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ECOSYSTEM INDICATORS AND LINKS WITH RECRUITMENT VARIABILITY FOR TUNAS

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1. INTRODUCTION

Recruitment estimates for tunas show significant variability at all time scales, which is not well described by any biologically meaningful relationship with spawning stock biomass. While it is logical to assume that such a relationship exists, at least for very low values of biomass not so far observed, the primary source of observed recruitment variability is most likely to be variability in natural mortality during the early life history stages, i.e. larvae and pre-recruits. For this reason there has been much research globally into environment-recruitment relationships, larval fish feeding and growth.

There are several factors that contribute to larval and early juvenile mortality. Growth rate depends on the encounter rate with food and on temperature. Encounter rate is determined by food abundance and availability. Tuna larvae feed on microzooplankton, which themselves feed on phytoplankton and are tightly coupled with spatio-temporal variability in primary production. Therefore we would expect there to be a direct relationship between primary production, larval growth and recruitment.

However, for larval tuna to grow, food must available as well as abundant, i.e. the larvae must be able to detect and capture it. Detection depends on the visual acuity and spectral sensitivity of the predator. In the case of tuna larvae, visual acuity is highly developed and spectral sensitivity is greatest in the green wavelengths (Loew et al. 2002); they are therefore perfectly adapted to detecting microzooplankton that have been grazing on phytoplankton. However, the ocean is not a static environment on any scale, and both predator and prey can swim. The encounter rate therefore also depends on their relative velocities and on water velocity at turbulent microscales. Turbulence is directly related to the input of wind energy from atmosphere to ocean (Niiler & Kraus 1977).

Temperature has a direct thermodynamic effect on physiology, i.e. rate of food energy absorption and metabolism leading to growth. Temperature depends on spawning time and place and on the trade-off between the degree of solar energy input, which will warm surface waters, and wind energy input, which will cause stirring, mixing and cooling.

All these physical and biological interactions at meso- to microscales, ultimately determine larval growth rate. To the extent that inadequate nutrition for growth results in starvation, they therefore have a controlling effect on survival and recruitment.

The next controlling factor is predation and there may well be density dependent effects due to cannibalism, as faster growing or older individuals may consume slower growing and younger, smaller ones. This is very hard to quantify in natural systems but predation may, in the case of density dependent effects, dampen the response of recruitment to otherwise positive conditions for growth, or it may account for some variability in recruitment that is not otherwise explained by observed environmental variability.

The aims of this study are to explore the relationships between observed environmental variability and estimated recruitment success for tunas, recognising that our scales of observation are far greater than those at which the relevant mechanisms are acting. We were particularly interested to investigate decadal scale variability and the potential effect on recruitment of so-called “regime shifts” in the environment, often suggested by comparison of ecological time series with the Pacific Decadal Oscillation (PDO; see Annex 1), but we have also carried out analyses on annual and quarterly time scales.

2. METHODS

2.1 Study area

The study was carried out for two sub-regions of the Western and Central Pacific Ocean (WCPO), corresponding to assumed spawning habitat for tunas: the area between 120°E–170°W, 10°N–10°S encompassing the core of the western Pacific warm pool was chosen for the tropical species (yellowfin, bigeye, skipjack); a more southerly area between 140°E–150°W, 10°S–20°S was chosen for the sub-tropical albacore (Fig. 1).

2.2 Datasets

Estimates of recruitment are routinely provided by the MULTIFAN-CL model developed at SPC-OFP (Fournier *et al.* 1998). MFCL is a spatially disaggregated, length-based, age-structured model used for stock assessments in the WCPO. MFCL recruitment estimates are derived from times series of fishery catch, effort and length/weight frequency data. The model is stratified by regions, which reflect the distribution of the various fisheries defined in the model and the spatial resolution of some of the data. Spawning appears to occur year-round for tropical tunas, so the time intervals used for yellowfin, bigeye and skipjack stock assessments are quarters (Jan–Mar, Apr–Jun, Jul–Sep, Oct–Dec). For albacore, which only spawn during austral summer (Nov–Mar), only one recruitment event is estimated each year. Recruitment estimates are available since 1952 for yellowfin, bigeye and albacore and since 1972 for skipjack. Recruitment estimates from the 2006 assessments were used; however, the 2005 estimates were also investigated.

The environmental data used here come from three 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 run to compute primary production. These models have been developed at ESSIC (Earth System Science Interdisciplinary Center, Maryland) and data provided to SPC-OFP. Secondly, epipelagic forage concentration was predicted using the Spatial Ecosystem And Population Dynamics model (SEAPODYM) developed at SPC-OFP. The resolution of these environmental data fields are 30 days and 0.5° square. Temperature, primary production, east-west current component, north-south current component and forage biomass computed at different depths were available for the 1948–2004 period. Thirdly, historical wind data on a monthly scale for the 1958–2001 period were obtained from the ECMWF (European Centre for Medium Range Weather Forecasting) Re-Analysis ERA-40 (http://www.ecmwf.int/research/era/). *U* and *V* wind components at 10 meters height and east-west surface stress were obtained on 2.5° square resolution. Estimates of absolute wind speed *W* were calculated using the formula: $W = \sqrt{(U^2 + V^2)}$. An index of turbulence was also calculated, using the fact that turbulent kinetic energy is proportional to the third power or cube of absolute wind speed (Niiler & Kraus, 1977).

Environmental data were chosen for analysis according to their anticipated impact on tuna recruitment, as concluded from a general understanding of environmental variability and fish early life history. Thus, mean temperature between 0–100 m (*T*100), primary production (*PP*), absolute values of east-west and north-south current components between 0–100 m (*U*100 and *V*100 respectively**)**, epipelagic prey concentrations during daytime (*epid*), east-west surface stress (*ewss*), wind speed and turbulence were extracted and spatially averaged over the chosen regions to generate time series for each variable.

2.3 Data analysis

Recruitment and environmental time series were observed on different temporal scales: Long term variability was first investigated in both total annual tuna recruitment and environmental time series in order to define possible decadal scale regime shifts in the WCPO. There are a number of methods designed for a detection of regime shifts for individual time series and for multiple time series characterisic of entire ecosystems.

We choose the STARS method (Rodionov 2004) to investigate possible regimes shifts in individual time series of recruitment. This method is based on a sequential algorithm with an incorporated *t*-test analysis that can signal a regime shift in real time. The test detects discontinuities in the mean of each time series using two main parameters, which are the probability level and the cut-off length. The probability level represent 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. Because of the strong interannual variability, the significance level was set at $p = 0.2$, and the cut-off length was defined to 10 years for all series in order to investigate decadal varaibility.

Multivariate analysis was then performed on the environmental data in order to detect common patterns of temporal variability within each of the two zones (tropical and subtropical) over the period 1958–2001. Principal components analysis (PCA) is particularly well suited for regime shift detection, as it reduces the dimensionality of a data matrix to a small number of uncorrelated and possibly meaningful time series named (PC scores) and loading vectors (Mantua 2004). Loadings vectors shows the extent to which original variables are related to PCs. The PC scores plotted against time shows the underlying patterns of a specific PC and thus if and when a sudden change occurred.. Rodionov analysis was used on PCs time series to corroborate the shift points. Chronological clustering defined by Legendre *et al.* (1985) is another good way to detect regime shifts and confirm the results found by the PCA (Weijerman *et al.* 2005). Chronological clustering results in groups of sequential years, defined by two parameters, namely the connectedness and the fusion level alpha, which is a clustering sensitivity parameter. Identification of breakpoints is usually investigated using different values of alpha for the same connectedness level (Legendre *et al.*1985). In order to detect regime shifts in our environmental times series, we first standardized each variable and used the euclidean distance function to calculate the dis(similiraty) between years. Then we investigated the main breakpoints in the whole environmental time series using small values of alpha (0.01 to 0.3) with a constant connectedness level set at 50%. The software package Brodgar (www.brodgar.com) was used for these calculations.

