

Large-scale climatic variability affects the dynamics of tropical skipjack tuna in the Western Pacific Ocean

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The role of climate variability in determining the fluctuations of fish populations had been a traditional problem in ecology. In this paper, we studied the role of the Southern Oscillation Index (SO) and the Pacific Decadal Oscillation (PDO) on the population dynamics of the western stock of the skipjack tuna *Katsuwonus pelamis*. Our analysis was based in three sequential steps: a diagnostic approach to deduce what kind of population dynamic model should be more appropriate, the modelling of capture per unit of effort data through a logistic model, and the use of population dynamic theory for analyzing the effect of exogenous perturbations. We find that direct and one-year lagged negative PDO effects and one-year lagged negative SO effects were needed to explain annual tuna fluctuations. Models including the combined effects of these climatic indexes explain 80% of the variance in tuna fluctuations. In addition, these models provided very accurate predictions of independent skipjack tuna observed dynamics. This result is encouraging because the inherent variability in CPUE data and the not well determined link between climate and ecological processes. Finally, this study demonstrates that simple models can offer reasonable explanations and accurate predictions of tuna fluctuations, provided they are based on a sound theoretical framework.

Understanding and predicting the influence of climate on the animal population fluctuations has been the subject of numerous past studies among fisheries biologists (Hjort 1914, 1926) and population ecologists (Elton 1924). Nowadays, because the pressing issue of predicting the effect of climatic change there is an increasing amount of empirical evidence determining the effects of climate on natural populations (Stenseth et al. 2002, Walther et al. 2002). In particular, several studies had determined the close relationship between climate variability and marine ecosystem dynamics (Hayward 1997, Walther et al. 2002, Ledohey et al. 2006). The common approach for studying the influence of climatic-oceanographic variables on population dynamic processes in marine ecosystems had been the use of statistical relationships between time series of population processes (recruitment or catch rates) and environmental variables (MacKenzie and Köster 2004, Stein and Borovkov 2004, Waluda et al. 2004) or correlation analyses based in the time or frequency domain (Ravier and Fromentin 2001, Ménard et al. 2007). Although these procedures can be useful for detecting relationships between variables and for showing common signatures in the time or frequency domain, they fail to provide explanations based in general and basic population dynamic principles (Berryman 1999, Turchin 2003, Ginzburg and Colyvan 2004).

Previous studies have reported the influence of climatic variables on the population dynamics of different tuna species. For example, in the Indian Ocean a strong association has been observed between catch rates of the bigeye *Thunnus obesus* and the yellowfin *Thunnus albacares* tunas and the El Niño Southern Oscillation (ENSO) and the Indian Oscillation Index (IOI) (Ménard et al. 2007). In the Atlantic Ocean, the long-term fluctuations in catches of the bluefin tuna *Thunnus thynnus* seem to be negatively related to trends in sea surface temperature (Ravier and Fromentin 2001). In the Pacific Ocean, the abundance and spatial distribution of tuna populations are influenced by the pervasive influence of the El Niño Southern Oscillation (ENSO) phenomenon (Ledohey et al. 1997, 2003). Previous studies have shown strong effects of the ENSO on the spatial movements and the vertical distribution of the skipjack *Katsuwonus pelamis* and the yellowfin tuna (Ledohey et al. 1997, 2003). In terms of total fluctuations in stock size and recruitment rates, both species appear to be positively influenced by the El Niño events and by the warm phases of the Pacific Decadal Oscillation (Ledohey et al. 2003). The understanding of the relationships between environmental variability, productivity and tuna abundance in the Western Central Pacific pelagic ecosystem had been approached by using a spatial environmental population model (SEPODYM) (Bertignac et al. 1998).

This is a coupled population dynamic model that combines information on prey production and tuna age-structure in a spatial dynamic setting described by an advection-diffusion equation (Lehodey et al. 2003).

In sum, we may ask whether something new can be done for understanding the relationships between tropical Pacific tuna populations and climate. Certainly, we think that there are some important reasons for analyzing tuna fluctuations under another perspective. First, models previously used are complex and need a large amount of data to be parameterized, which is usually not available in many populations. In contrast, here we propose the use of theoretical population dynamics models as a platform for deciphering the ecological effects of climatic oscillations (Berryman and Lima 2006, Lima and Berryman 2006). The advantage of using theoretical models is that they provide a solid and simple background to analyze and interpret fluctuations in animal population (Royama 1977, 1992, Berryman 1999, Ginzburg and Colyvan 2004, Ginzburg and Jensen 2004). Moreover, models used in the present study are easy to fit to data, parameters are ecologically interpretable, and their predictions can be tested against independent data. Second, we used the year as the time unit in the time series analyses, while previous studies correlated monthly CPUE estimates with monthly climatic indexes. We chose this time unit because inter-annual fluctuations can be more useful for revealing ecological processes in nature (Berryman 1999). Third, no study to the date has considered the possibility that the combined effects of North and South Pacific Ocean could explain tropical tuna fluctuations. Our analysis of the western stock of the skipjack tuna *Katsuwonus pelamis* Pacific populations is based in three sequential steps: a diagnostic approach to determine what kind of population dynamic model is most appropriated (Berryman 1999), the modelling of the observed dynamic through a simple theoretically-based model, and the use of a theoretical framework for analyzing exogenous perturbations (Royama 1992).

