariate methods, e.g. for shift detection. This study uses principal components analysis (PCA) to derive quantitative indicators of ecosystem state (PC scores) from physical and biological oceanographic variables for 4 different areas of the WCPO. The variables and areas are selected based on their relevance to the tuna recruitment GLMs. A test is then applied to determine the existence of regime shifts in the mean and variance of these indicators, and correlations with basin and regional scale climate indices are determined.

2. METHODS

2.1 Study area

The study was carried out for the equatorial western and central Pacific Ocean (WCPO) (125°E–170°W; 20°N–10°S) corresponding to assumed spawning and feeding habitat for the tropical tunas. This area encompasses a large part of the western Pacific warm pool and cold tongue system (Fig. 1a). Four sub-areas were investigated (Fig. 1b), having been selected by a generalised linear model (GLM) that uses oceanographic variables to predict recruitment for yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*Thunnus obesus*) (Langley et al. in press; see 2.3 below).

2.2 Datasets

Initial selection of environmental variables (Table 1) was based on a general understanding of environmental variability and fish early life history; final selection (Table 2) was according to their significance in a statistical model of tuna recruitment (see 2.3 below). The environmental data come from two sources. Firstly, surface ocean current vectors and temperature fields were generated using a physical ocean general circulation model (OGCM); a biogeochemical NPZD (nutrients-phyto-zooplankton-detritus) model was then run to compute primary production (Christian et al. 2002a,b; Christian & Murtugudde 2003). The resolution of these environmental data fields are 30 d and 1°×1°. Temperature, east-west current component, north-south current component (averaged over 0–100 m depth) and primary production (averaged over 0–400 m depth) were available for the 1948–2004 period. Secondly, wind data were obtained from the NCEP/NCAR Reanalysis provided by NOAA Earth System Research Laboratory³. The *u* and *v* wind components at 10 m height were obtained at 2.5°×2.5° resolution. In addition, 2 composite variables were derived: annual average wind direction was calculated by unit vector averaging, and an index of turbulence was calculated assuming that turbulent kinetic energy is proportional to absolute wind speed cubed (Niller & Kraus 1977).

2.3 Data analysis

Generalised linear model (GLM)

The GLM methodology and results are described in detail in a companion paper (Langley et al. in press). Briefly, yellowfin and bigeye recruitment estimates were obtained from stock assessments using the MULTIFAN-CL model (MFCL: Fournier et al. 1998). GLMs relating these estimates to oceanographic variables were constructed for the period 1980–2003, for which bigeye and yellowfin MFCL recruitment estimates are considered reliable. The GLMs were then hindcast for the period 1948–1980. The most informative spatial scale selected by the model for both yellowfin and bigeye tuna was 10° latitude × 30° longitude, with zero time lag, i.e. the quarter during spawning. However, the most informative zones selected by the models differ between the species (Fig. 1b). The GLM for bigeye predicted 4 out of range values during 1952–1961 due to values of some oceanographic variables being beyond the range observed during the model building period. For the purpose of this paper, these outliers were substituted with the average recruitment for the same quarter in the preceding and following years.

³ www.cdc.noaa.gov/cdc/data.ncep.reanalysis.derived.surface.html

Principal components analysis (PCA)

Principal components analysis (PCA) was used to analyse the temporal variability of the ten most influential oceanographic variables selected by the GLM for the different zones (Table 2). PCA is particularly well suited for multivariate datasets, as it reduces dimensionality to a small number of uncorrelated and possibly meaningful time series of PC scores and loading vectors (see Hare & Mantua 2000, Mantua 2004). The analysis was performed on the environmental data in order to detect the predominant patterns of temporal variability within the selected zones over the period 1948–2004.

Loading vectors show the extent to which the original variables are related to each of the PCs (Tables 3 & 4). A number of PCs are identified and there are several ways to discern their significance. Scree plots (Figs. 2 & 3) rank the PCs by the variance for which they account (x -axis) and their eigenvalues (y -axis); if the latter are <1 that PC may be discarded (Norman & Streiner 1994). The temporal variability of the significant PC scores can then be characterised and tests applied to detect statistically significant shifts.

Sequential t -test analysis of regime shifts (STARS)

Sequential t -test analysis of regime shifts (STARS; Rodionov 2004) was applied to investigate possible regimes shifts in PC scores and in recruitment time series. The test detects discontinuities in the mean of each time series using two main parameters: the probability level represents the level at which the null hypothesis (that the mean values of the two regimes are equal) is rejected by the two-tailed Student test. The cut-off length determines the minimum length of the regimes that will be detected and is similar to the cut-off point in low pass filtering. The significance level was set at $p = 0.2$ and the cut-off length defined to 10 yr for all series, because of the strong interannual variability.