Finally, relationships between the various environmental variables and recruitment were investigated by fitting generalized additive models (GAMs). GAMs are nonparametric generalizations of multiple regression techniques (Hastie and Tibshirani, 1990). These types of models are better suited than linear models for studying the link between marine organisms and their environment because non-linearity of responses is expected and can be estimated in the model (Maury *et al.* 2001). The analyses were made on both annual and quarterly time scale using the R software *gam* package (R Development Core Team) and a polynomial spline function *s* to describe the relationship. Simple cross-correlations were also computed to detect significant interactions between the environmental factors.

3. RESULTS

3.1 Interdecadal variation in recruitment

The results of Rodionov analysis on total annual recruitment for each species as estimated in the 2006 MFCL assessments are presented in Fig. 2.

For tropical tuna, shift points in recruitment were not found for the same years. Yellowfin recruitment appears to have shifted four times over the study period. Recruitment started with high values then decreased abruptly to lower values in 1965. Mean values increased after 1976 and 1986 then dropped again in 1997. Bigeye underwent only one apparent shift in 1994, with higher values of recruitment after this year. For skipjack, recruitment shifted twice in 1982 and 1997 with two successive increases in the mean level.

For albacore, shifts points were found in 1965, 1978 and 1995. These shifts points began at about the same time as those found in yellowfin recruitment but the effect on recruitment was inversely related for the two first regime shifts in 1965 and in 1978.

It is interesting to note that a signature of the main climatic regime shift documented for the North Pacific in the late 1970s (Hare & Mantua 2000; see Annex 1) can be found in some of the tuna recruitment time series, with a different impact on tropical (yellowfin) and temperate (albacore) species.

3.2 Long term environmental variability in tropical and subtropical zones

Results from the PCA presented in Table 1 and Fig. 3 show the main patterns of variability obtained in tropical and subtropical time series. In the tropical zone, the first principal component accounted for 48.12% of the total variance and the second pattern for 22.69%. Wind speed, turbulence, *ewss* and *U*100 are well represented by PC Factor 1 (loadings >|0.60|) and their spatial projection on the factor plot shows a strong correlation, which means that their temporal variability must be very similar. Primary production, *V*100 and temperature are best represented by PC Factor 2, with loadings also > |0.60|. Primary production and *V*100 are positively correlated with each other but inversely correlated with temperature.

In the temperate zone, both axes accounted for about the same proportion of the variance, with eigenvalues of 29.44% for PC1 and 28.46% for PC2. Wind speed and turbulence are well represented on PC1 (loadings >|0.70|), whereas *U*100, *ewss* and primary production are best represented on PC2 and are all positively correlated. It should be noted that the difference in the PCA results may be related to the fact that in the temperate area the environmental values were averaged over the austral summer months in order to best represent the temporal spawning period for albacore.

Figs. 4-5 illustrates possible environmental regime shifts in the tropical and subtropical zones, using Rodionov analysis on the PC time series and results of chronological clustering analysis.

In the tropical zone, PCs series shows rapid changes from positive to negative phase, with no real decadal scale temporal structure. The regime shifts documented for the North Pacific are not evident, except maybe for 1998 shift, which is detected as a breakpoint by the chronological clustering analysis (alpha = 0.1 and 0.3) and is represented by a abrupt transition to a strong negative phase on PC1 time series. A supplementary analysis made on the PCs showed that PC2 was strongly correlated (R = –0.78) with the annual southern oscillation index (SOI; Annex 1). This may explain the rapid changes in environmental conditions, as El Niño Southern Oscillation (ENSO) is known to be responsible for tropical interannual variability on a 2 to 7 year time scale (Horel & Wallace 1981).

In the subtropical zone, three breakpoints were detected by the chronological clustering in 1978, 1989 and 1994 at alpha = 0.2 and 0.3. Another possible breakpoint is found in 1968 at alpha = 0.01, 0.05 and 0.3. Three of these shift points (1967, 1978, 1994) were also found on PC2, where the whole time series could be summarised as a succession of four regimes with strong negative phase, neutral negative phase, positive phase and strong positive phase. The shift points found in 1978 and 1989 reminds the regime shifts described by Hare & Mantua (2000) in the North Pacific region. PC1 shows two others breakpoints in 1981 and 1998. A supplementary analysis made on the PCs shows that PC1 is positively correlated with SOI (R = 0.59) and PC2 are positively correlated with the Pacific Decadal Oscillation with R = 0.46 (Annex 1).

3.3 Relationship between recruitment and environmental variables

Annual analysis

Relationships between annual recruitment and environmental variables in the tropical zone as described by GAMs are summarized in Table 2a and plots showing the most significant relationships (P<0.01) are presented in Fig. 6. For the tropical species, primary production, temperature and epipelagic prey concentration are the 3 factors which have a significant effect on recruitment.

For bigeye, primary production accounts for the largest part of the recruitment variability. The contribution of primary production is highest with a one year lag (22.6% compared to 10.20% without any lag), with a clear monotonous positive effect on recruitment (Fig. 6a). Recruitment is higher than average when the primary production in the previous year was greater than 40 mmol m^{-2}. Epipelagic prey concentration is also significant but this is strongly correlated with $PP0$ and $PP1$ ($R_{epid/PP0}$= 0.72 and $R_{epid/PP1}$= 0.81), which could explain its significant relationship with bigeye recruitment.

Instantaneous primary production is also an important factor for skipjack recruitment and accounted for 50% of the deviance. As for bigeye, the relationship with $PP0$ is globally positive and exhibits an increasing shape (Fig. 6b). Recruitment of skipjack appears to be above average in waters where primary production values exceed 36–37 mmol m^{-2}.

For yellowfin, temperature between 0–100 m was the only factor which had a significant impact on annual recruitment, accounting for 25.40% of the deviance. However, when 2005 recruitment estimates were used instead of those from 2006, primary production became significant, accounting for 14.9% of the deviance with lag 0 and 9.82% with lag 1. The effect of instantaneous primary production on recruitment is then the same as for the other tropical species, with a positive slope and highest values of recruitment obtained for $PP0 > 35$ mmol m^{-2} d^{-1} (Fig. 6c). Temperature was less significant when using 2005 estimates but still accounted for 20.9% of the deviance. However, it is difficult to draw any meaningful conclusions from the shape of the relationship with temperature (Fig. 6d) over such a narrow range of temperature (28.46–29.33°). As for bigeye, epipelagic prey was also signifcant, accounting for 8.96% of the deviance.