Data and methods

Focal species, fisheries, and abundance data

Pacific skipjack tuna fisheries

Skipjack tuna is a common inhabitant of the tropical and subtropical waters of the Pacific Ocean (Hampton 2002). In the Western Central Pacific Ocean (WCPO) the large scale movement and mixing rates suggest a single stock (Lehodey et al. 1997, Sibert et al. 1999), which was the focus of our analyses (Fig. 1). Skipjack tuna is a rapid growth species compared with other tunas and it has a shorter life cycle with a maximum life-span of 4–5 yr (Hampton 2002). In the Pacific Ocean, skipjack tuna fisheries can be classified into the Japan distant-water and offshore pole-and-line fleets, domestic pole-and-line fleets based in island countries, artisanal fleets based in the Philippines, eastern Indonesia and the Pacific Islands, and distant-water and Pacific-Island-based purse seine fleets (Hampton 2002). Purse seine fleets usually operate in equatorial waters from 10°N to 10°S (Fig. 1). The distant-water fleets from Japan, Korea,

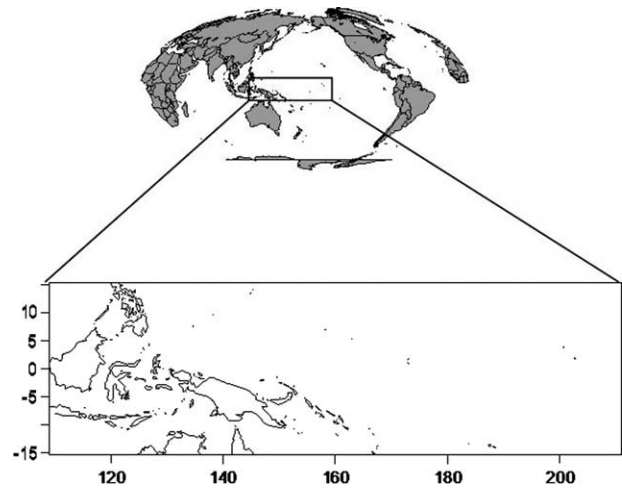


Figure 1. In Western Central Pacific Ocean most of the skipjack tuna catches from purse seine fleets come from the area in the rectangle (15°S–15°N and west to the 150°W of longitude).

Taiwan and the USA capture most of the skipjack in the WCPO (Fig. 1). Skipjack tuna catches in the WCPO have increased steadily since 1970, more than doubling during the 1980s and continue increasing to the present (Hampton 2002).

CPUE data

Data on skipjack tuna catches from the tropical Pacific Ocean were provided by the Oceanic Fisheries Programme, Secretariat of the Pacific Community on behalf of the Western and Central Pacific Fisheries Commission. The data consist in annual catches in tonnes of skipjack, effort (days fished or searched), and CPUE (tonnes d⁻¹), for the Japanese (1976–2006), United States (1981–2006), Korean and Chinese Taipei (1994–2006) purse-seine fleets in the Western and Central Pacific Ocean (west of 150°W longitude and between 15°S and 15°N of latitude). The use of CPUE data for analyzing population dynamics of fish presents some problems, CPUE data is not a reliable estimator of population abundance or biomass and it is influenced by several factors that change the catchability of fish. In consequence, we are aware that the observed CPUE fluctuations are the results of changes in both, the availability (abundance/biomass) and catchability of tunas. For example, the catchability (i.e. the fraction of a stock which is caught by a standardized unit of fishing effort) of skipjack tuna appears to be influenced by climate. It is known that ENSO variability influences the vertical (catchability) distribution within the Tropical Pacific Ocean of the skipjack tuna western stock (Lehodey et al. 1997, Langley et al. 2006). In addition, the reliability of CPUE as an index of fish stock abundance is proportional to the homogeneity of the fishing vessels in their features and operating behavior in space and time. In consequence, we used only Japanese and United States purse seine CPUE data because both are mobile fleets using similar fishing techniques and they are the longer time series data of CPUE (Lehodey et al. 1997). These two fleets operate in the entire distribution of the western stock (Langley et al. 2006) being

two of the most important in terms of catches (41% of the overall during the period 1986–2006).

Climatic data

Southern Oscillation Index (SOI)

Fluctuations in tropical Pacific sea surface temperature (SST) are related to the occurrence of El Niño (EN), during which the equatorial surface waters warm considerably from the International Date Line to the western coast of South America. The atmospheric phenomenon linked to EN is termed the Southern Oscillation (SO), which involves exchanges of air between the eastern and western hemispheres centered in tropical and subtropical latitudes. El Niño and the SO are linked so closely that the term ENSO is used to describe the atmosphere–ocean interactions throughout the tropical Pacific. Various SO indices exist, mostly based on Sea Level Pressure (SLP) time-series data. The most common one is defined by the normalized SLP anomalies of Tahiti (17°33'S, 149°37'W) minus those of Darwin (12°28'S, 130°51'E). During an EN event, SLP tends to be higher than usual at Darwin and lower than usual at Tahiti, making the SO index negative.