As the existence of strong autocorrelation in the time series can lead to an increased number of incorrectly identified regime shifts, we first performed a so-called ‘pre-whitening’ procedure on the PC scores (Rodionov 2006) to remove ‘red noise’, i.e. apparent long-period variability that is actually induced by cumulative short-period variability. The sequential t -test was then performed on the filtered time series.

Regime shifts in the variance of PC scores was also investigated, to corroborate the shifts found in the mean. The procedure is similar to that used for shifts in the mean, except that it is based on the F -test instead of the t -test (Rodionov 2005).

Correlation analysis

The relationship between PC scores, recruitment estimates and climate indices (SOI, PDO) was investigated by linear correlation. In addition, because the areas selected by the GLM for yellowfin recruitment include the northern and eastern boundaries of the western Pacific warm pool (Fig. 1), the correlation between tuna recruitment and warm pool area was also investigated.

3. RESULTS

3.1 Areas 1 & 2

PCA results for variables selected by the GLM for yellowfin from Areas 1 & 2 (Fig. 1b) are presented in Fig. 2 and Table 3. There are 4 significant principal components (PCs; Fig. 2a): PC1 accounts for 34.18% of the total variance, PC2 for 19.44%, PC3 for 14.94% and PC4 for 11.41%. The most influential variables in the GLM *Currentavg1* and *Tempavg1* are well represented on PC1 (Table 3) with similarly high loadings, which means that their temporal variability is similar and follows the trend of PC1. *Currentvrage2* and *Currenturage2* are also well represented on PC1 and closely related to each other; however, their loadings are negative indicating that their temporal trend has the opposite sign to the PC score itself. *Windvavg2* and *Currentvavg2* are well represented on PC2 but inversely related to each other; while both variables therefore follow the PC2 trend, *Currentvavg2* has the opposite sign. *PPavg1* has a strong, positive loading on PC3 and a smaller positive loading on PC2. *Tempavg2* is best represented on PCs 1 & 3 while *Temprange1* and *Turbulence1* are best represented on PC4.

The temporal trends of the PCs and possible regime shifts, as detected using STARS analysis, are illustrated in Fig. 2b. PC1 has two main shifts (1964 & 2001) with a succession of three regimes, with a strong negative phase, a strong positive phase and a neutral phase; the same shifts are detected in the variance (not shown). For PC2, two main shifts in the mean were detected, in 1989 & 1998. The time series is less obviously structured than PC1 and shows rapid changes from positive to negative phase within some of the regimes described. The biggest shift is found in 1998, where PC2 changes abruptly from a strong positive phase to a negative phase. This is followed by a shift in the variance in 1999 (not shown). PC 3 shows two positive shifts in the mean, for 1977 and 2002, and 3 shifts in the variance (1958, 1969 and 2002; not shown). PC4 has a positive shift in 1957 and a negative shift in 1964, after which there is little structure to the variability. There is also a shift in the variance for 1964 (not shown).

STARS analysis on yellowfin recruitment estimated by the GLM (Fig. 4a) finds the same two shifts in both recruitment and PC1, i.e. an increase in 1965 and a decrease in 2002. Recruitment is also strongly correlated with PC1 ($R^2 = 58\%$). There are 2 other shifts in recruitment, a small decrease in 1957 and a small increase in 1976, that coincide with positive shifts in PC4 and PC3 respectively, and a small decrease in 1991 that does not coincide with shifts in any of the PCs.

The correlation between warm pool area and yellowfin tuna recruitment was strongest between annual recruitment and the annual mean area enclosed by the >28.5 degrees isotherm ($R^2 = 52\%$), or the mean area enclosed by the >28.0 degrees isotherm from November through March ($R^2 = 45\%$). There is no significant correlation between PC1, PC2 or PC4 and SOI or PDO, though PC3 is strongly correlated to both climate indices ($R^2 = 39\%$). Two of the same positive shifts (1965 & 1976) are found in warm pool area and yellowfin recruitment (Fig. 4 c) and the negative shift in warm pool area in 1999 is followed by a negative shift in recruitment in 2002.