The relationship between annual albacore recruitment and the environmental variables for the temperate zone (averaged over the austral summer months) is presented in Table 2b. During November to March, recruitment seems mostly affected by environmental parameters related to wind (*ewss* and turbulence) or current (*U*100). All these environmental parameters have a negative impact on recruitment and all are positively and significantly correlated with each other ($R_{ewss/U100} = 0.57$; $R_{ewss/turbulence} = 0.36$). Turbulence and *ewss* have the most significant effects on albacore recruitment, accounting for 19.0% and 19.80% of the model deviance respectively. Figure 7 shows that albacore recruitment is higher when values of turbulence are quite low (< 300 m^3s^{-3}).

Quarterly analysis

In the tropical zone, the significance of relationships between environmental variables and tuna recruitment change when looking on a smaller temporal scale (Table 3). Environmental variables linked to wind (wind speed, turbulence) or current (*V*100) have a very significant impact on all tropical species on a quarterly scale.

For bigeye, epipelagic prey concentrations are also an important factor, accounting for 10.20% of the variance and having a positive impact on recruitment. *V*100, wind speed and turbulence (deviance ≈ 7%), which are all intercorrelated ($R_{V100/winspeed} = 0.61$; $R_{V100/turbulence} = 0.75$; $R_{turbulence/windspeed} = 0.93$) also have a very significant impact on recruitment, with a negative effect. Figure 8 shows that bigeye recruitment is above average for very low values of turbulence (< 250 m^3s^{-3}).

For yellowfin tuna, the same variables *V*100, wind speed and turbulence are also significant (deviance > 12%) but the relationship with recruitment is different for the 2006 estimates; Figure 8 shows that recruitment first increases with turbulence and seems to be favoured for values of turbulence > 300 m^3s^{-3}. Then, after a certain threshold around 900 m^3s^{-3}, the relationship reverses and turbulence then has a negative effect on recruitment. This could suggest an ‘optimal environmental window’ for the effects of turbulence (Cury & Roy 1989), but the windspeeds at the inflection point are higher than in any other studies. Furthermore, when the 2005 recruitment estimates are used the relationship that follows is the same as for the other tuna species. We are more inclined to believe that yellowfin has the same generally negative relationship with turbulence as the other tuna species. *PP* has an significant positive impact on yellowfin recruitment.

For skipjack, a great number of variables linked to wind (wind speed, *ewss*, turbulence) and current (*V*100) seems to influence recruitment, with the greatest deviances accounted for by *V*100 (18.80%) and wind speed (18.10%). All these variables have a negative impact on recruitment except for *V*100, where a statistically significant result was obtained but the functional form of the relationship is difficult to interpret. This result may be spurious but may also derive from some higher order property of *V*100, such as divergence, which would bring about upwelling and an increase of nutrients into surface waters. This possibility will be investigated further. Figure 8 also shows that values of recruitment are above average for turbulence < 300 m^3s^{-3}. As for yellowfin, *PP* has a positive and significant impact on skipjack recruitment. Finally, *T*100 is found to have a negative impact on recruitment. It is however difficult to formulate conclusions with this variable, because once again the range of values observed is very small (<1.5°).

4. DISCUSSION

Long-term variability is clearly apparent in both recruitment and environmental time series (Figs. 2,4,5). Whether or not these constitute statistically significant shifts between relatively stable regimes depends on the significance levels used in the analysis (for the STARS method and for chronological clustering) but nonetheless there is evidence in both single and mutivariate time series for decadal scale changes in the environment and in recruitment, most notably in the late 1970s and late 1990s. A climate signature appears to be present in recruitment for tunas in both tropical and subtropical zones. The effect of this seems to be reversed for tropical and temperate species but this is not always true.

In the tropical zone the multivariate index PC2 is strongly correlated with SOI and in the sub-tropical zone PC1 is similarly strongly correlated with SOI. This confirms the importance of the El Nino Southern Oscillation (ENSO) as a very significant mode of variation in both physical and biological components of Pacific Ocean ecosystems. The strong influence of ENSO-related variability may explain the changes in recruitment after El Nino events in 1982 and 1997 for skipjack, and after 1986 and 1997 for yellowfin. PC1 for the tropical zone is best interpreted as a generally flat signal of interannual variability in zonal winds and related variables (Fig. 3a); the pattern (Fig. 4a) suggests that there have been occasional pulses in westward winds/currents since the early 1970s but little long-term variability except for post-1999, when there was a very strong rebound to the 1997/8 El Nino, generating several years of La Nina. This is also captured on PC2, except the intitial effect was not so strong and it is not diminishing.

In the subtropical zone the significant relationship between PC2 and the PDO suggests that this climate index has some relevance as an ecosystem indicator in this zone, especially as its change of phase precedes the 1978 shift in albacore recruitment (Fig. 2). However, the further shift downward in albacore recruitment in 1995 is not preceded by a similar shift in PDO but such a shift is seen for PC2, which suggests that the multivariate index we have derived here would be a better predictor of regime shifts in recruitment variation for albacore than the PDO.

Shift points in multivariate ecosystem indicators do not always explain shift points in recruitment. For example, the 1965 shift points in yellowfin and albacore recruitment are not related to any of the shifts in PC scores. However, single variables do show simlar patterns around this time, notably temperature and $V100$ for yellowfin and albacore respectively. There is also a shift point for primary production in 1992 that may be related to the shift point in bigeye recruitment in 1994 (see Annex 2).

Shifts point in recruitment for tropical species are not always synchronized, and when they are, the direction of change is not always the same (e.g. 1997 for yellowfin and skipjack). This could mean that the behavior of spawners or the adaptations of larvae to environmental variability are different among species. However, the GAM analysis shows that there appears to be some consistency in the link between environment and recruitment for tropical species, and that is the relationship between primary production (i.e. food for larvae) and recruitment (Fig. 6). For bigeye this relationship is most significant with a lag of 1 year, whereas yellowfin and skipjack depend principally on the primary production of the year. The significant positive relationship for epipelagic prey with bigeye and yellowfin recruitment (not shown) is consistent with a lagged effect of primary production, but may also imply that spawning adults were looking for forage-rich areas to satisfy the energy demands of reproduction.

Compared to tropical tunas, albacore have a more conservative reproductive strategy, reproducing during a more defined season, as they are adapted to a colder and more variable environment (Fromentin & Fonteneau 2001). They are not necessarily looking for periods or places of high productivity, which would be found during the austral winter months, and no relationship was found here between primary production and recruitment. It has been hypothesised that their strategy derives from their evolutionary origins, whereby they still require warm waters for their larvae to grow, and it has also been suggested that this strategy is to avoid predation on their larvae (Bakun & Broad 2003).

Albacore recruitment success seems to be mostly dependant on east-west current component and turbulence during the austral summer months. Both have a negative impact on recruitment. This could be due to dispersion of eggs or larvae to unfavorable areas, where temperature is colder and predation is higher. Strong winds imply mixing of the upper layer which, as discussed in the Introduction, may have a detrimental effect on feeding rate if it is too high (Rotschild & Osborn 1988; Cury & Roy 1989; Kiorboe & Saiz 1995; Porter et al. 2005). For albacore as for bigeye and skipjack on a quarterly time scale, recruitment success is better for low turbulence values ($<300\ m^3s^{-3}$). Values of 200–400 m^3s^{-3} are consistent with wind speeds of 3–5ms^{-1}, just below the threshold wind speed (~5 ms^{-1}) used to distinguish biological (low turbulence) from physical (high turbulence) control of phytoplankton patchiness (Therriault & Platt 1981). Cury & Roy (1989) suggest an ‘optimal environmental window’ hypothesis for the effects of turbulence on recruitment, whereby it is positive up to an extent and negative thereafter: this is exactly the kind of relationship that was obtained here for yellowfin using the 2006 recruitment estimates (Fig. 8). However, the inflexion point is for wind speeds between 8 and 10 ms^{-1}. When the 2005 recruitment estimates were considered, the functional form of the relationship was quite different and instead of the dome-shaped curve there was a general decrease in recruitment with turbulence. The results presented here will be compared with experimental work carried out at IATTC (Margulies et al. in press).