Pacific Decadal Oscillation Index (PDO)

A very important index of wintertime climate fluctuations over the North Pacific is the Pacific Decadal Oscillation (PDO) of Mantua et al. (1997). This index is defined by the leading principal component of SST anomalies north of 20°N. A striking feature of the PDO index is the occurrence of extended periods (two to three decades in duration) of predominantly positive or negative departures from the long-term mean. Very little is known about the mechanisms producing these nominal 50–60 yr variations.

Diagnostic analysis

Population dynamics of skipjack tuna is the result of the combined effects of feedback structure (ecological interactions within and between populations), limiting factors, climatic influences, and stochastic forces. To understand how these factors may determine skipjack population fluctuations, we model both system-intrinsic processes (both within the population and between various trophic levels) and exogenous influences, as a general model based on the R-function (Berryman 1999). The R-function represents the realized per capita population growth rates that represent the processes of individual survival and reproduction (Berryman 1999). Defining $R_t = \ln(N_t) - \ln(N_{t-1})$, we can express the R-function (sensu Berryman 1999) as:

$$R_t = \ln\left(\frac{N_t}{N_{t-1}}\right) = f(N_{t-1}, N_{t-2}, \dots, N_{t-i}, C_{t-i}, \varepsilon_t) \quad (1)$$

Here N_{t-i} is the CPUE at different time lags; C_{t-i} is climate effects; and ε_t is a random normally distributed variable. This model represents the basic feedback structure and integrates the stochastic and climatic forces that drive population dynamics in nature. Our first step was to

estimate the order of the dynamical processes (Royama 1977), that is how many time lags, N_{t-i} , should be included in the model for representing the feedback structure. To estimate the order of the process we used the partial rate correlation (PRCF(i)) between R and $\ln N_{t-i} = X_{t-i}$ after the effects of shorter lags have been removed. We write (1) in logarithmic form to calculate the partial correlations.

$$R_t = \ln\left(\frac{N_t}{N_{t-1}}\right) = A + B_1 \times X_{t-1} + B_2 \times X_{t-2} + \varepsilon_t \quad (2)$$

where R , the realized per-capita rate of change, is calculated from the data, we fitted a multiple regression between the per capita growth rates and lagged population density to estimate the PRCF_{t-d} coefficients at each lag (B_i , $i = 1, 2, \dots, 3$), for statistical convenience we assumed a linear relationship between R and X_{t-i} (Royama 1977). The CPUE fluctuations of the skipjack tuna were characterized by irregular oscillations and a linear positive trend during all the period studied ($r^2 = 0.50$; $F_{1,30} = 31.39$; $p < 0.0001$; Fig. 2a). Because the increasing trend in CPUE is in part caused by the increasing effort, efficiency, and mobility of the fleet (Langley et al. 2006), we de-trended the observed time series by using the residuals of the linear regression between $\ln$ CPUE and time and adding the mean $\ln$ CPUE value (Fig. 2b), which is a common practice in the analysis of population dynamic data (Berryman 1999). A first-order negative feedback [PRCF (1)] was the most important component of per capita growth rates (Table 1). This result suggest a simple feedback structure, and low order dynamics of the skipjack tuna population (Fig. 2c).

The model

Our starting point in the analyses was to model tropical tuna populations using simple population dynamic models (Royama 1977, 1992). The PRCF analysis suggests that tuna fluctuations can be caused by a first-order population process, which indicates that population dynamics may be the result of intra-population processes (Results). To understand how these processes determine tuna fluctuations, we will use the called exponential form of the discrete logistic model (Ricker 1954, Royama 1992):

$$N_t = r_m \times N_{t-1} \times e^{(-c \times N_{t-1}^a)} \quad (3)$$

In this model N_t represents the fish abundance or biomass at time t (represented by the CPUE data), r_m is a positive constant representing the maximum finite reproductive rate, c is a constant representing the competition intensity and resource depletion and a indicates the effect of interference on each individual as density or biomass increases (Royama 1992); values of $a > 1$ indicates that interference intensifies with density, while values of $a < 1$ indicates habituation to interference. By defining the above equations in terms of the R-function, by defining $R_t = \ln(N_t/N_{t-1})$, and by log transforming the equation 1, we obtain:

