POLISH JOURNAL OF NATURAL SCIENCES
Abbrev.: Pol. J. Natur. Sc., Vol 33(1): 131–154, Y. 2018

CLIMATE-RELATED VARIABILITY AND STOCK – RECRUITMENT RELATIONSHIP OF THE NORTH PACIFIC ALBACORE TUNA*

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Key words: recruitment, spawning stock biomass, sea surface temperature, Pacific decadal oscillation, El Niño southern oscillation.

Abstract

The stock-recruitment relationship is biological in nature and it is evident that one affects the other. However, fish life cycle, growth, abundance and distribution is dependent on a complex relation with various biotic and abiotic variables inclusive of environmental factors. The stock-recruitment relationship and environmental influences was investigated for the North Pacific albacore tuna (*Thunnus alalunga*). Statistical investigation revealed the presence of different density-dependent effects in the relationships of recruits per spawning biomass (RPS) and recruitment (R) against the female spawning stock biomass (SSB). Significant relationship of R, RPS and SSB were determined with the sea surface temperature (SST), Pacific Decadal Oscillation (PDO) and multivariate El Niño Southern Oscillation (ENSO), with SST being the principal variable. This makes the stock recruitment behavior multidimensional. The results suggest significant influence of the environmental conditions on the stock recruitment relationship of the North Pacific albacore tuna including a possible regime shift.

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* This study was supported by the Research and Publication Committee (URPC), Fiji National University, Koronivia, Fiji, grand number: URPC060.

WPŁYW KLIMATU A ZALEŻNOŚĆ STADO – UZUPEŁNIENIE NA PRZYKŁADZIE TUŃCZYKA PÓŁNOCNOPACYFICZNEGO *THUNNUS ALALUNGA*

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Słowa kluczowe: uzupełnienie stada, biomasa stada tarłowego, temperatura powierzchni morza, pacyficzna cyrkulacja powietrza, El Niño – oscylacja południowa.

Abstrakt

Modele stado – uzupełnienie wyjaśniają jedynie pewną część obserwowanej wariancji rekrutacji. Cykl życiowy, tempo wzrostu, liczebność i rozmieszczenie ryb wiążą się z różnymi zmiennymi biotycznymi i abiotycznymi, w tym z czynnikami klimatycznymi. W pracy zbadano proces naturalnej rekrutacji w zależności od zmieniających się parametrów środowiska. Wyniki wskazują na istotny wpływ warunków klimatycznych na zależność stado – uzupełnienie.

Introduction

The North Pacific albacore is a temperate tuna species distributed in the North Pacific which is of significant economic importance to the Pacific Island Nations, territories as well as various fishery industries that obtain license to harvest albacore stock from these waters (SUND et al. 1981, MIYAKE et al. 2004, GILLETT 2009, CHILDERS et al. 2011, SPC 2012, BELL et al. 2013). Albacore stock in the Northern Pacific has been shown to be as discrete and reproductively isolated (UEYANAGI 1969, SUZUKI et al. 1977, CHOW and USHIAMA 1995, RAMON and BAILEY 1996, TAKAGI et al. 2001, ICHINOKAWA et al. 2008). Tuna fisheries provides employment to over 13,000 Pacificic islanders and represents a significant proportion of governmental revenue (more than 40% in some cases) from tuna licensing fees alone (GILLETT 2009). In the Western and Central Pacific Ocean (WCPO), longline landings of albacore represents approximately 1/3rd of annual tuna catch. The North Pacific albacore accounts for ~50% of total global albacore harvests (LAURS and POWERS 2010, WILLIAMS and TERAWASI

2013). The ecological properties and behavior of albacore is not well understood despite having a long fishery history in the Pacific.

Oceanic regime shifts are long lasting and sudden large scale spatial changes in ecological conditions often characterized by changes in abundance and spatial variability of various aquatic species (MÖLLMAN et al. 2014). A regime shift in a commercial fish species stock abundance and/or distribution characteristics across a time series can be in response to high levels of anthropogenic activities such as fishing pressure or environmental and climatic regime shifts (LEHODEY et al. 2003, CAHUIN et al. 2009, LITZOW et al. 2016). LEHODEY et al. (2015) showed that the stock abundance of the South Pacific albacore tuna is significantly affected by both the applied levels of fishing pressure and alteration in environmental and climatic conditions. The spawning behavior of albacore was shown to be related to the spatial variability of the optimal ambient spawning sea surface temperature (SST). LEHODEY et al. (2003) compared the annual recruitment patterns over decadal scales in the Western and Central Pacific Ocean (WCPO) for skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*) and the South Pacific albacore tuna and detected long-term sustained trend change in the recruitment time series for all three species. The changes or regimes were shown to have responded to regime shifts in the inter-decadal climatic variability of the El Niño Southern Oscillation (ENSO).The spatial distribution and abundance of the South Pacific albacore tuna has been shown to be related to the environmental and climatic variables of the SST, Multivariate El Niño Southern Oscillation Index (ENSO) and the Pacific Decadal Oscillation (PDO) (LEHODEY et al. 2003, ZAINUDDIN et al. 2004, GANACHAUD et al. 2011, LE BORGNE et al. 2011, LEHODEY et al. 2011, SPC 2012, BELL et al. 2013, GANACHAUD et al. 2013, PHILLIPS et al. 2014, ZHANG et al. 2014, LEHODEY et al. 2015, SINGH et al. 2015, SINGH et al. 2017). Multivariate El Niño Southern Oscillation Index (ENSO) is a sub-decadal time scale and important climatic variability with effects spanning over most parts of the tropics and sub-tropics. Multiple variables of surface wind indexes, atmospheric conditions, sea-level pressure, SST and surface air temperature are used for the calculation of ENSO (WOLTER and TIMLIN 1998).

PHILLIPS et al. (2014) determined an abrupt change (regime shift) in the spatial distribution of the juvenile North Pacific albacore in the waters of the US west coast in response to alteration in the condition of the SST and PDO. SINGH et al. (2017) determined significant influence of the SST, PDO and ENSO variability on the recruitment and spawning biomass of the North Pacific albacore from 1970 to 2012. In the North Pacific Ocean there is a major dominant mode of climate index called the Pacific decadal oscillation (PDO) which occurs over decadal time scales and affects oceanic temperatures both in the Northern and the Southern Pacific (MANTUA et al. 1997, ZHANG et al. 1997, DESER et al. 2004, CHHAK et al. 2009, LINSLEY et al. 2015).

The objectives of this study were 1) to elucidate the relationship between the recruitment (R), female spawning stock biomass (SSB) and the reproductive success (RPS) of the North-Pacific stock of the albacore tuna, 2) to determine if the albacore R, SSB and RPS time series experienced a regime shift due to a regime shift in environmental conditions, 3) to determine if inter-decadal environmental and climatic variation of the sea surface temperature (SST), El Niño Southern Oscillation (ENSO), and the Pacific decadal Oscillation (PDO) have significant impact on the stock-recruitment relationship of the North Pacific albacore tuna.