This analysis suggests that while ‘regime shifts’ are not well justified by correlating recruitment with SOI and PDO, and the concept may be too simple to properly reflect the variability observed in environmental and recruitment time series, there is still significant and coherent variability in these series at multiple time scales. The most promising general relationships presented here are the positive correlation between recruitment of tropical tunas and primary productivity and a negative relationship for all species with turbulence. This permits a better understanding of recruitment variability and generates a warning for future recruitment, since primary productivity has fallen back to long-term average levels since 1998, after being above average since the early 1980s (Annex 2.).

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Table 1 Loading factors related to the first two Principal Component (PC) scores obtained from principal component analysis on environmental time series extracted from tropical and subtropical zones

	Tropical zone		Sub tropical zone	
Environmental variables	PC1	PC2	PC1	PC2
T100	0.220	–0.667	0.473	0.479
PP	–0.504	0.707	0.096	0.593
U100	–0.677	–0.218	0.482	0.790
V100	–0.249	0.638	–0.676	–0.103
epid	–0.744	0.355	–0.487	–0.155
ewss	–0.862	–0.398	–0.069	0.727
wind speed	–0.914	–0.338	–0.814	0.411
turbulence	–0.945	–0.134	–0.727	0.583

Table 2 Results from GAM analysis showing the annual relationships between species recruitment R and environmental parameters in a) tropical zone and b) subtropical zone. ** means very significant (P<0.01);* means significant (P<0.05) and n.s. means non significant. PP0 and PP1 represent primary production at lag 0 and 1, respectively. YFT# means that recruitment estimates are from the 2005 stock assessment .

		a)				b)
annual	Explanatory variables	BET	YFT	YFT#	SKJ	ALB
	T100	n.s.	**	*	n.s.	n.s.
	PP0	*	n.s.	*	**	n.s.
	PP1	**	n.s.	*	n.s.	
	U100	n.s.	n.s.	n.s.	n.s.	*
	V100	n.s.	n.s.	n.s.	n.s.	n.s.
	epid	*	n.s.	*	n.s.	n.s.
	ewss	n.s.	n.s.	n.s.	n.s.	**
	wind speed	n.s.	n.s.	n.s.	n.s.	n.s.
	turbulence	n.s.	n.s.	n.s.	n.s.	**

		Explanatory variables	Prob.	Deviance	Global effect
a)	R(BET)	PP1	0.005	22.60%	+
		PP0	0.037	10.20%	+
		epid	0.034	10.20%	+
	R(YFT)	T100	0.008	25.40%	-/+
	R(YFT)#	T100	0.033	20.90%	-/+
		PP0	0.042	14.90%	+
		PP1	0.038	9.82%	+
		epid	0.048	8.96%	+
	R(SKJ)	PP0	0.000	50.00%	+
b)	R(ALB)	ewss	0.002	19.80%	-
		turbulence	0.010	19.00%	-
		U100	0.035	9.85%	-

Table 3 Results from GAM analysis showing the quarterly relationships between tropical species recruitment R and environmental parameters.** means very significant (P<0.01);* means significant (P<0.05) and n.s. means non significant. YFT# means that recruitment estimates are from the 2005 stock assessment .

Explanatory variables	R(BET)	R(YFT)	R(YFT)#	R(SKJ)
T100	n.s.	n.s.	*	**
PP	n.s.	*	n.s.	*
U100	n.s.	n.s.	n.s.	n.s.
V100	**	**	**	**
epid	**	n.s.	**	n.s.
ewss	n.s.	n.s.	**	**
wind speed	**	**	**	**
turbulence	**	**	*	*

	Explanatory variables	Prob.	Deviance	Global effect
R(BET)	epid	0.000	10.20%	+
	V100	0.007	7.58%	-
	wind speed	0.000	7.43%	-
	turbulence	0.003	7.01%	-
R(YFT)	turbulence	2.73E-07	20.20%	+/-
	wind speed	1.46E-07	20.20%	+/-
	V100	0.000	12.90%	+/-
	PP	0.046	4.35%	+
R(YFT)#	V100	2.47E-05	17.10%	+/-
	wind speed	0.000	12.90%	+/-
	ewss	9.83E-05	8.19%	-
	epid	1.00E-03	6.86%	+
	turbulence	0.017	6.08%	-
	T100	0.021	5.75%	-
R(SKJ)	V100	0.004	18.80%	+/-
	wind speed	0.002	18.10%	-
	T100	0.001	13.40%	-
	ewss	0.008	9.98%	-
	turbulence	0.023	7.30%	-
	PP	0.013	4.95%	+

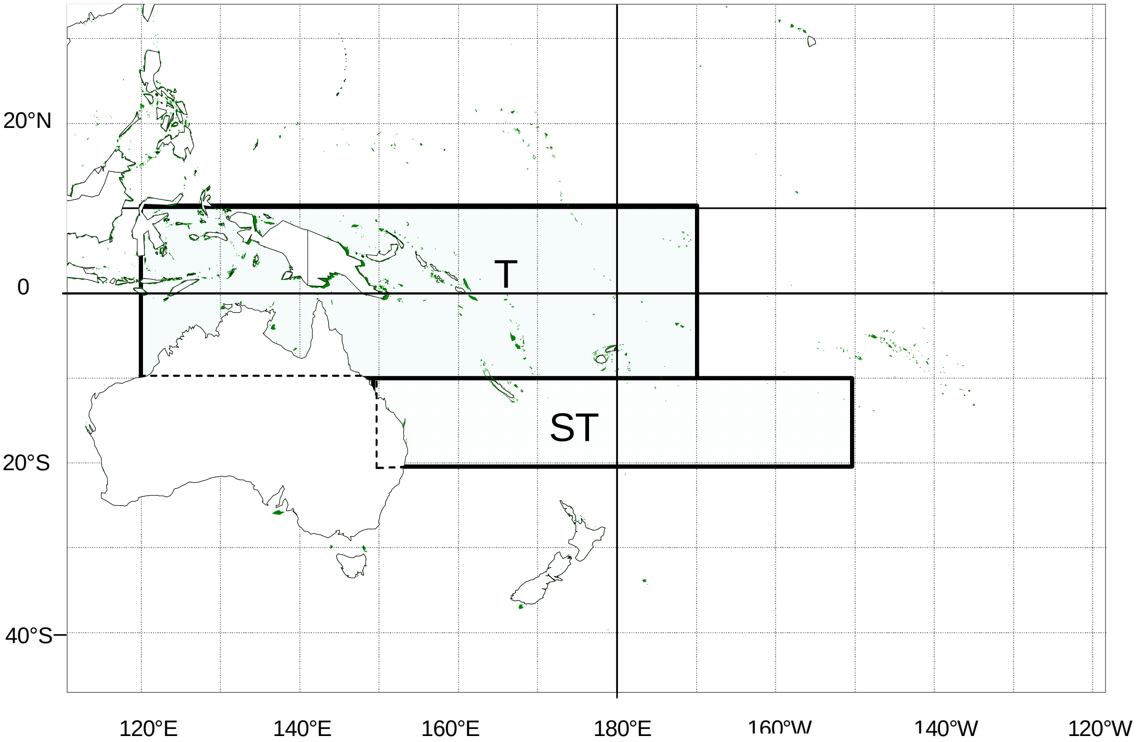


Fig. 1 Map of the study area and selected tropical (T) and subtropical (ST) zones used for the environmental analyses.