3.2 Areas 3 & 4

PCA results for variables selected by the GLM for bigeye from Areas 3 & 4 (Fig. 1b) are presented in Fig. 3 and Table 4. There are 3 significant principal components (PCs; Fig. 3a): PC1 accounts for 46.23% of the total temporal variance, PC2 for 18.00% and PC3 for 13.49%. *Tempavg3* and *Tempavg4* have very high positive loadings on PC1. This indicates that temperature in both zones has the same temporal trend and follows the temporal projection of PC1. The variables *Currentvrangle4*, *Turbulence4* and *Currenturange3* are well represented on PC1 but with negative loadings. These variables therefore follow the same temporal pattern but in the opposite sense as PC1. *PPavg3* and *Currentdir3* are strongly associated with PC2 with high negative loadings. *Windvavg3* is also well represented on PC2, but with positive loadings. *Windvavg4* is strongly represented on PC3, but also has a fairly strong positive loading on PC1. *Tempvrangle3* is a highly significant variable in the GLM but is not strongly represented on any single PC, but rather it is evenly loaded between PCs 1 & 3, and to a lesser extent PC2.

The temporal trends of the PCs and possible regime shifts, as detected using STARS analysis, are illustrated in Fig. 3b. PC1 has 2 main shifts (1963 & 1976), with a strong negative phase, followed by a moderate negative or neutral phase, and finally a high positive phase from 1976 onwards. There is also a shift in the variance in 1963 (not shown). PC2 shows higher interannual variability than PC1, and also has 2 regime shifts, in 1983 & 1998. The time series starts with a moderately positive phase, shifts to a moderately negative phase in 1983 and ends with a more pronounced negative phase from 1998, after a strong positive score for 1997. A shift in the variance of PC2 is also detected in 1997. PC3 has little temporal structure other than a positive shift in 1999, which is preceded by a shift in the variance in 1998 (not shown). PC3 also records a shift in the variance in 1959 (not shown), with no matching shift in the mean.

Over the whole series, bigeye GLM recruitment estimates show only 2 shifts with 3 distinct phases. Recruitment starts relatively high, showing a slight decrease in 1959 before remaining relatively stable over 3 decades (1960s, 1970s, 1980s); it then almost doubles in 1994 and remains at a high level until the end of the series. None of these shifts are coincident with shifts in PC scores.

The recruitment time series is not well correlated with any of the PCs (PC1: $R^2 = 11\%$; PC2: $R^2 = 5\%$), there was little correlation between bigeye recruitment and PDO ($R^2 = 10\%$) and none with SOI. There was no correlation between bigeye recruitment and warm pool area. There is quite strong correlation between PC1 and the PDO ($R^2 = 50\%$) and between PC1 and SOI ($R^2 = 37\%$). However, only a slight correlation is detected between PC2 and SOI ($R^2 = 13\%$) and no correlation is found with the PDO. PC3 is slightly correlated with SOI ($R^2 = 23\%$) but less so with PDO ($R^2 = 10\%$).

4. Discussion

4.1 Areas 1 & 2

The shifts found in 1989 and 1998 in PC2 are consistent with the shifts described by Hare & Mantua (2000), Benson & Trites (2002) and Peterson & Schwing (2003) in the North Pacific Ocean. The 1989 shift is strongest for *Windvavg2* and *Currentvavg2*. There is a modest biological response in *PPavg1*, though this variable is best described by PC3 and correlated to the PDO or SOI.

No significant correlation was found between yellowfin recruitment and SOI or PDO. These climate indices shift in 1976 (Fig. 4d,e) but there is no corresponding shift in the physical variables that are strongest on PCs 1 & 2. However, the shift in 1976 for PC3, *PPavg1*, yellowfin recruitment and warm pool area coincides with the shift in SOI and PDO, and with the shift in the North Pacific (Beamish et al. 1999, Hare & Mantua 2000, Benson & Trites 2002, Mantua 2004).

The correlation between warm pool area and yellowfin tuna recruitment is significant and strong. Warm pool area is a good indicator of decadal scale recruitment variability, but it does not capture interannual or seasonal variability. However, it is probably the best single indicator for monitoring or predicting the long-term effect of environmental variability on yellowfin recruitment, accounting for as much variance as the first 4 variables selected by the GLM (*Tempavg1*, *Currentuavg1*, *PPavg1*, *Turbulencel*).

4.2. Areas 3 & 4

The regime shifts in PC1 are well pronounced, and the shift in 1976 corresponds to the regime shift observed for the North Pacific. The variables most affected by this shift are *Tempavg3*, *Tempavg4*, *Turbulence4*, *Currentvrange4*, and *Currenturange3*. There are no shifts in 1989 but there is a strong shift in PCs 2 & 3 in 1998/9, affecting *PPavg3* and zonal wind *Windvavg4* respectively.

The shift for PC1 in 1963 has approximately the same timing as those recorded in Fig. 2b for PCs 1 & 4 (1964) and for warm pool area (Fig. 4c). A shift at this time has not previously been reported and may be worthy of further investigation.