Materials and Methods

Data sources

Stock assessment of commercial North Pacific albacore tuna harvests are compiled and reported by the Albacore Working Group of the International Scientific Committee for Tuna and Tuna-like Species (ISC) (ISC 2014). Data is gathered from the ISC member countries of Japan, USA, Korea, Chinese Taipei and Canada. Also included is information from Inter-American Tropical Tuna Commission (IATTC) and China as well as some countries under the Western and Central Pacific Fisheries Commission (WCPFC). Fishing gears and methods used include gillnet, pole and line, purse seine, troll, longline including harpoons, handlines and recreational gear. From 1970 to 2012, the annual recruitment (R) and female spawning stock biomass (SSB) data was estimated by the ISC using an age-structure, length-structure and sex-structured Stock Synthesis assessment model fitted to time series of catch and size structure data (ISC 2014). R and SSB data from the base case assessment model wereextracted from the ISC report and the annual recruits per spawning biomass was calculated from this. Further details on the techniques and methods for the collection and calculation of the annual R and SSB data are described in ISC (2014). The R and SSB estimates by the ISC are assumed to be reliable with the deviations noted in ISC (2014). The geographical range for the albacore stock distribution was restricted to the North Pacific region defined within the coordinates of 50°N – 120°E, 10°N – 120°E, 50°N

– 120ºW, 10ºN – 120ºW presented in Figure 1. Previous studies have identified the North Pacific albacore stock as discrete and reproductively isolated from other albacore stocks (UEYANAGI 1969, SUZUKI et al. 1977, CHOW and USHIAMA 1995, RAMON and BAILEY 1996, TAKAGI et al. 2001, ICHINOKAWA et al. 2008).

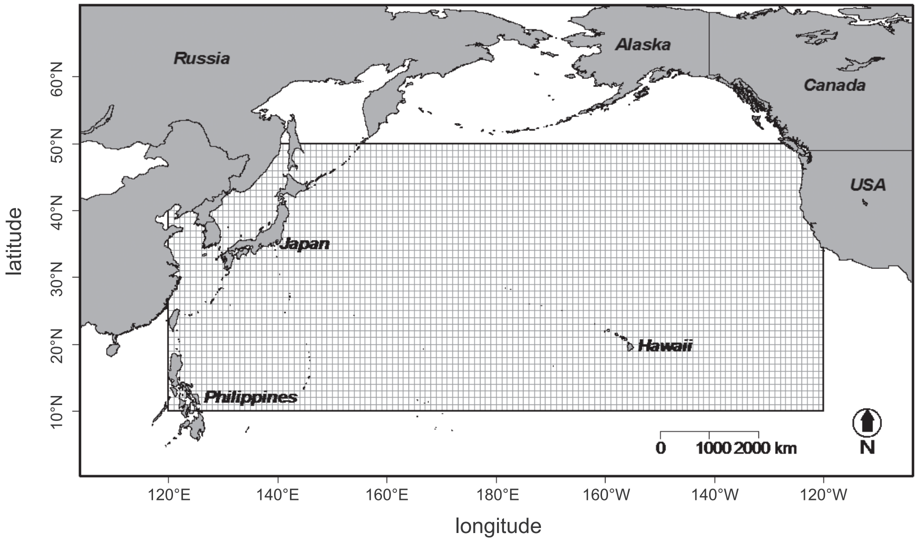

Fig. 1. Area of the study of North Pacific albacore tuna recruitment and spawning stock

For each year the recruitment is estimated as the number fish at age-0 and the SSB represents the total weight of reproductively mature female specimens at the initiation of the spawning season. Pacific albacore tuna recruitment and spawning period typically occurs only once per year as determined by CHEN et al. (2010). UEYANAGI (1957) determined that 50% of the North Pacific albacore reaches maturity at age-5 and 100% by age-6 and this maturity ogive was used for the calculation of the SSB as reported in ISC (2014). Recent work of FARLEY et al. (2014) and assessments by ISC (2011) also support these estimations. The spawning zone for albacore occurs in the North Pacific between Taiwan, Hawaii and Philippine waters within the latitudes of 10ºN and 25ºN and longitudes of 155ºW and 120ºE (UEYANAGI 1957, OTSU and UCHIDA 1959, YOSHIDA 1968, CHEN et al. 2010) – Figure 1. Like most fishery populations, the stock-recruitment pattern of the North Pacific albacore displays a scattered distribution (Figure 2).

For comparing the North Pacific albacore tuna stock variability with environmental variables, the SST and other temperature related climatic anomalies data set were obtained. SST monthly data on a 1º by 1º resolution for the years 1970 to 2012 was extracted for the study area (Figure 1) from Hadley Centre Sea Ice and Sea Surface Temperature data set (HadISST) with further description and compilation details available from RAYNER et al. (2003). The NOAA/ESRL Physical Sciences Division

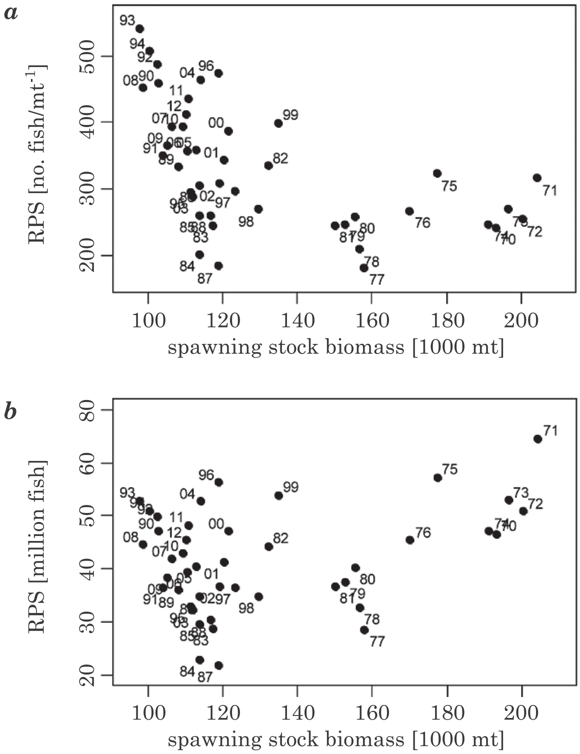

Fig. 2. Pattern of the recruits per spawning biomass (RPS) against the spawning stock biomass (SSB) (*a*) and the stock-recruitment distribution (*b*) for the albacore tuna (*T. alalunga*) in the North Pacific Ocean for the years ranging from 1970–2012

(Boulder, Colorado, USA), website (http://www.esrl.noaa.gov/psd last accessed 02 March 2016) was accessed to obtain monthly grouped time series data on the climatic indexes of the Pacific decadal oscillation (PDO) and the Multivariate El Niño Southern Oscillation Index (ENSO).

Regimes and density-dependent effects

SAKURAMOTO (2012), SINGH et al. (2014) and WADA and JACOBSON (1998) outlined the method for identifying different regimes in the fish stock parameters and determining the presence of density dependent effects in time series data. North Pacific albacore R, SSB and RPS time series were explored for observable and sustained differences in trend over the years from 1970 to 2012. Existence of any such trends would indicate a possible "regime shift". An observable regime shift in a fish stock usually results in response to changes in environmental conditions and as such a regime shift should also be present in environmental conditions which have relationship with the North Pacific albacore stock time series.

We carried out statistical analysis to investigate the stock recruitment relationship of albacore tuna for the presence of different density-dependent effects. Simple least-squares regression was applied for log(RPS) against log(SSB). This technique has limitations as the presence of possible observational errors in R and SSB can cause overestimation and underestimation of the RPS (SAKURAMOTO and SUZUKI 2012, STÖCKL et al. 1998). For validation of the results we applied regression of log(R) against log(SSB) as this method is more robust and less sensitive to observational errors. Results indicating slopes which are significantly different from unity at $p < 0.05$ were considered positive for the presence of different density dependent effects and a regime shift in the albacore tuna stock-recruitment relationship.