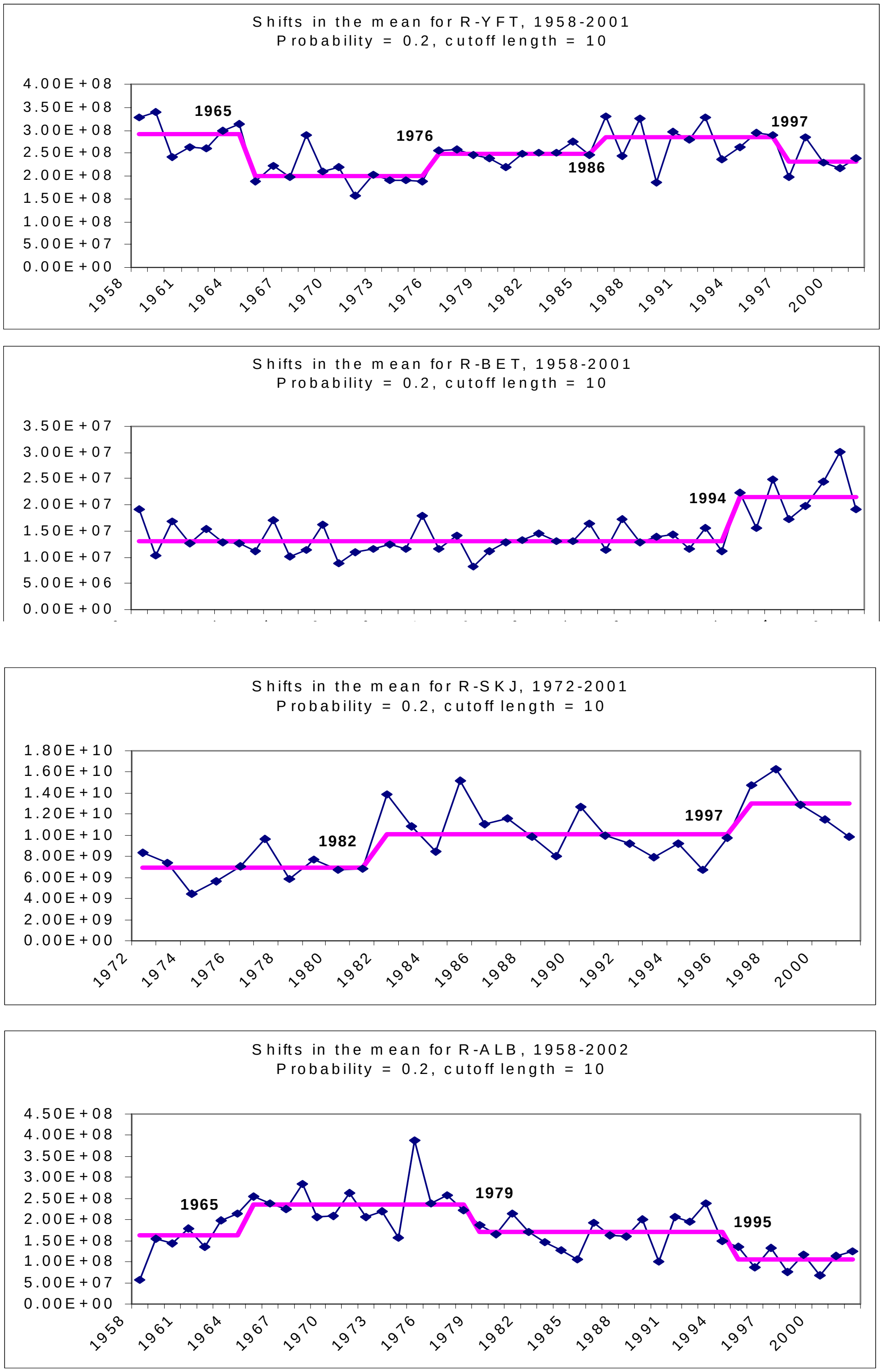


Fig. 2. Apparent regime shifts in annual recruitment of a) yellowfin, b) bigeye, c) skipjack and d) albacore tuna. Shift points were calculed using the Rodionov STARS method, with the cutoff length of 10 years and significant level of 0.2 for all species.

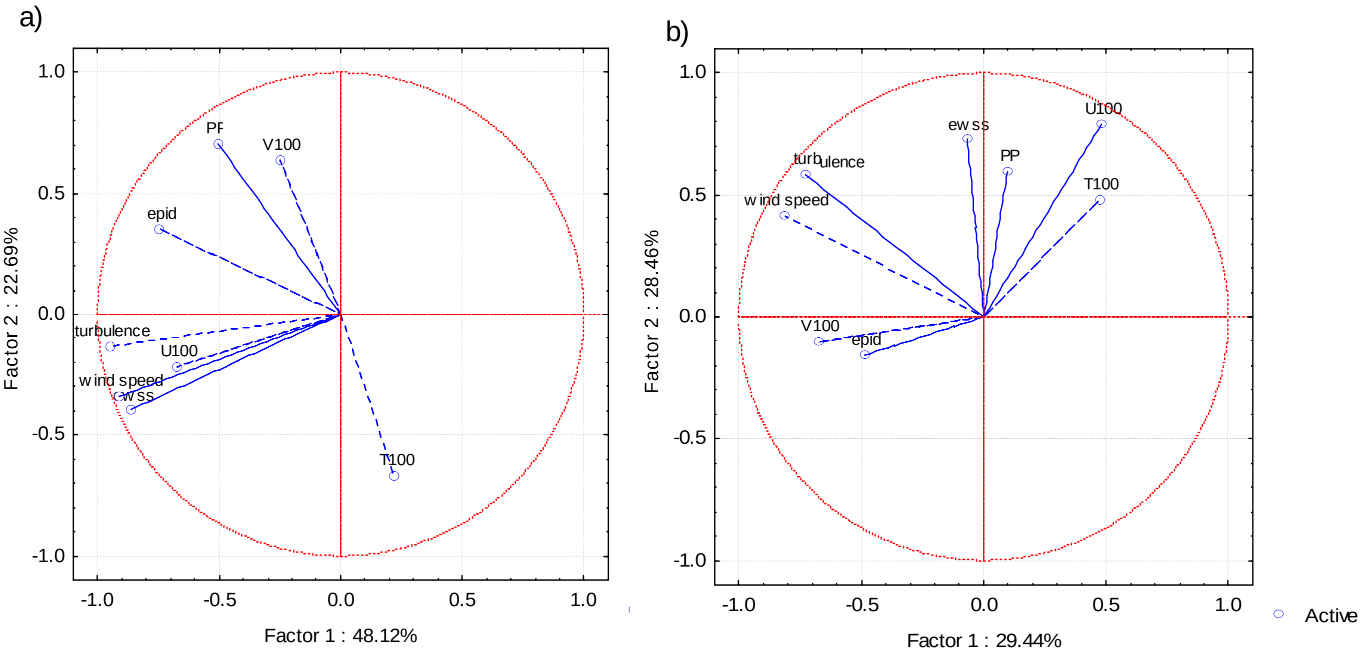


Fig. 3 Principal component analysis on enviromental variables over the period 1958–2001 for a) tropical region and b) subtropical region.