The timing of shifts in bigeye recruitment does not correspond to shifts found in PCs for the environmental data. Indeed the small shift in recruitment 1959 could be induced by the out of range values predicted by the GLM around this time, or from our method of substituting for obvious outliers.

4.3. General conclusions

In this paper we have objectively analysed decadal scale variability of oceanographic variables for the WCPO and successfully identified shifts in low-dimensional, multivariate indicators of ecosystem state. The combination of PCA and STARS is a good way of objectively classifying environmental variability and is a great improvement on less rigorous or subjective methods. It is still possible to vary the parameters of the regime shift test to make it more or less sensitive, thus generating more or less shifts, but we have deliberately held those parameters constant in this analysis to only detect decadal scale change. The pre-whitening procedure (Rodionov 2006) also

allows confidence that apparent variability is real and regime shifts significant. However, without more comprehensive in situ data it is still not conclusive that these oceanographic regime shifts also constitute regime shifts in ecosystem structure and function. Furthermore, the selection of oceanographic variables and scale/area definition was based upon their significance in predicting tuna recruitment. An alternative approach to determine the existence of regime shifts in the WCPO, regardless of their role in tuna recruitment, could select variables at certain scales and from certain areas based on their regime shift signal strength, i.e. the degree to which they exhibited bi-modal behaviour.

It is important also to recognise that climate variability signals such as the PDO are based only on surface quantities such as SST, whereas the ocean almost certainly has a response in subsurface fields such as thermocline depth. While the eastern Pacific is known for its SST and thermocline signal (Guilderson & Schrag 1998, McPhaden & Zhang 2004), the western Pacific has no significant spatial loading in the PDO pattern but is known for its response to ENSO events in terms of primary and new production variations (Turk et al. 2001). Recall that the surface variables used here are integrated over the top 100 m and may therefore not be sufficient to detect changes at depth.

The results reported here for the WCPO are broadly consistent with other studies of regime shifts in the north Pacific but it is obvious that even where the timing of such shifts is similar to those identified in other studies (e.g. Areas 1 & 2: 1989 & 1998 in PC2, Fig. 2; Areas 3 & 4: 1976 & 1998 in PC1 and PC2 respectively, Fig. 3) the effects are not equally strong for all variables and the predominant modes of environmental variability are not necessarily those that are most influential for tuna recruitment. In the western equatorial Pacific (Areas 1 & 2) it appears that there is only a small signal of a 1976 regime shift in primary production, while shifts in wind and currents are evident in 1989 and 1998. Yellowfin tuna recruitment does apparently respond to these shifts, though the 1965 shift in warm pool area appears to have a stronger effect. There is a strong shift in the physical variables of the central equatorial Pacific (Areas 3 & 4) in 1976, and a strong shift in current direction and primary production in 1998. Bigeye tuna recruitment does not appear to be directly affected by these shifts and the role of oceanographic variability, while clearly being important, given the explanatory power of the final GLM ($R^2 = 76\%$; Table 2), is obviously more complex than the analysis here, and the regime shift concept more generally, can capture.

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Table 1. Summary of oceanographic data and sources and a description of composite variables used in building the GLM.

Attribute	Description	Units	Source
<i>tempavg</i>	Mean sea temperature within 0–100 m depth	°C	ESSIC
<i>temprange</i>	Range in sea temperature within 0–100 m depth.	°C	
<i>currentuavg</i>	Mean zonal (E-W) current velocity within 0–100 m depth.	ms ⁻¹	ESSIC
<i>currentrange</i>	Range in zonal current velocity within 0–100 m depth.	ms ⁻¹	
<i>currentvavg</i>	Mean meridional (N-S) current velocity within 0–100 m depth.	ms ⁻¹	ESSIC
<i>currentvrange</i>	Range in meridional current velocity within 0–100 m depth.	ms ⁻¹	
<i>currentdir</i>	Current direction	quadrant	ESSIC
<i>ppavg</i>	Mean primary production within 0–400 m depth.	mmol m ² day ¹	ESSIC
<i>winduavg</i>	Mean zonal (E-W) wind at 10 m altitude	m s ⁻¹	NCEP
<i>windvavg</i>	Mean meridional (N-S) wind at 10 m altitude	m s ⁻¹	NCEP
<i>turbulence</i>	Index of turbulent kinetic energy –wind speed cubed	m ³ s ⁻³	NCEP

Table 2. Environmental variables successively selected in the final GLM for each species (YFT: yellowfin tuna; BET: bigeye tuna) along with overall R^2 as each variable was added (see Langley et al. in press). See Table 1. for description of variables; number suffix refers to area (see Fig. 1).