Simple least-squares regression has some drawbacks as it does not assume the presence of observation errors in the independent variable and without observation error the parameter estimates derived from least squares regression will have high tendency to exhibit bias according to STÖCKL et al. (1998). The Deming regression method (MARTIN 2000) assumes the presence of errors in both the independent and the dependent variables. The Deming regression algorithm developed by AOKI (2012) was applied to log(RPS) against log(SSB) and log(R) against log(SSB), with the assumption that the variance ratio in R and SSB is equal to 1. Variance ratios of 1, 2, 3, ..., 5 were also used for sensitivity tests. The parameters of Deming regression were compared with the least-squares regression.

The Ricker model (RICKER 1954) shown below (Equation 1) was used to further investigate the stock recruitment relationship. An error term was included as an assumption for the presence of observational and/or process errors. A multiplicative error term was added to the model instead of an additive one as the variability was expected to be different in different areas of data.

$$R = a \cdot SSBexp^{-bSSB} \cdot exp^{\epsilon} \tag{1}$$

Where a and b represent the density independent and density dependent parameter respectively. The term is the assumption of variability around the model. To fit the model using the R statistical software the linearized form of Ricker model (Equation 2) was used (QUINN and DERISO 1999):

$$\log(R) = \log(a \cdot SSBexp^{-bSSB}) + \epsilon \tag{2}$$

The R and SSB data was divided into different year ranges between 1970 to 2012 to determine if density dependent patterns exist in the stock recruitment relationship. Different stock-recruitment models using environmental variables were also investigated and discussed. All statistical analysis was performed using the language "R" software version 3.4.0 (R CORE TEAM 2017).

Results

Regimes and density-dependent effects

The stock trajectory of the albacore tuna RPS in Figure 3 shows a sustained change in the time series trend which occurs between 1987 to 1990 with a lower RPS average from 1970 to 1988 and a higher average from 1989 to 2012 which coincides with the trend for R where a difference in trend can also be between 1970 to 1988 and 1989 to 2012. For SSB there is a trend difference between the years 1970 to 1982 and 1983 to 2012.

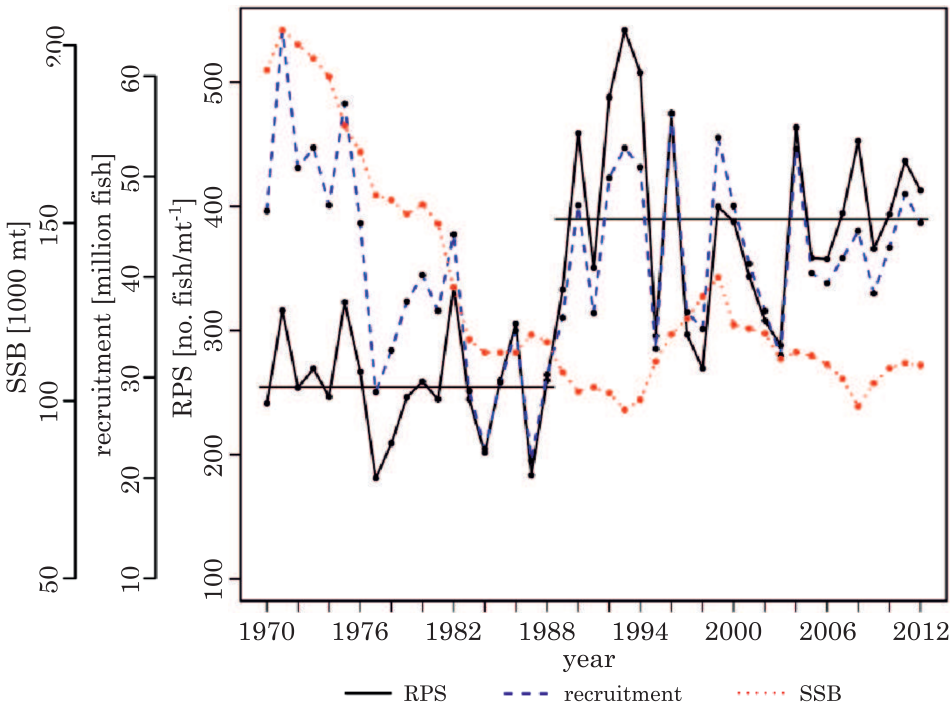

Fig. 3. The recruitment (R), spawning stock biomass (SSB) and recruits per spawning biomass (RPS) time series trajectory of the albacore tuna (*T. alalunga*) in the North Pacific Ocean for the years ranging from 1970–2012

Such changes in the stock trend indicate the possibility of different density-dependent effects and a possible regime shift. The changes or regimes of the stock parameters is possibly resulting from changes in environmental conditions and should coincide with environmental conditions exhibiting relationship with the albacore stock (SAKURAMOTO 2012).

From Figure 3, it can be seen that for some years, when the SSB is low, R is high and so is RPS. This may be a result of the smaller number of larvae which experience an abundance of food and significantly reduced competition and cannibalism, which would lead to a larger survival rate of the larvae from the initial high natural mortality. Figure 4 shows

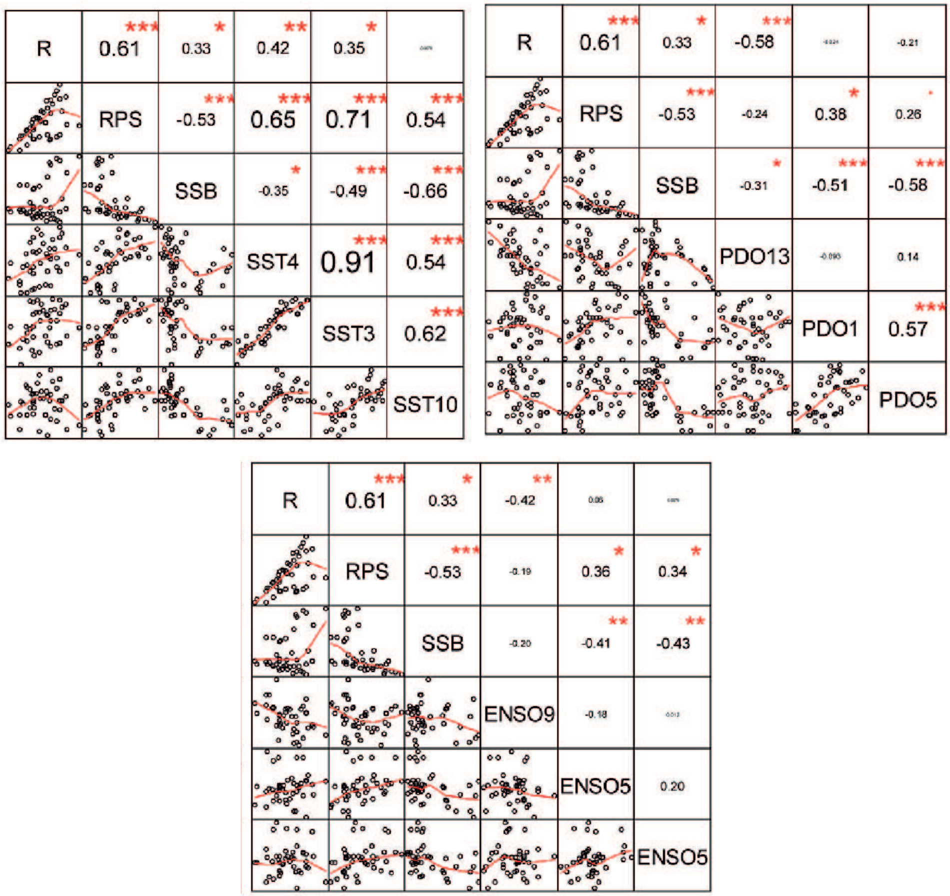

Fig. 4. Scatterplot matrix showing absolute correlations, kernel density overlays with significance asterisks ($p < 0.05$*, $p < 0.01$**, $p < 0.001$***) of the relation between the recruitment (R), recruits per spawning biomass (RPS) and spawning stock biomass (SSB) of the North Pacific albacore tuna (*T. alalunga*) with the environmental variables of SST, PDO and ENSO for the years ranging from 1970–2012. The numbers refer to the months (1, 2, ..., 12) and the number 13 is the annual average