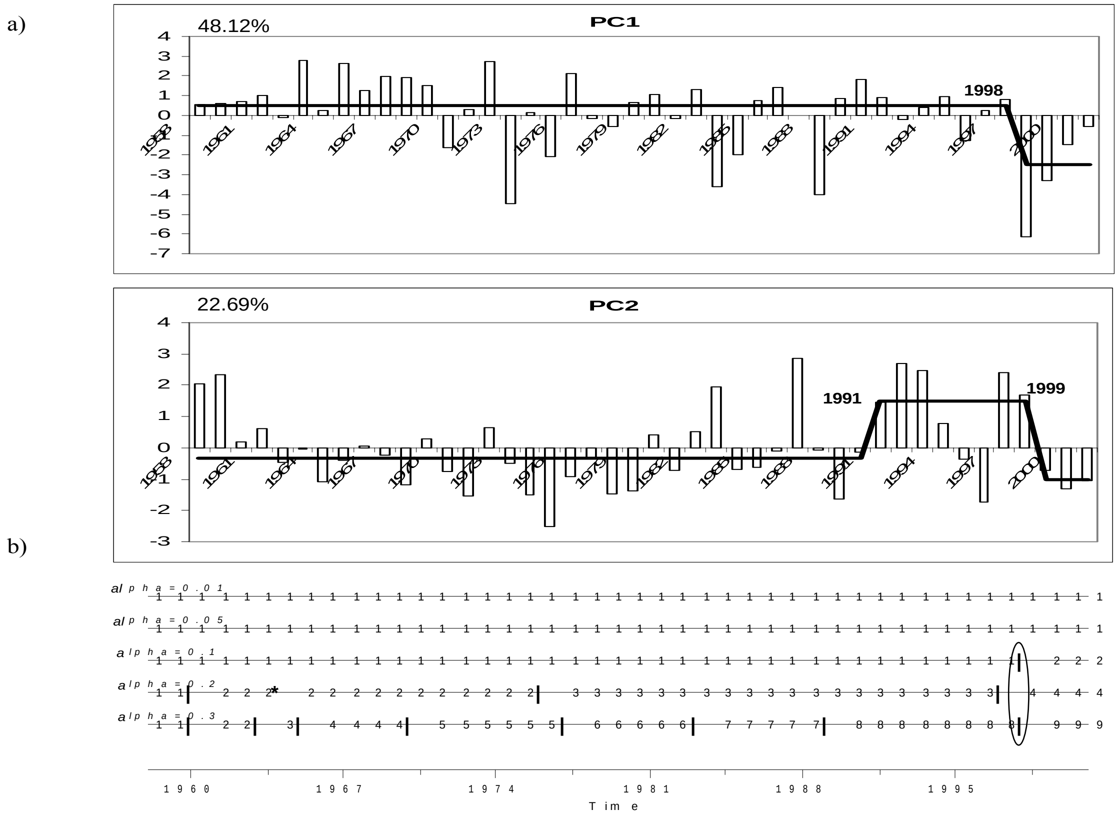


Fig. 4 Regime shift analysis on environmental variables in the tropical zone based on annual means for 1958–2001 period, using a) Rodionov analysis of PCA results, with cutoff length =10 years and alpha=0.2, b) chronological clustering.

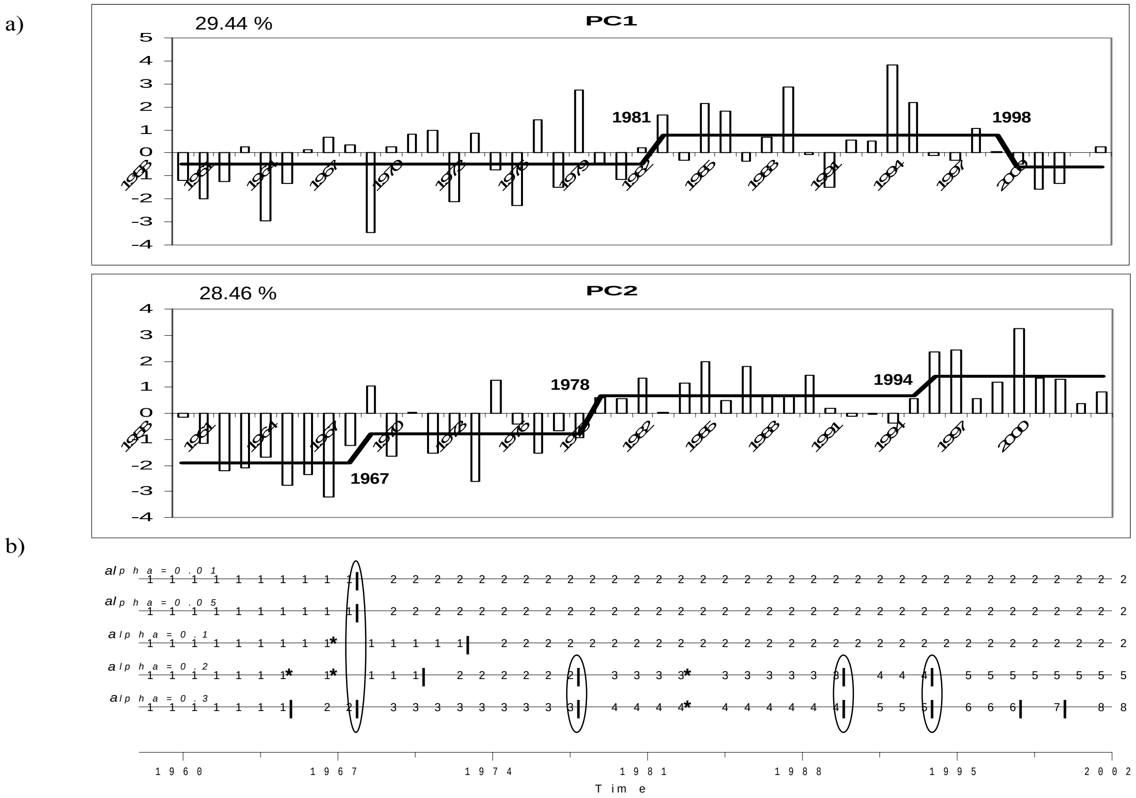


Fig. 5 Regime shift analysis on environmental variables in the sub-tropical zone based on january mean for 1958–2002 period, using a) Rodionov analysis of PCA results, with cutoff length =10 years and alpha=0.2, b) chronological clustering..