Variables YFT	R^2	Variables BET	R^2
<i>Tempavg1</i>	0.16	<i>Tempavg3</i>	0.08
+ <i>Currentuavg1</i>	0.26	+ <i>Temprange3</i>	0.42
+ <i>PPavg1</i>	0.32	+ <i>Tempavg4</i>	0.50
+ <i>Turbulence1</i>	0.35	+ <i>Currentvrage4</i>	0.57
+ <i>Currentvrage2</i>	0.41	+ <i>Currenturange3</i>	0.63
+ <i>Temprange1</i>	0.47	+ <i>Windvavg3</i>	0.68
+ <i>Currenturange2</i>	0.52	+ <i>PPavg3</i>	0.71
+ <i>Currentvavg2</i>	0.59	+ <i>Currentdir3</i>	0.73
+ <i>Windvavg2</i>	0.65	+ <i>Windvavg4</i>	0.75
+ <i>Tempavg2</i>	0.68	+ <i>Turbulence4</i>	0.76

Table 3. Areas 1 & 2: loadings for environmental variables on each of the significant principal components (PC)

Variable	PC1	PC2	PC3	PC4
Tempavg1	0.83	-0.29	-0.29	0.10
Temprange1	0.47	-0.33	0.16	0.51
Currentavg1	0.85	-0.17	-0.20	0.08
PPavg1	0.04	0.43	0.84	0.06
Turbulence1	-0.15	0.27	-0.09	-0.67
Tempavg2	0.60	0.38	0.57	0.10
Currentvavg2	-0.06	-0.79	0.45	-0.21
Windvavg2	-0.05	0.78	-0.32	0.38
Currenturange2	-0.83	-0.29	0.04	0.33
Currentvrage2	-0.87	-0.10	0.01	0.31

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Table 4. Areas 3 & 4: loadings for environmental variables on each of the significant principal components (PC)

Variables	PC1	PC2	PC3
Tempavg3	0.95	-0.07	-0.19
Temprange3	-0.48	0.27	-0.52
PPavg3	-0.26	-0.84	0.35
Windvavg3	-0.57	0.57	0.37
Currentrange3	-0.67	-0.13	-0.04
Currentdir3	0.14	-0.78	-0.30
Tempavg4	0.96	0.10	-0.13
Windvavg4	0.43	-0.07	0.76
Turbulence4	-0.90	-0.24	-0.22
Currentvrange4	-0.84	-0.05	0.18

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Fig. 1. Map of the study area showing (a) annual mean sea surface temperature and location of the warm pool-cold tongue system in the western equatorial Pacific. (b) Spatial stratification used in the final GLMs for yellowfin and bigeye tuna recruitment (Langley et al. in press). Light dashed lines represent the different areas explored by the GLM. Areas 1–4 were the most informative areas and resolution (10° latitude \times 30° longitude) used in the final GLM for yellowfin (bold dashed line) and bigeye (solid line).