$$R_t = R_m - e^{(a \times X_{t-1} + C)} \quad (4)$$

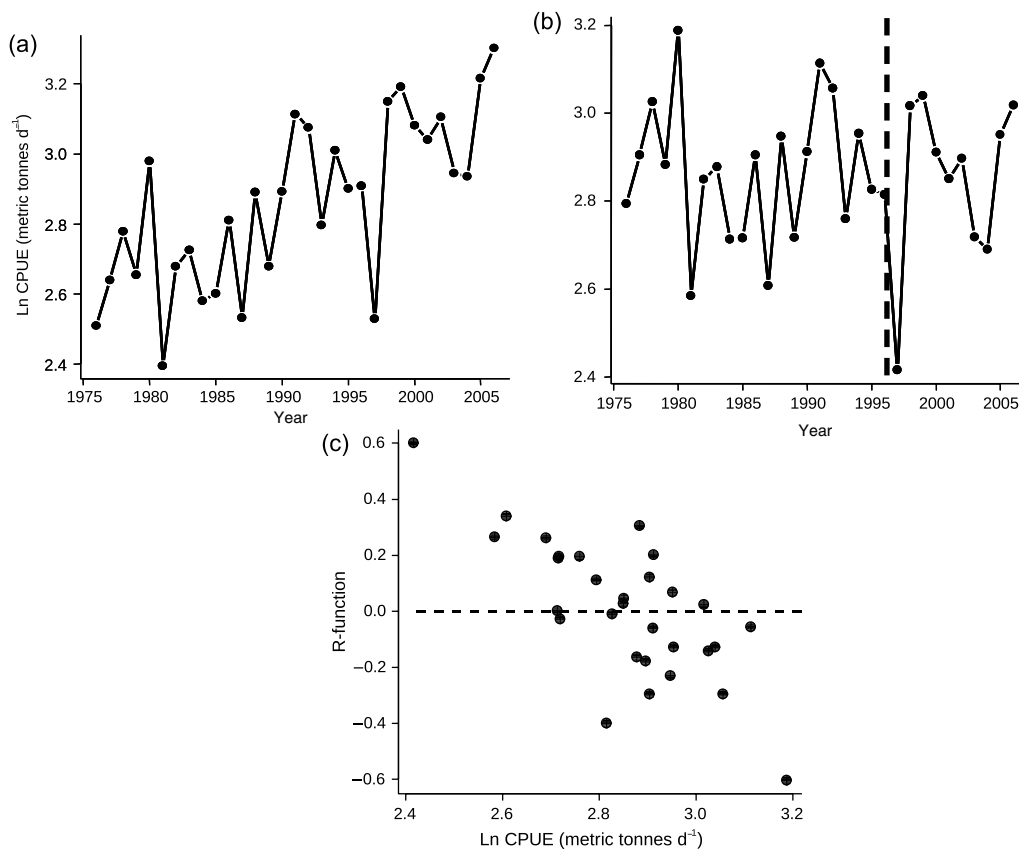


Figure 2. (a) Annual estimates of skipjack tuna ln CPUE for the period 1976–2006 in the studied area. (b) Detrended data, the vertical line shows the division of data used to fit the models (1976–1996) and data used for validation of model predictions (1997–2006). (c) R-function plot of the detrended data.

where R_t is the realized per capita growth rate $R_t = \ln(N_t/N_{t-1})$, $R_m = \ln(r_m)$, a is the same parameter as in equation 1, $C = \ln(c)$, and $X = \ln(N)$. This model represents the basic feedback structure determined by intra-population processes. In this model the three parameters R_m , a and C have an explicit biological interpretation and we can include climatic perturbations by using the framework of Royama (1992). For example, simple additive climatic perturbation effects can be represented as “vertical” effects, which shift the relative position of the R-function by changing R_m in the y axis (Royama 1992); this can be expressed as:

$$R_m + g(\text{PDO}, \text{SO}) \quad (5)$$

where g is a simple linear function (+ or –) of the climatic variables at different lags. Another kind of climatic perturbation is when the equilibrium point of the population is influenced by the climate. In this case the climatic factor shifts the R-function curve along the x-axis without

changing the slope at the equilibrium; that represents a “lateral” perturbation in the Royama (1992) framework:

$$C + g(\text{PDO}, \text{SO}) \quad (6)$$

We fitted eq. 2 using the nls library in the program R by means of nonlinear regression analyses (Bates and Watts 1988). In addition, we included the climatic variables in the parameters R_m and C as linear functions (eq. 5, 6). All the models were fitted by minimizing the Akaike information criterion corrected for low sample size, $AIC_c = -2 \times \log(\text{likelihood}) + 2p + 2p(p+1)/(n-p-1)$, where p is the number of model parameters and n is the sample size. Models with lowest AIC_c values were selected. We tested how well models fit with data from the sequence 1976–1996 and use the sequence 1997–2006 for model prediction. As an additional analysis, we used the de-trended time series of the CPUE data extracted from Korean and Chinese Taipei fleets to compare with model predictions for the period 1994–2006. In order to make data comparable the CPUE data of Korean and Chinese Taipei fleets were de-trended, log-transformed and the average value was tuned to the average CPUE value observed for the Japanese and USA fleet. Observed and predicted dynamics were compared using the standard deviations of the difference between observed and predicted data and calculated as:

Table 1. Diagnostic analysis of the feedback structure of skipjack tuna dynamics. PRCF_{t-i} = the partial correlation between R and $\ln N_{t-i}$ (with $i = 1, 2$ and 3). We interpret this to be a measure of the importance, or the relative contributions, of feedback at lag i to the determination of R (see the text).