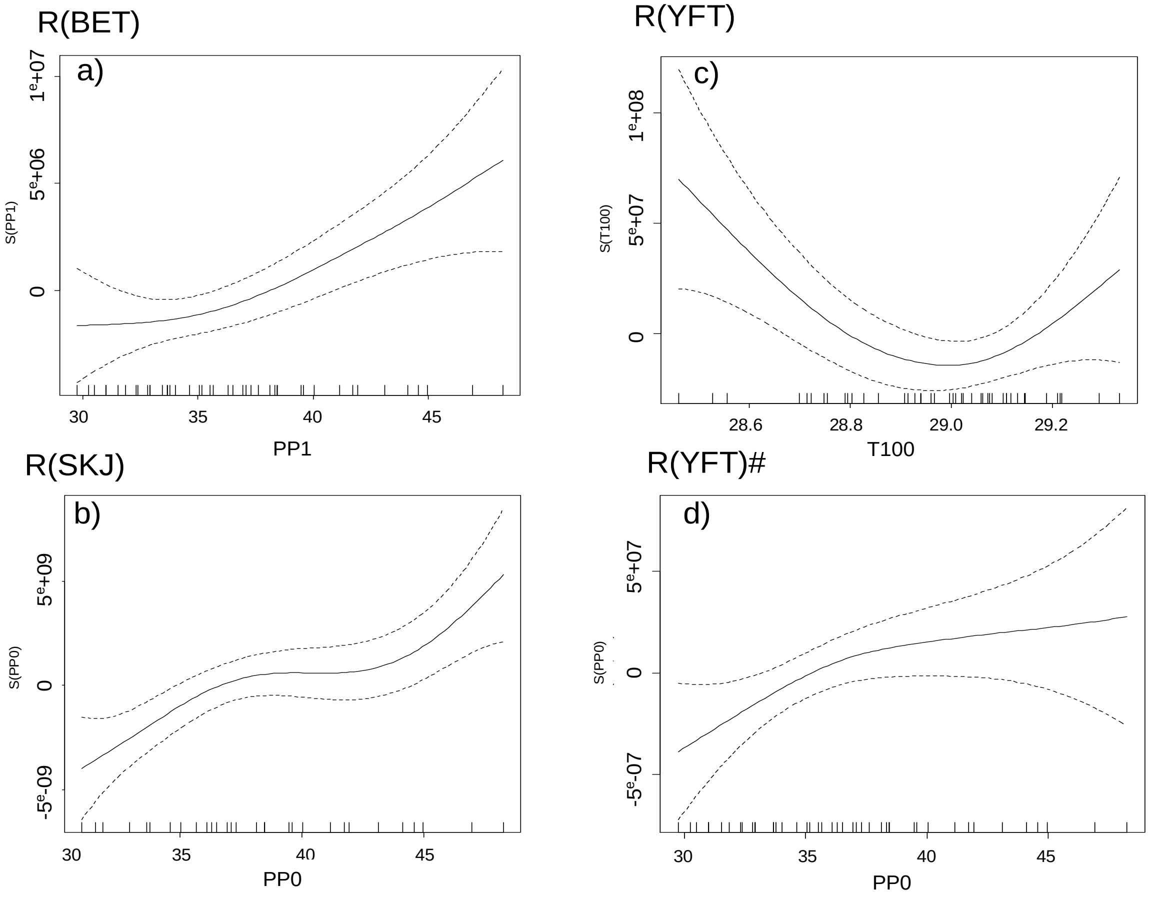


Fig. 6 GAM regression showing the annual effect of environment on tuna recruitment in the tropical zone during 1958–2001 for bigeye and yellowfin and during 1972–2001 for skipjack. The most significant parameters were plotted for the different species. a) primary production with lag 1 with bigeye recruitment; b) primary production of the year with skipjack recruitment; c) temperature between 0–100m with yellowfin recruitement; d) primary production of the year with yellowfin recruitment. # means that recruitment data comes from the previous stock assessment 2005.

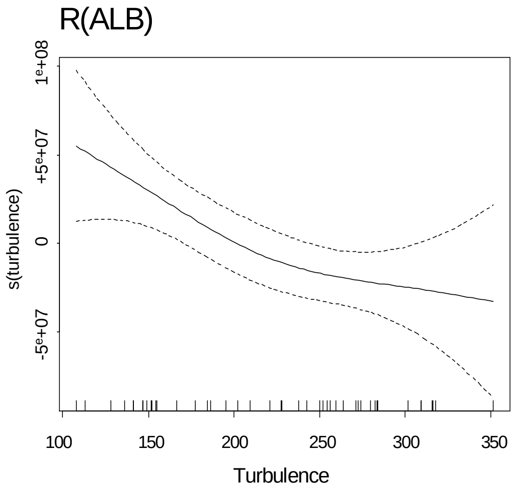


Fig. 7 GAM regression showing the effect of turbulence on albacore recruitment in subtropical zone during austral summer months of 1958–2002.