the correlation between the R, RPS and SSB of the North Pacific albacore tuna with the environmental factors of the SST, PDO and ENSO. SST of the study area (Figure 1) was identified as the principle environmental factors correlating with the North Pacific albacore tuna stock. Figure 5

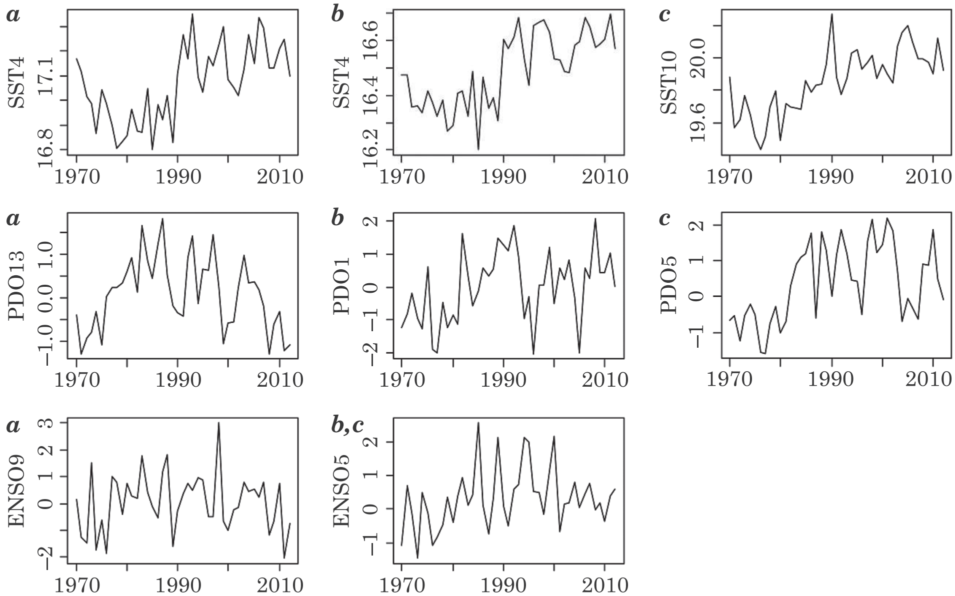

Fig. 5. Environmental conditions time series trend for SST, PDO and ENSO from 1965 to 2012 which exhibited significant correlation with R, SSB, and RPS as shown in Figure 4. The letters refer to the stock parameter for which the particular environmental condition shows the highest correlation (*a* – R, *b* – RPS, *c* – SSB).The numbers refer to the months (1, 2, … 12) and the number 13 is the annual average.

shows the time series trend of the environmental variables from Figure 4, where it can be seen that there is a visible change in the trend of the SST time series around the years 1987–1989 which corresponds to the change in trend for the R and RPS.R and RPS trajectories plots with their respective correlated SSTs are shown in Figure 6. The changes in trajectories coincide quite well indicating that significant proportion of changes in stock behavior of the North Pacific albacore tuna are in response to SST time series dynamics including the observed regime shift.

Figure 7 shows the results of regression analysis applied to log(RPS) against log(SSB) and log(R) against log(SBB). The slope of the regression line adopted for log(RPS) against log(SSB) was -0.714 (p = 1.12 $\cdot 10^{-4}$) and 95% confidence interval of (-1.052, -0.377). The negative slope was statistically significant and positive for the presence of different density dependent effects and indicated a regime shift. According to the simulations by

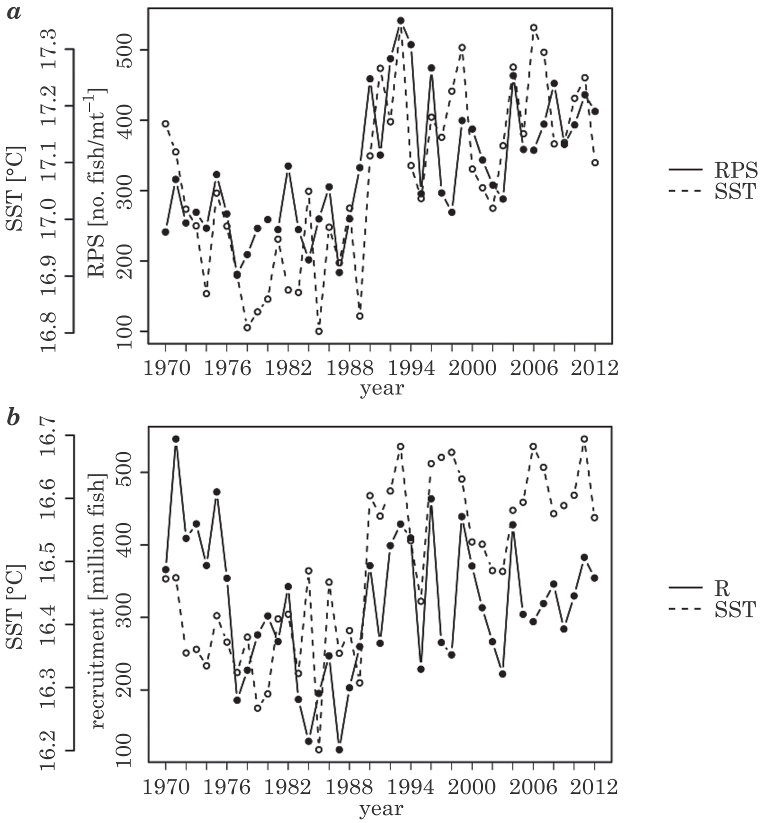

Fig. 6. The recruitment (R) and recruits per spawning biomass (RPS) time series plots of with the respective correlated SSTs from Figure 4 and Figure 5. The similarities in the trend and coinciding shift in trend pattern can be seen indicating significant influence of the SST on albacore tuna (*T. alalunga*) R and RPS trajectory

(SAKURAMOTO 2012) and as shown by STÖCKL et al.(1998), using RPS for regression analysis can lead to potentially flawed results in cases where observation errors are present. To validate the results, we applied regression analysis to log(R) against log(SSB) which is a more reliable method. The regression line slope was 0.110 (p = 3.01×10^{-2}) with 95% confidence interval of (0.010, 0.192) which was significantly less than unity.