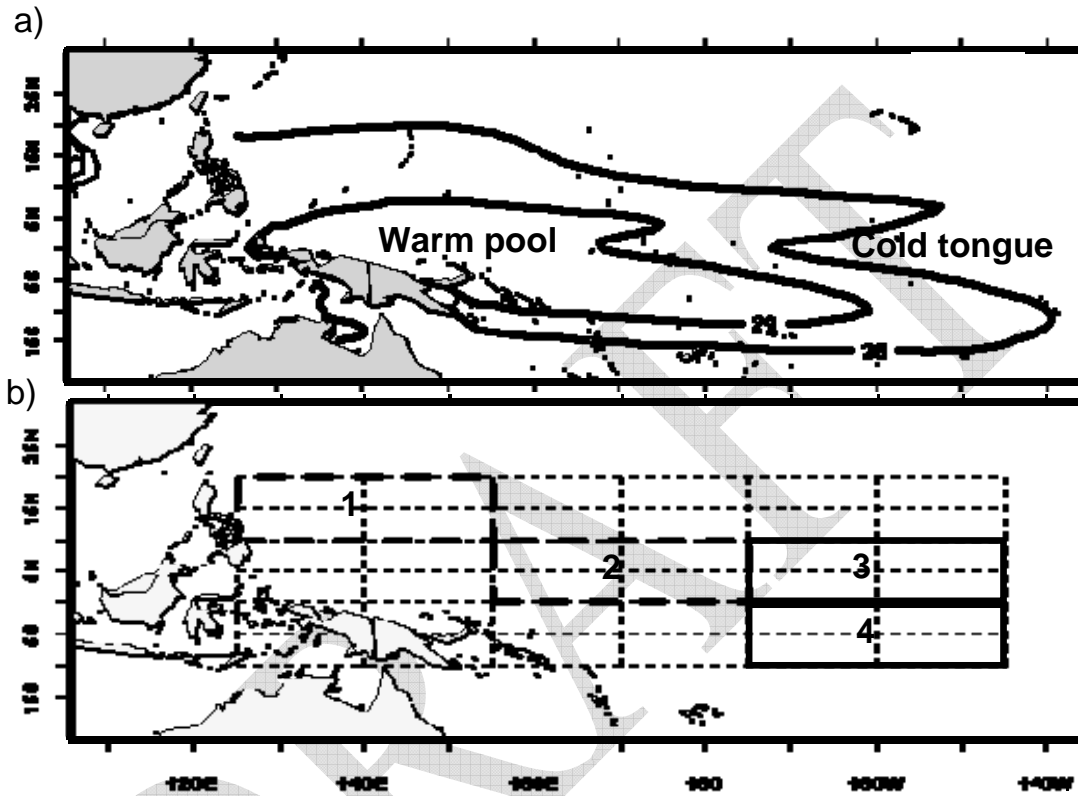
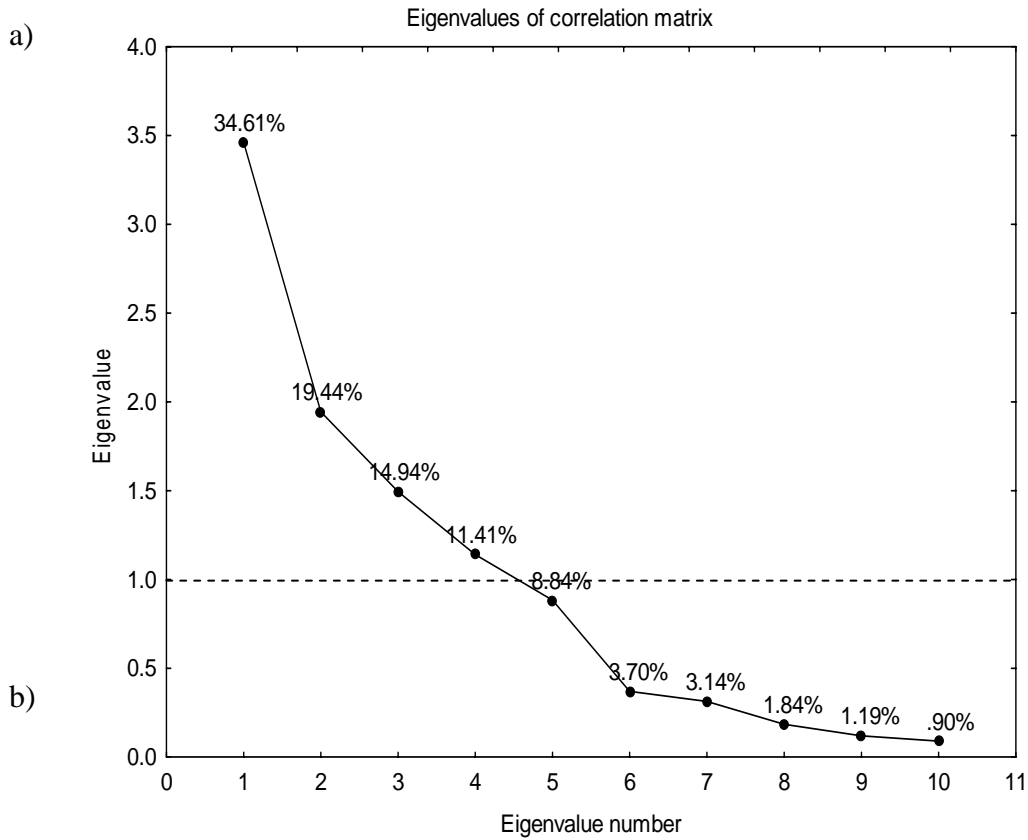


Fig. 2. Areas 1 & 2: (a) 'scree' plot showing all principal components ranked in order of variance accounted for. (b) Sequential *t*-test analysis of regime shifts (STARS; solid line, dates) on the temporal projections of the 4 significant principal components (PCs; bars)