PRCF_{t-1}	PRCF_{t-2}	PRCF_{t-3}
–0.73	–0.029	–0.089

$$SD = \sqrt{\frac{\sum_{i=1}^n (O_i - P_i)^2}{n}} \quad (7)$$

where O_i is observed data and P_i is predicted data. In addition, we used the Pearson's correlation coefficient between the observed and predicted numbers to assess model predictions.

Results

According to our analyses, the logistic model without exogenous effects accounts for 48% of the observed variation in R-values of *K. pelamis* (Table 2; Fig. 2c). Our second step was to look for the climatic effect to explain the residual variation of the logistic model. The effects of SOI showed no significant correlation with the model residuals at any time lag [SOI_t : $r = -0.047$, $p = 0.84$; SOI_{t-1} : $r = -0.27$, $p = 0.22$; SOI_{t-2} : $r = 0.23$, $p = 0.31$], while the direct and one-year lagged PDO effects showed negative correlation with model residuals [PDO_t : $r = -0.45$, $p = 0.04$; PDO_{t-1} : $r = -0.40$, $p = 0.07$; PDO_{t-2} : $r = -0.29$, $p = 0.21$]. The Akaike weights indicate a very strong support for the role of PDO_t as the main exogenous perturbation effect. Specifically, the ratio between the models including this climatic index and the pure endogenous model ($w_4/w_1 = 2.18$ and $w_5/w_1 = 2.27$) suggests two times of support for the role of PDO (Table 2). However, after removing the effects of PDO_t , the one-year lagged effects of SOI also suggest the existence of climatic effects on model residuals [SOI_t : $r = -0.18$, $p = 0.43$; SOI_{t-1} : $r = -0.44$, $p = 0.046$; SOI_{t-2} : $r = 0.25$, $p = 0.28$]. In this sense, the addition of lagged SOI_{t-1} to model 5 improves model performance substantially, in particular when both climatic indices are included as lateral perturbation

effects (model 10 in Table 2). In this case, the decrease in the AIC_c is almost 5.3 units, and the Akaike weights ratio between this model and the pure endogenous model reach a value of 13.94. Thus, the best models appear to be those including the effects of direct and one-year lagged PDO and one-year lagged SOI (Table 2).

Predictions of independent data (i.e. the period 1997–2006 and Korean and Chinese CPUE data for the period 1994–2006) showed that the models including only one of the two climatic indexes were poor in predicting the observed dynamics (Fig. 3a, b and 4a, b; Table 2). However, model predictions were noticeably improved with the simultaneous inclusion of PDO and SOI effects (Fig. 3c, d; Table 2), and particularly in the model including the direct and lagged effect of PDO and the lagged effect of SOI (Fig. 3e, 4e; Table 2). Again, models including climatic variables as lateral perturbations give better predictions than models including climate as vertical perturbations (Table 2).

Discussion

Our modelling analyses suggest that the relevant ecological processes underlying the population dynamics of Western Tropical Pacific skipjack tuna are intra-specific competition and the combined effects of El Niño–Southern Oscillation and the Pacific Decadal Oscillation. In particular tuna CPUE fluctuations are much better described and predicted when the two most important climatic indexes operating at large spatial scale in the Pacific are included in combination. In this sense, it is noteworthy that delayed effect of SOI only are significant after to include the effect of PDO, suggesting that a variable may become important only if another variable is first included in the analysis. Although the influence of climatic variables such as the ENSO and the PDO on tropical tuna fluctuations have been previously reported (Ledohey et al. 1997, 2003, 2006, Ravier and

Table 2. Optimal population dynamic models for skipjack tuna, using the exponential form of logistic growth. The parameter values given in the equations were estimated by non-linear regression analysis in R-program using the nls library. The best model was chosen by using the Akaike information criteria for small sample size AIC_c . X_{t-1} = ln population abundance, SOI = Southern Oscillation Index, PDO = Pacific Decadal Oscillation, p = number of model parameters, ΔAIC_c = model AIC_c – lowest AIC_c , w_i = Akaike weights, r^2 = proportion of the variance explained by the model, SD = bias parameter estimated from the difference between the observed and predicted data (see the text), r simulations = Pearson's correlation coefficient between the observed and predicted dynamics (in parenthesis are the results of compare model predictions against the CPUE of Korean and Chinese Taipei fleets for the period 1994–2006).