When Deming regression was applied to log(RPS) against log(SSB) the slope was significantly different from unity with a slope of -1.560 at 95%confidence interval of (-2.618, -1.094). For log(R) against log(SSB) the slope was 1.475 and not significantly differ from 1.0 as the 95% confidence interval was -12.160, 7.127). The ratio of variance for Deming regression of log(R) against log(SSB) was assumed to be 1.0 and when the variance ratio was increased to 2.0 (Figure 8) the results did not significantly differ

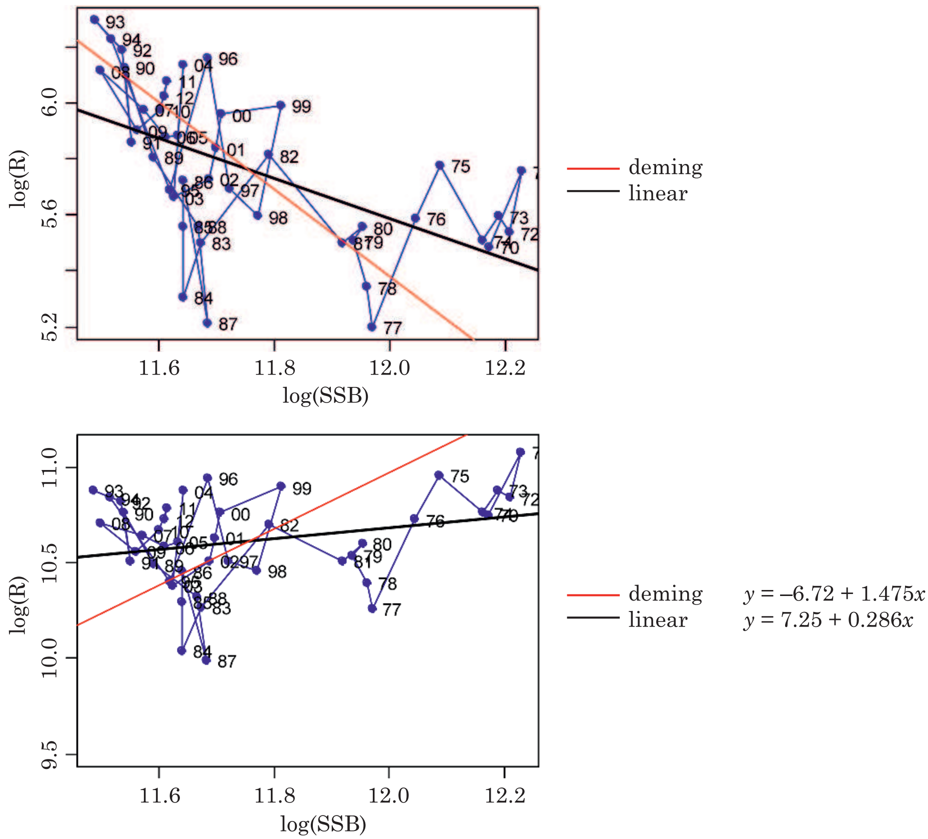

Fig. 7. The relationship between log(RPS) against log(SSB) and log(R) against log(SSB) using Deming regression and simple linear regression. For log(RPS) against log(R) the correlation coefficient was (cc = -0.555), for log(R) against log(SSB) (cc = 0.258)

indicating the absence of different density dependent effects and a proportional stock-recruitment relationship shown in Equation 3 and Equation 4

$$\log(R) = \log(l) + \log(SSB) + \varepsilon \quad (3)$$

$$R = l \cdot SSB + \varepsilon \quad (4)$$

where l is a parameter estimate and ε is an unexplained variable. However, when the ratio of variance was augmented to ≥ 3.0, the slope was significantly different from 1.0 (Figure 8). For the variance ratio of 3.0 the slope was 0.451 with 95% confidence interval of (-0.292, 0.842). By raising the variance ratio to ≥ 3.0 the slope was significantly different from unity indicating that a proportional model such as Equation 3 and Equation 4 cannot be used to describe the stock-recruitment relationship of the North

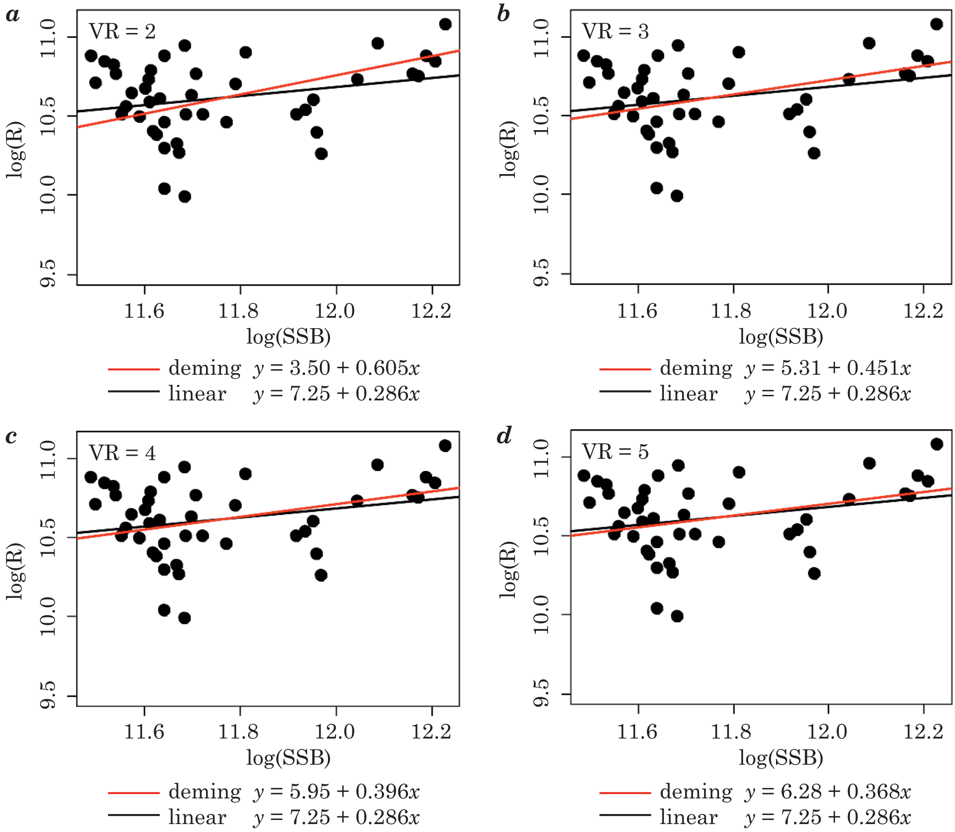

Fig. 8. For Deming regression of log(R) against log(SSB) with the slopes for different variance ratios (VR = 2, 3, …, 5) are shown. Correlation coefficient is (cc = 0.258)

Pacific albacore tuna. The estimated SSB and R by the ISC had significant annual standard deviations (SD) (ISC 2014). For example, the SD for SSB was 30,203 mt for 1993 and 73,551 mt for 1971. The SD for R was 7.4 million fish for 1987 and 18.8 million fish 1971. This would mean that the stock-recruitment variance would be expected to be high.

When stock recruitment relationship was fit using the Ricker model (Equation 2), a density dependent pattern was shown with $p < 0.001$ (Figure 9*a*). When Ricker model was applied to the different regimes, regime 1 (1970–1988)had a large *p*-value ($p = 0.450$) suggesting the density independent model as a better fit (Figure 9*b*) whereas regime 2 (1989–2012) showed density dependent pattern ($p < 0.001$) (Figure 9*b*).