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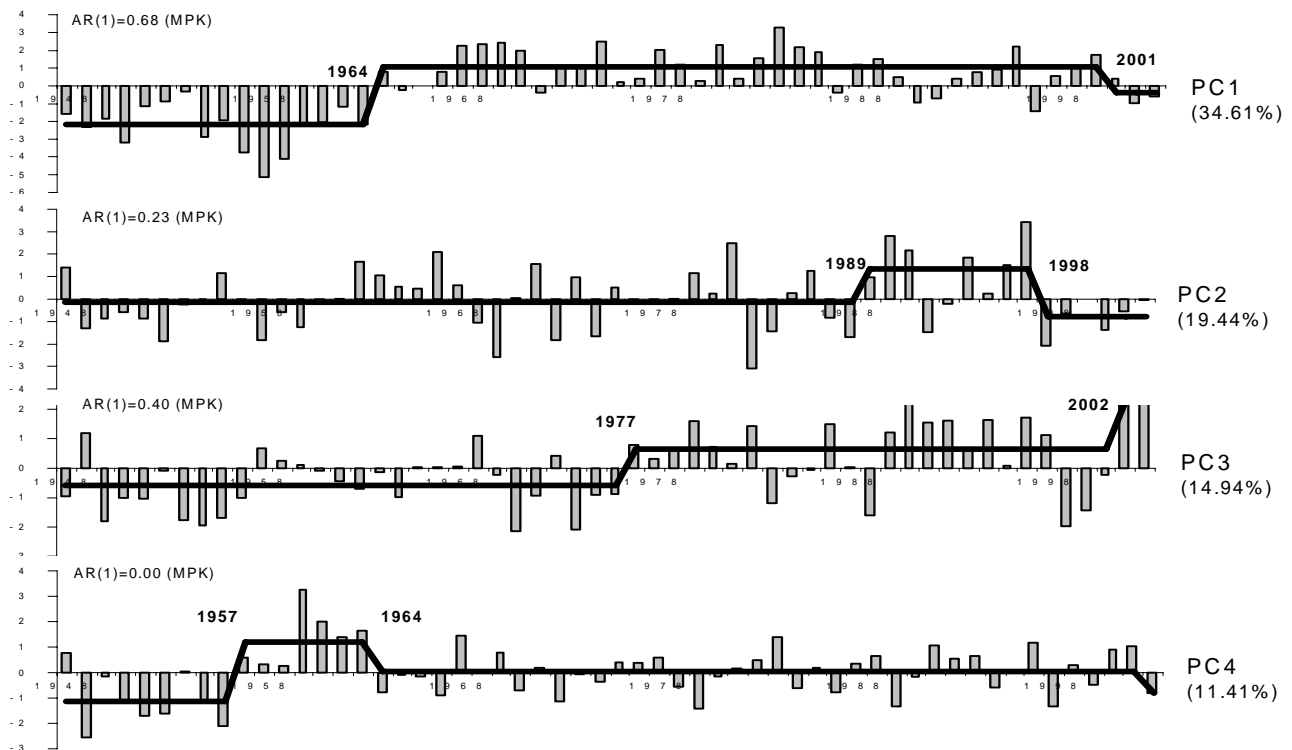
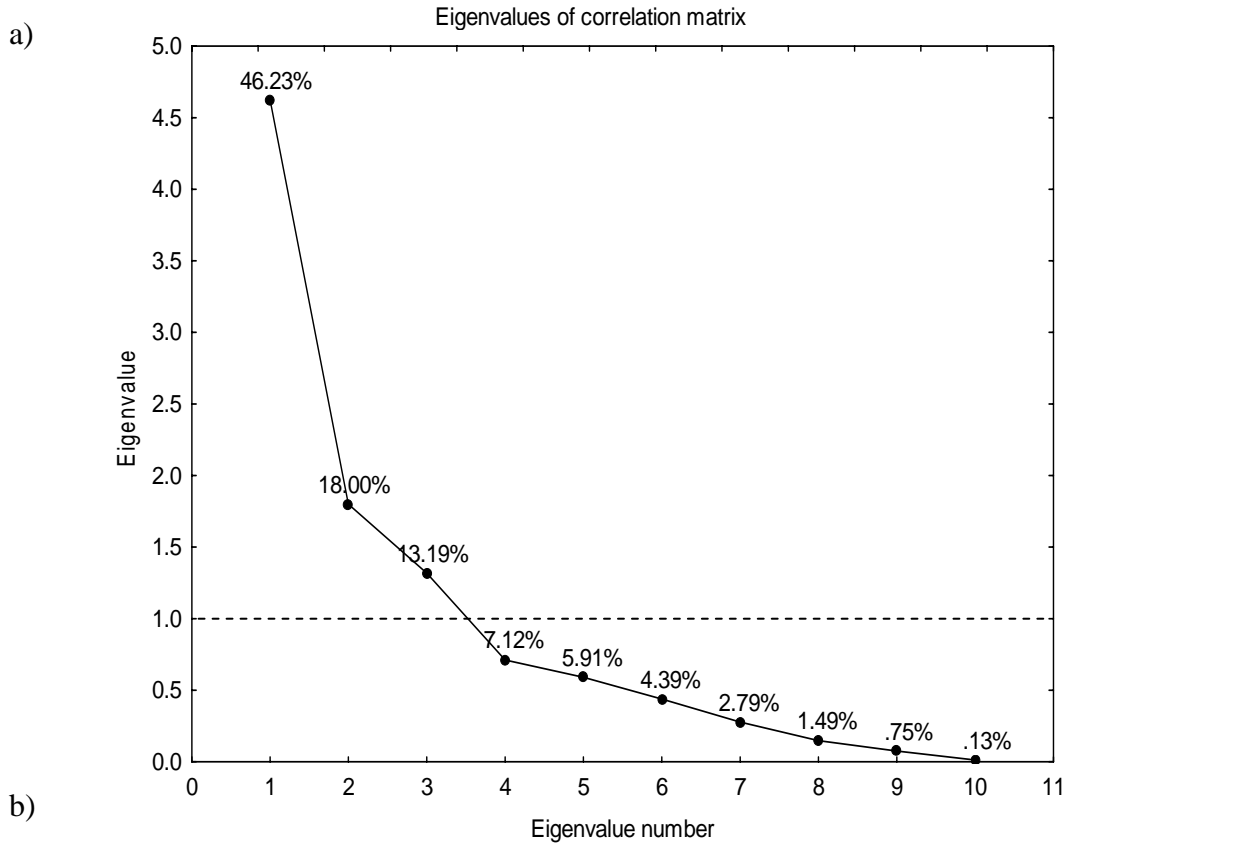