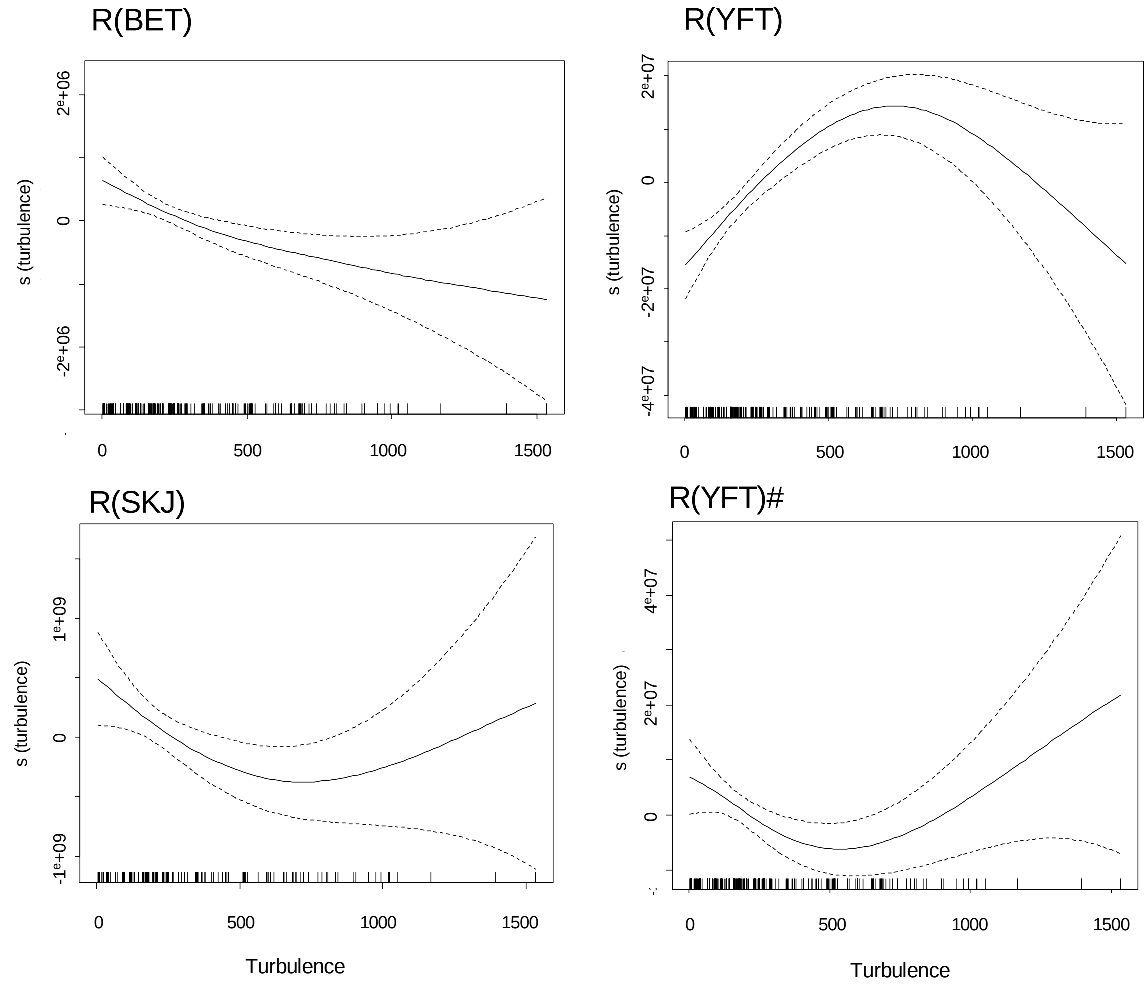
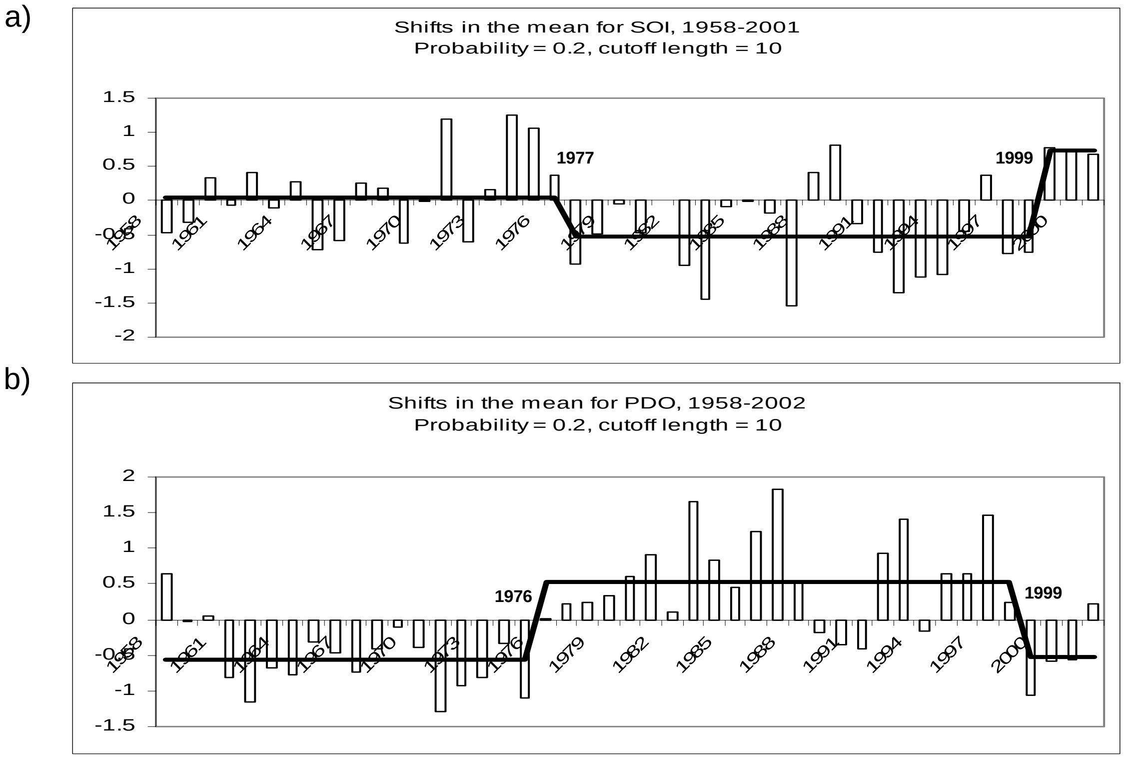
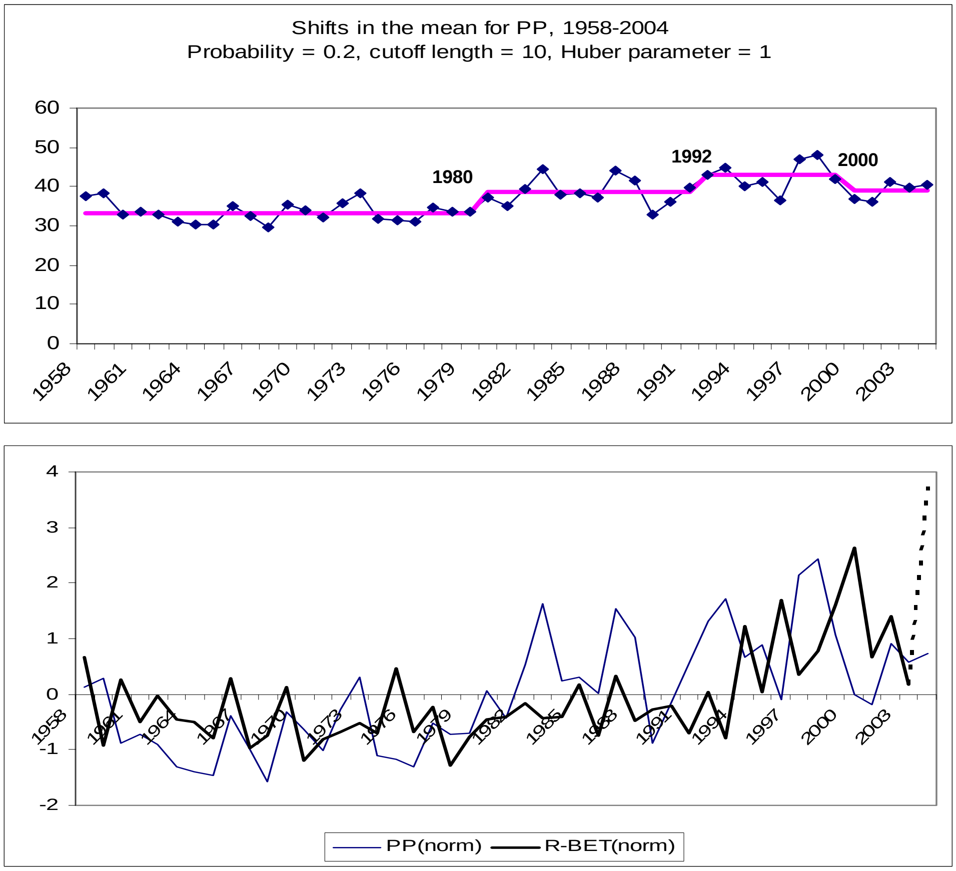


Fig. 8 GAM regression showing the effect of turbulence on the 2006 tuna recruitment estimates in the tropical zone for 1958–2001 for bigeye and yellowfin and 1972–2001 for skipjack. R(YFT)# means that recruitment estimates are from the 2005 stock assessment .

Annex 1 Interannual variability and regime shifts in the two principal climate oscillations in Pacific Ocean: a) Southern oscillation index and b) Pacific Decadal oscillation. Shift points were calculated using Rodionov STARS analysis, wih the cutoff length of 10 years and significant level of 0.2



Annex 2. Possible regime shifts and annual variation of primary production in tropical zone during 1958–2004 period compared to bigeye recruitment (data were standardized for comparison: norm. means normalized).



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