The inability of the proportional models from Equation 3 and Equation 4 to describe the stock-recruitment relationship of the North Pacific albacore tuna and the presence of different density dependent effects indi-

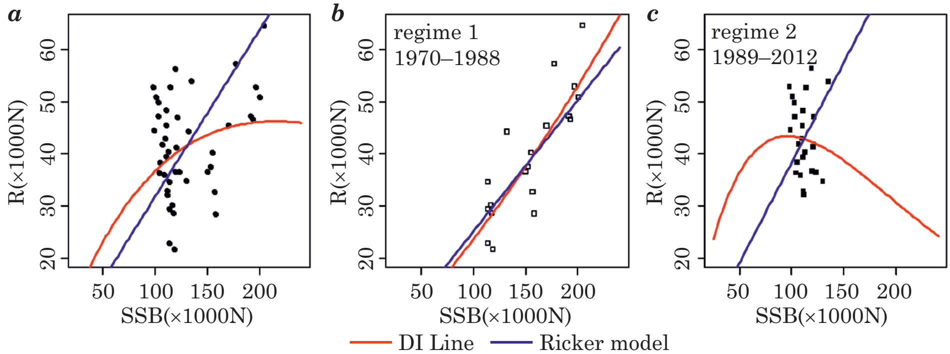

Fig. 9. The Ricker model fit to the stock recruitment relationship of the North Pacific albacore tuna. DI is the density independent line; (*a*) Data from 1970 to 2012 show density dependent relationship with $p < 0.001$; (*b*) regime 1 data from 1970 to 1988 had a large p-value ($p = 0.450$) suggesting the density independent model as a better fit; (*c*) regime 2 data from 1989–2012 had a small p-value ($p = 0.001$) suggesting the density dependent model as a better fit

cates strong influences of environmental condition on its stock characteristics. Equation 3 and Equation 4 can be modified to incorporate the environmental factors resulting in Equation 5 and Equation 6

$$\log(R_t) = \log(l) + \log(SSB) + f(y_{i,t-n}) + \varepsilon \quad (5)$$

$$R_t = l \cdot SSB_t, e^f \cdot f(y^{i,t-n}) + \varepsilon \quad (6)$$

where $f(.)$ denotes a function that takes into account the influence of the environmental conditions in the year t-n. y_i denotes the environmental factors as well as the ecological factors with $y_i=[y_1,y_2,\ldots,y_k]$. k is the number of environmental and ecological factors exhibiting relationship to the albacore tuna stock parameters. This case is apparent from the work of Singh et al. (2017) where the environmental factors of SST and PDO were incorporated into the generalized additive models to explain the R trajectory of the North Pacific albacore tuna as shown in Equation 7

$$\log(R_t) = 1{,}284 \cdot \log(SSB_t) + 0.450 \cdot SST4_{t-2} - 11.423 \cdot PDO13_t + \\ + 0.661 \cdot (SST4_{t-2} \cdot \mathrm{PDO}_{u,t}) + \varepsilon \quad (7)$$

where R represents the albacore recruitment for year t, SST and PDO are the independent variables of the sea surface temperature and the Pacific decadal oscillation and ε is a normally distributed unsolved random variable. In Singh et al. (2017), the individual and combined effects of the environmental conditions and SSB were tested using the equation 5 type. The combined effect of environmental conditions and SSB resulted in the most significant model through AIC and p-value comparison resulting in the selection of Equation 5, $R^2 = 0.606$ ($p = 1.41 \cdot 10^{-10}$). PHILLIPS et al. (2014) also came up with a threshold generalized additive mixed model (tGAMM) for the North Pacific albacore tuna from 1961 to 2008 in the US West coast which incorporated the environmental variables of SST and PDO with $R^2 = 0.290$ ($p \leq 1.00 \cdot 10^{-4}$). This provides further evidence that environmental factors of SST and PDO have significant influence on the stock-recruitment relationship of the North Pacific albacore tuna.

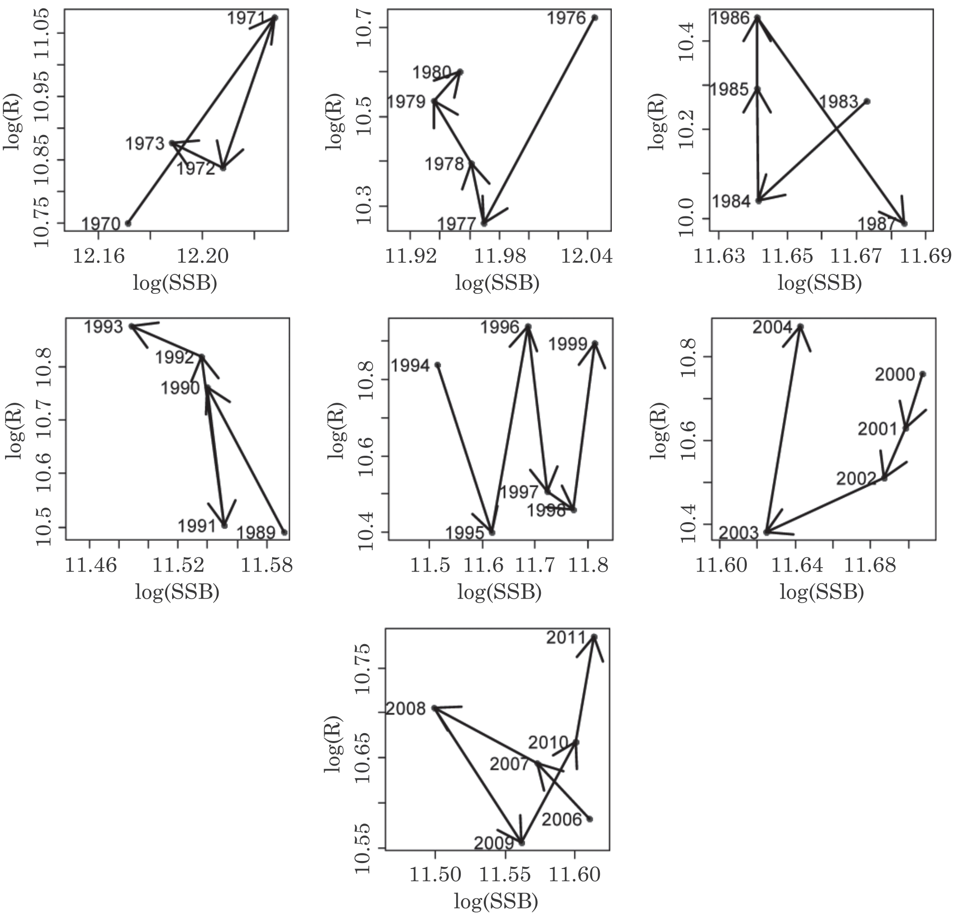

Fig. 10. Stock-recruitment relationship of the North Pacific albacore tuna. Log(R) and Log(SSB) denote the logarithm for the recruitment and female spawning stock biomass in year *t*. The clockwise and anticlockwise loops can be seen. (i) 1970–1973; (ii) 1976–1980; (iii) 1983–1987; (iv) 1989–1993; (v) 1994–1999; (vi) 2000–2005 (vii) 2006–2011

SAKURAMOTO (2015) studied the stock-recruitment relationship of the Pacific stock of the bluefin tuna (*Thunnus thynnus*) and Japanese sardine (*Sardinops melanostictus*). The study showed that the long-termcyclic fluctuations in environmental conditions result in clockwise and anticlockwise loops in the stock recruitment relationship. The characteristics of such relationships are dependent upon the cycle of the environmental conditions and the reproductive cycle of the fish species. Indeed, the presence of clockwise and anti-clockwise loops can be seen for the stock recruitment relationship of the albacore tuna (Figure 10).