Fig. 3. Areas 3 & 4: (a) 'scree' plot showing all principal components ranked in order of variance accounted for. (b) Sequential *t*-test analysis of regime shifts (STARS; solid line, dates) on the temporal projections of the 3 significant principal components (PCs; bars)



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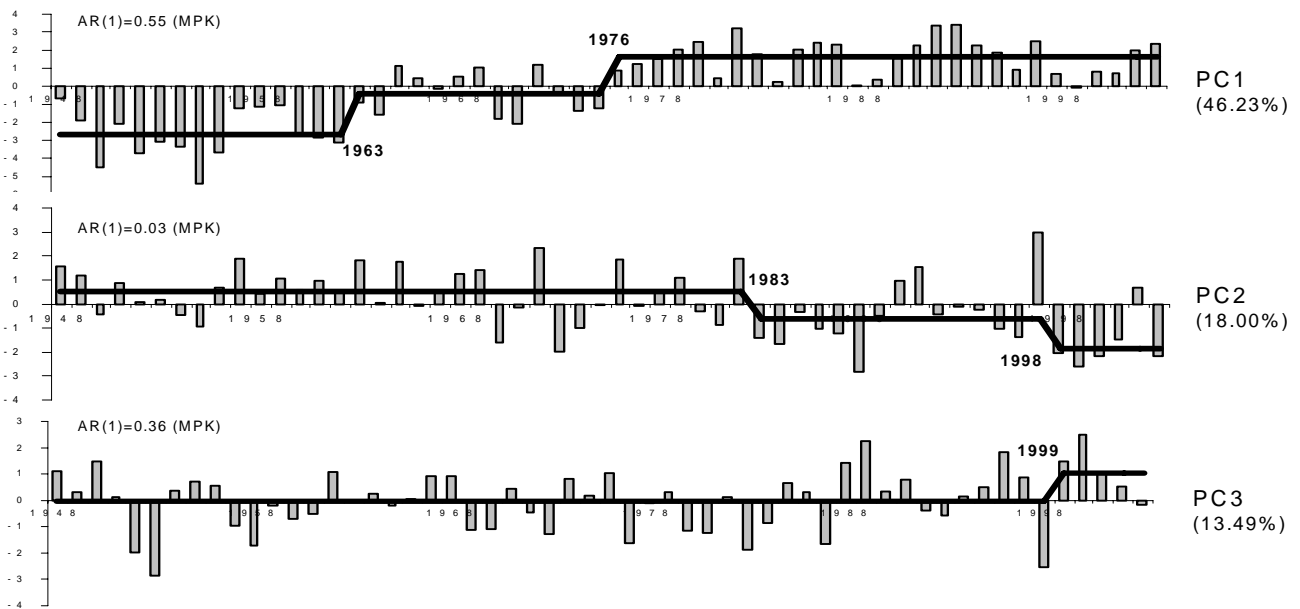


Fig. 4. Sequential t -test analysis of regime shifts (STARS; solid lines, dates) (a) yellowfin and (b) bigeye tuna recruitment predictions from the GLM, and WCPO climate indices: (c) warm pool area, (d) PDO and (e) SOI.