Models for skipjack tuna	Log-likelihood	AIC_c	p	ΔAIC_c	w_i	r^2	SD	r (simulations)
1. $R_t = 0.92 - \exp [1.18 X_{t-1} - 3.45]$	6.56	−2.51	4	6.82	0.0128	0.48		
SOI effects								
2. $R_t = 0.94 - \exp [1.19 X_{t-1} - 3.44] - 0.0067 SOI_{t-1}$	7.44	−0.88	5	8.55	0.054	0.52		
3. $R_t = 0.77 - \exp [1.51 X_{t-1} - 4.54 + 0.009 SOI_{t-1}]$	7.52	−1.04	5	8.39	0.058	0.53	0.14 (0.12)	0.70 (0.27)
PDO effects								
4. $R_t = 0.70 - \exp [1.53 X_{t-1} - 4.85] - 0.13 PDO_t$	9.10	−4.19	5	5.24	0.028	0.59		
5. $R_t = 0.87 - \exp [1.09 X_{t-1} - 3.35 + 0.15 PDO_t]$	9.14	−4.27	5	5.16	0.029	0.60	0.75 (0.15)	0.75 (0.09)
6. $R_t = 3.91 - \exp [0.31 X_{t-1} + 0.46] - 0.10 PDO_t - 0.10 PDO_{t-1}$	10.40	−2.80	6	6.63	0.014	0.64		
7. $R_t = 0.66 - \exp [1.65 X_{t-1} - 5.32 + 0.14 PDO_t + 0.16 PDO_{t-1}]$	10.94	−3.90	6	5.53	0.024	0.66	0.16 (0.14)	0.68 (0.21)
8. $R_t = 0.46 - \exp [2.66 X_{t-1} - 8.74 + 0.27 PDO_{t-1}] - 0.10 PDO_t$	11.10	−4.20	6	5.23	0.028	0.66		
PDO and SOI effects								
9. $R_t = 0.72 - \exp [1.52 X_{t-1} - 4.75] - 0.16 PDO_t - 0.010 SOI_{t-1}$	11.65	−5.32	6	4.10	0.050	0.68		
10. $R_t = 0.39 - \exp [2.61 X_{t-1} - 8.60 + 0.45 PDO_t + 0.033 SOI_{t-1}]$	12.94	−7.91	6	1.52	0.18	0.72	0.14 (0.17)	0.73 (0.23)
11. $R_t = 5.24 - \exp [0.26 X_{t-1} + 0.90] - 0.12 PDO_t - 0.15 PDO_{t-1} - 0.013 SOI_{t-1}$	15.46	−8.29	7	1.13	0.22	0.78		
12. $R_t = 0.83 - \exp [1.48 X_{t-1} - 4.55 + 0.15 PDO_t + 0.16 PDO_{t-1} + 0.015 SOI_{t-1}]$	16.02	−9.43	7	0.00	0.39	0.79	0.10 (0.14)	0.86 (0.46)

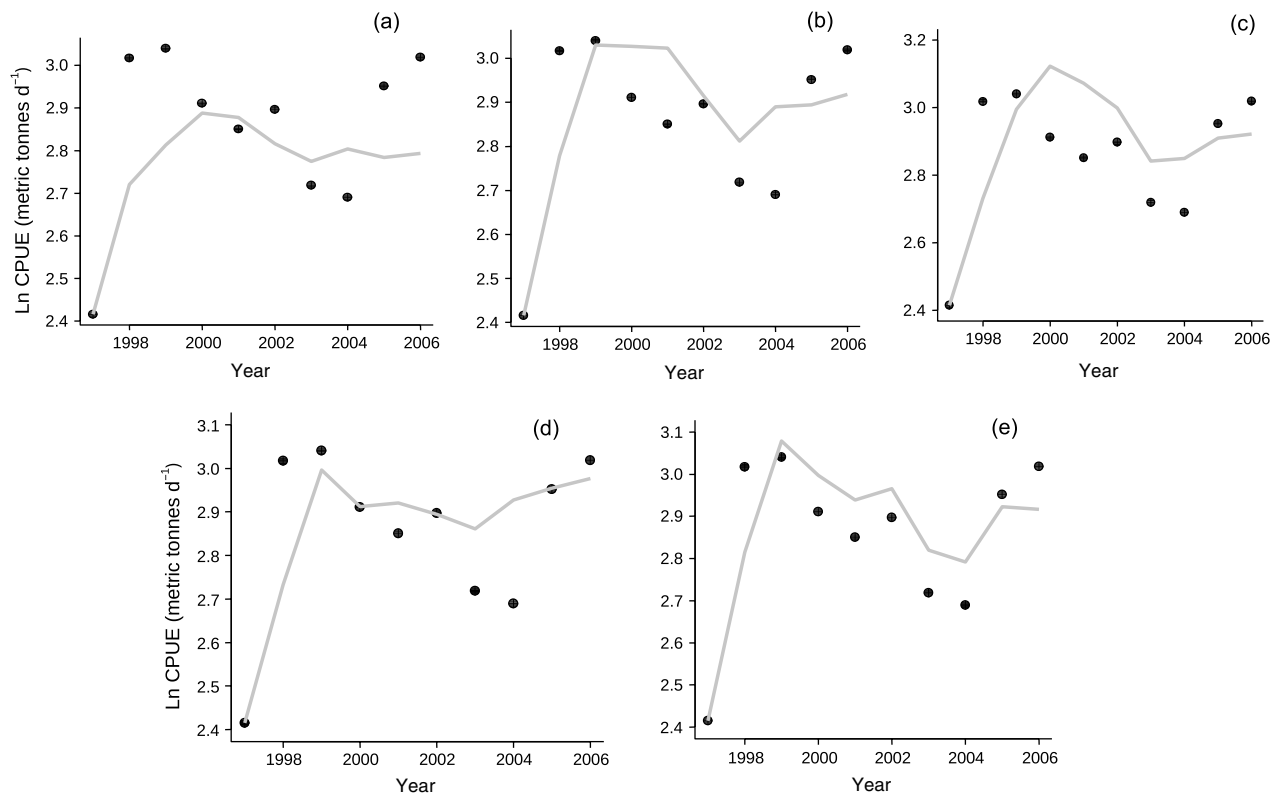


Figure 3. Comparison of observed skipjack tuna biomass (solid circles) for the period 1997–2006 with predictions from models fitted to the data until the year 1996 (grey lines). (a) Model 3 (SOI_{t-1}); (b) model 5 (PDO_t); (c) model 7 (PDO_t and PDO_{t-1}); (d) model 10 (PDO_t and SOI_{t-1}) and (e) model 12 (PDO_t , PDO_{t-1} and SOI_{t-1}).