If we take Equation 5 as our main model then the stock recruitment relationship of albacore tuna will be more than 2-dimensional. Figure 11*a* shows the 3-dimensional plot when log(R) is plotted with log(SSB) and SST in April from Equation 5. Due to the large number of data points, a clear relationship cannot be observed. Figure 11*b* shows that increase in SSB and SST causes R to increase. As it can be seen, the complete relationship is better represented by the 3-dimensional construct compared to the

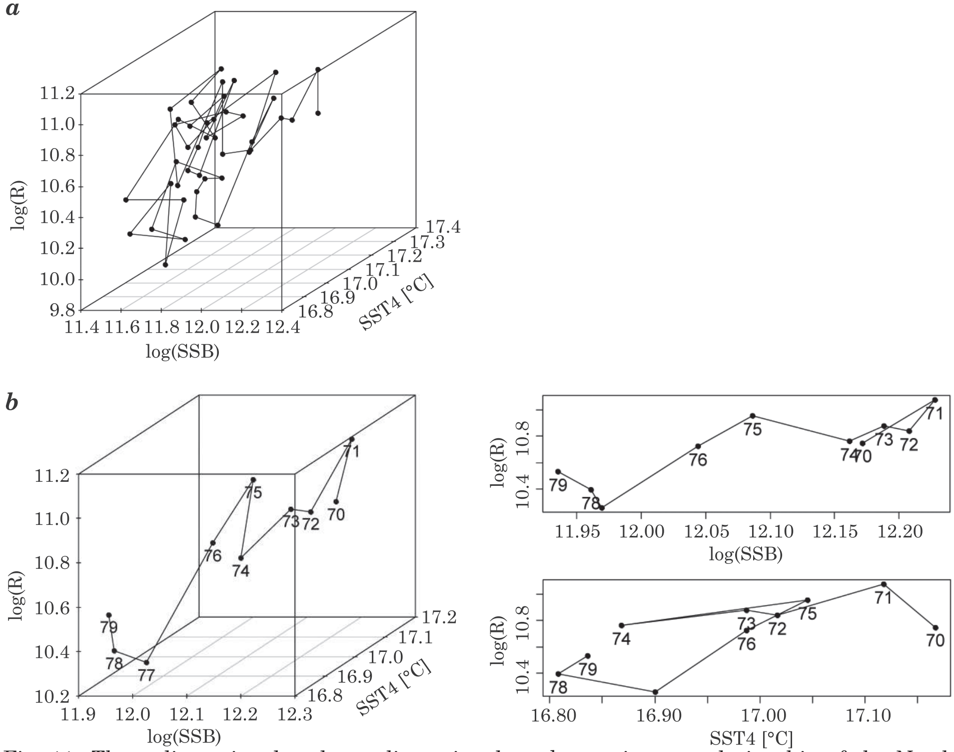

Fig. 11. Three dimensional and two dimensional stock-recruitment relationship of the North Pacific albacore tuna; (*a*) R, SSB and SST in April from 1970–2012; (*b*) 1970–1979

2-dimensional construct. Figure 12*a* shows the 3-dimensional construct of log(R) against log(SSB) and annual average PDO. In Figure 12*b* the looping characteristics of the stock-recruitment relationship in relation to

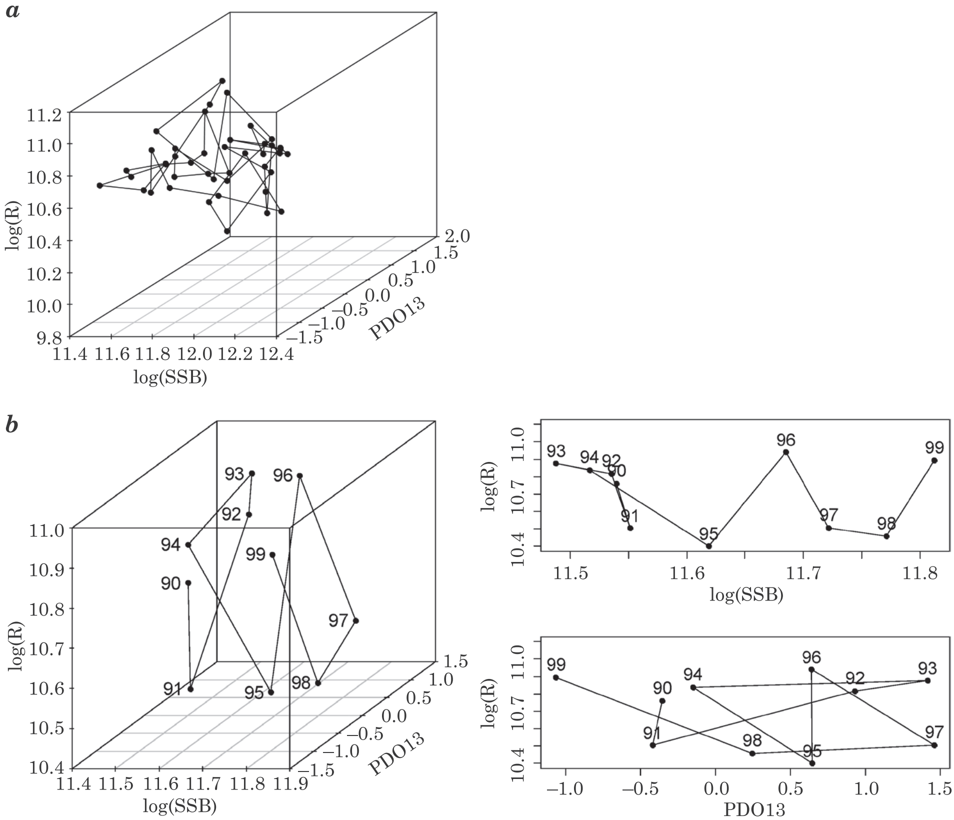

Fig. 12. Three dimensional and two dimensional stock-recruitment relationships of the North Pacific albacore tuna; (*a*) R, SSB and annual average PDO from 1970–2012; (*b*) 1990–1999

the PDO can be seen. This cannot be seen in the 2-dimensional models. Figure 11 and Figure 12 make it evident that the recruitment dynamics of the North Pacific albacore tuna cannot be determined by the SSB alone but together with the environmental conditions as shown by Equation 7.

Discussion

This work was undertaken to identify if the stock-recruitment relationship of albacore tuna exhibit density-dependent effects and indicate a possible regime shift in the environmental conditions. Significant density-dependent effects of the SSB were detected on the North Pacific albacore tuna R and RPS. The changes in R and RPS pattern coincide with the annual trajectory of the SST (Figure 5, Figure 6) where a shift in the trajectory pattern was observed for the same period as that for the R and RPS

(Figure 3). This indicates that a possible regime shift in the North Pacific SST for the geographical coordinates of 50ºN – 120ºE, 10ºN – 120ºE, 50ºN – 120ºW, 10ºN – 120ºW (Figure 1) has occurred and has had significant impact on the stock-recruitment relationship of albacore tuna. Indeed, highly significant relationship between R, RPS, SSB and SST can be seen in Figure 4. PHILLIPS et al. (2014) investigated the correlation between the spatial distribution of the North Pacific albacore tuna and the local environmental variability of the SST in the US West Coast for a period of 48 years from 1961 to 2008. SST had significant and spatially variable correlation with albacore tuna CPUE and a significant geographical shift in the relationship was identified before and after the threshold year of 1986. Most significant tGAMM model was formed using SST and PDO as the independent variables. SST was the principal component that exhibited a regime shift which was mostly responsible for the shift in the spatial distribution of the albacore tuna juvenile CPUE before and after the threshold year.

With reference to Figure 3 and Figure 6, SST trend and R, RPS trends show changes in the same period from 1987 to 1989. Since the albacore R is estimated as age-0 fish, it makes sense that albacore R as well as RPS level will be affected in same period of the SST regime-shift. For the SSB, a change in the trend can be seen before and after 1982 for SSB which is a lag of 5–7 years when comparing with trend change of the R and RPS. This lag period coincides with the maturity ogive for North Pacific albacore tuna which is between 5–6 years (UEYANAGI 1957, ISC 2011, FARLEY et al. 2014). LEHODEY et al. (2003) showed shifts in trajectory patterns and the presence of regime shift indicators in the recruitment time series of skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*) in the Western and Central Pacific Ocean (WCPO) and the South Pacific albacore tuna from the early 1960s to the late 1990s. These patterns were shown to correlate to the positive and negative PDO phases and the ENSO time series pattern. The relationship of the climatic variables of PDO and ENSO with South Pacific albacore tuna has also been shown by SINGH et al. (2015). Indeed, significant correlations were detected between the albacore tuna R, RPS and SSB and the climatic variability of PDO and ENSO (Figure 5).

When simple regression analysis was applied, density-dependent effect was detected for log(RPS) versus log(SSB) as well as for log(R) versus log(SSB). When Deming regression was applied assuming the presence of observation errors, density-dependent effect was detected for log(RPS) versus log(SSB) but not for log(R) versus log(SSB). If we assume a variance ratio of < 3.0 in R and SSB then the findings of simple linear regression and Deming regression do not synchronize. However, if we assume a variance ratio of ≥ 3.0 then the results for simple linear regression and Deming regression coincide well with each other and both indicate the presence of different density-dependent effects in the stock-relationship. The Ricker model revealed different stock recruitment relations for the two albacore stock regimes. This further supports the occurrence of different density dependents effects in the stock recruitment relationship of the North Pacific albacore tuna stock indicating the likely influences of extrinsic factors on the trajectory of the albacore tuna.

The relationship between R and SSB is biological in nature and there is no doubt that one affects the other. Environmental factors influence the stock characteristics of albacore tuna between the successive generations of R and SSB. It is evident that using environmental factors leads to the improvement of the stock-recruitment relationship (Equation 7) for the North Pacific albacore tuna. The stock-recruitment relationship can be represented by Equation 5. That is,

$$\log(R_t) = \log(l) + \log(SSB) + f(y_{i,t-n}) + \varepsilon \tag{5}$$

The stock recruitment relationship in this case is multidimensional, incorporating the influences of various biotic and abiotic variables.

The results presented here still remain semi-conclusive and form the platform for further studies. The models presented are based on the best estimates of variables that are available and come with their own sources of possible errors. The stock-recruitment variability and uncertainties are expected as the estimates of R and SSB are based on fishing activity data from different countries with fishing methods differing between as well as within countries. The fishing season, period and area also differ among different data sources used for the estimates (ISC 2014). The actual stock--recruitment relationship can be masked by observation and/or process errors (SAKURAMOTO and SUZUKI 2012) which likely exist in the data used in this study and further work is needed to elucidate this. Different fishing regimes will have variable influence on albacore population structure inclusive of the spawning stock structure, spawning success and various other variables under the stock recruitment variability. The key uncertainties noted in the data used in this study are insufficient sex-specific size data and the unavailability of updated parameters of maturity and natural mortality (ISC 2014). The time series data ranges over a period of more than four decades. Over this period there has been changes in fishing technology and data recording system have also developed. The efficiency of one unit of effort would be expected to improve with improvement of technology. For example, in the 1970s the efficiency of a fishing hook would be expected to have been lower compared to a fishing hook in 2010. As such, a unit of effort in 1970 may not be the same as a unit of effort in 2010. Data recording and storage systems have also seen improvement. One would expect higher reliability (lower stock-recruitment variability) of recent data in comparison to earlier recorded data.

Estimates derived from the stock-recruitment relationships are fundamental for fisheries stock management. Quantities derived from the relationship are used to set fishing quota limits and overexploitation reference points. Stock-recruitment parameter estimates are significantly influenced by measurement errors in recruitment and spawning biomass including time series bias. Such uncertainties make the determination of stock-recruitment relationships is a challenging task for fisheries stock assessors (HILBORN and WALTERS 1992, SAKURAMOTO and SUZUKI 2012).

The SST data for the study area was based on the HadISST as described in RAYNER et al. (2003). HadISST was based on a combination of SST data from a diversity of methods. The necessary bias adjustments were made to the data. For the SST up to 1981 the reduced space optimal interpolation (RSOI) method was applied (KAPLAN et al. 1997). For SST from 1982 to 2012, RSOI was applied to the combination of in situ and satellite SST. Further bias adjustments were made to the data following the method of JONES et al. (2001) to homogenize the SST grid-scale variance. PDO index is estimated using the SST in the Pacific north of 20°N (MANTUA et al. 1997). ENSO calculation is determined using the variables of wind indexes, sea-level pressure, SST, atmospheric conditions and surface air temperature (WOLTER and TIMLIN 1998) with each variable having its own possible sources of bias such as that mentioned in ZHANG et al. (2013).

WANG and LIU (2005) tested the reliability of AIC in selecting the model fit for various stock-recruitment relationships. The results ascertained the validity of AIC in selecting the most suitable relationship. SINGH et al. (2017) used the AIC for model selection, resulting the model represented by Equation 7. This gives validity to the stock-recruitment relationship presented in this work represented by Equation 5. Log transformation of the relationship represented by Equation 5 stabilizes the residual variance of the dependent and independent variables and reduces the effects of possible observation and process errors present in the variables (HILBORN and WALTERS 1992).

The stock–recruitment models presented here may are based on dependent and independent variables. As outlined previously, each variable comes with its own bias. The estimated variables are adjusted for bias as efficiently as presently possible. Based on this and the modeling techniques used, the models can be expected to have sufficient reliability, however bias is still expected to be present in the stock-recruitment relationship. Detailed studies of the North Pacific albacore tuna age-class and its relation to the SST are needed to conclusively determine the stock-recruitment relationship of the North Pacific albacore tuna and the environmental regime shift. With the results presented here, albacore tuna fishery managers need to be wary of the influences following an environmental regime shift especially for the SST where albacore R and RPS trajectory pattern closely follow the SST behavior. Such events can influence stock abundance both with time and distribution and managers need to adjust their harvesting plans accordingly.

Acknowledgements

This work was supported by the University Research and Publication Committee (URPC), Fiji National University, Koronivia, Fiji. The University of Fiji is also acknowledged for providing the resources and administrative support necessary for carrying out the write-up of the project. We thank all the researchers, scientists and all the individuals involved in the collection of the North Pacific albacore tuna data for the International Scientific Committee for Tuna and Tuna-like Species. The team at the Hadley Center in the United Kingdom is acknowledged for collecting and disseminating oceanic temperature data. We also acknowledge the efforts of The National Oceanic and Atmospheric Administration (NOAA) team for compiling climatic data and making it available.

Accepted for print 18.08.2017

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