Fromentin 2001, Ménard et al. 2007), we think that our results bring a new perspective and interpretation of skipjack biomass oscillations at the western tropical Pacific Ocean. This is because we were able to describe tuna population dynamics by using a simple logistic model (Ricker 1954), with only six ecological parameters. In fact, recent studies in terrestrial mammals showed that simple models are helpful for understanding the causes of population fluctuations and can make very accurate predictions (Berryman and Lima 2006, Lima and Berryman 2006, Lima et al. 2008a, b). In addition, our results agree with some previous analyses that find close statistical associations between biomass indices and climatic variables of ocean top predators (Maunder and Watters 2003).

An increasing numbers of studies have determined the role of climate-induced fluctuations in catches of commercial fish (Cushing and Dickson 1976, Cushing 1995, Hjermann et al. 2004, 2007, MacKenzie and Köster 2004, Stige et al. 2006), and tuna stocks (Ledohey et al. 1997, 2003, Bertignac et al. 1998, Ravier and Fromentin 2001, Ménard et al. 2007). Climate fluctuations have been shown to influence: 1) the catchability, i.e. the fraction of a stock which is caught by a standardized unit of fishing effort; 2) the spatial dynamics of migrating fish populations (Corten 1990, 2001, Ledohey et al. 1997) and 3) population dynamic processes, such as, mortality, reproduction and recruitment. For the particular case of skipjack tuna western stock it is well known that ENSO variability influences organisms' vertical (catchability) and spatial distribution (Ledohey et al. 1997, Langley et al.

2006). Given that the positive PDO (warm) phases appear to be related with a reduction in the equatorial upwelling and a deeper thermo-cline at the equatorial Pacific Ocean (McPhaden and Zhang 2002), we think that the direct negative effect of PDO on CPUE could be related to changes in tuna vertical distribution, skipjack tuna moves to deeper areas and there is also a decrease in their catchability. On the other hand, because the large spatial scale of our study, we think that longitudinal displacement were not important in determining temporal variability in our analysis. Therefore, we think that the positive one-year lagged effects of El Niño phase and the cool phase of the PDO represent real effects on per capita rates of change of skipjack tunas.

Indeed, our analyses at annual time scale agree with previous studies relating lagged positive effects of El Niño phase, suggesting the role of ENSO variability influencing skipjack tuna recruitment within the warm pool area (Ledohey et al. 2003). During El Niño years the expansion experienced by the warm pool and the subsequent enlargement of the spawning grounds appears to benefit skipjack tuna recruitment processes (Ledohey et al. 2003), which is consistent with the one-year lagged SOI effect detected in our analyses. In the same vein, Ledohey (2001) suggests that the higher zooplankton biomass in the western Pacific during the El Niño phase represents a highly favorable environment for larval survival and development of the skipjack tuna, which is expected to produce strong tuna recruitment to the fisheries around one year later. In addition, skipjack tuna appears to be influenced by the

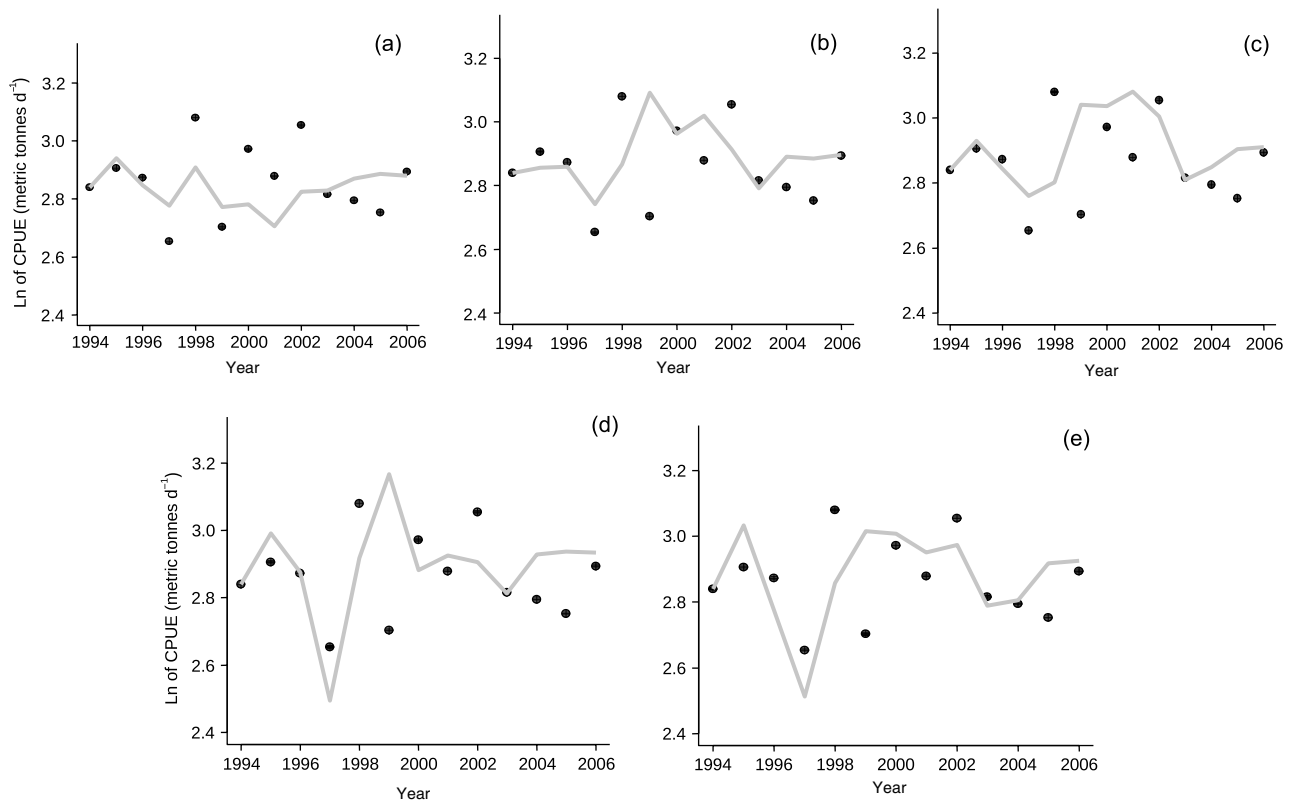


Figure 4. Comparison of observed skipjack tuna biomass (solid circles) for the period 1994–2006 extracted from the Korean and Chinese Taipei purse-seine fleet with predictions from models fit to 1976–1996 data from Japanese and USA fleet (grey lines). (a) Model 3 (SOI_{t-1}); (b) model 5 (PDO_t); (c) model 7 (PDO_t and PDO_{t-1}); (d) model 10 (PDO_t and SOI_{t-1}) and (e) model 12 (PDO_t , PDO_{t-1} and SOI_{t-1}).

Pacific Decadal Oscillation (Ledohey et al. 2003, Langley et al. 2006). Specifically, we observed a negative one-year lagged effects of PDO on skipjack tuna CPUE, a result that is consistent with the hypothesis that cool phases of PDO (i.e. negative PDO values) would have positive effects on tuna populations inhabiting the warm pool of western tropical Pacific Ocean (Chavez et al. 2003). According to this hypothesis, the negative effects of PDO on skipjack tuna could be associated with the observation that during the warm phases of PDO (i.e. positive PDO values) there is a reduction in the equatorial upwelling and a rise of the sea surface temperatures at the equatorial Pacific Ocean (McPhaden and Zhang 2002). Therefore, this reduction in the ocean productivity could be influencing negatively the recruitment of skipjack tuna that are perceived the next year when the individuals recruit to the fishery. It seems that changes in sea surface temperature and ecosystem processes within the equatorial Pacific Ocean are influenced by the decadal oscillation within the North Pacific Ocean (Linsley et al. 2000, McPhaden and Zhang 2002). In sum, we determined one-year lagged effects of SOI and PDO that can be related with ecological effects on recruitment, whereas the direct PDO effects could be caused by the effect of oceanographic conditions on tuna catchability.

On the other hand, models including climatic indexes as lateral (non-additive) perturbations appear to perform better than models including climate as a vertical (additive) effect. This result is expected when climate is influencing a limiting factor, for example, when rainfall influence the

biomass of plants or seeds in arid ecosystems, it is very likely that, in those cases, rainfall represents a lateral perturbation effect for the herbivore populations (Royama 1992). The problem with this kind of exogenous effect is that it affects the availability of some limiting factor or resource (e.g. food); hence, the per capita resource share of individuals is also influenced (Royama 1992). In consequence, the effect of the climatic variable cannot be evaluated independently of the population density level, because the exogenous effect acts jointly with population density or biomass (Royama 1992, Berryman and Lima 2006, Lima and Berryman 2006, Lima et al. 2006, 2008a, b, Previtali et al. 2009), resulting in potentially nonlinear responses of populations to changes in climate. Some recent studies in fish populations have emphasized the role of non-additive and indirect climatic effects (Hjermann et al. 2004, 2007, Dingsør et al. 2007). This is consistent with other recent studies in small rodents and insects showing that the effect of rainfall (or temperature) on primary productivity can be easily incorporated as a lateral perturbation effect using simple population models (Lima et al. 2006, 2008a, b, Estay et al. 2009, Previtali et al. 2009). The same approach has been used to predict the dynamics of large mammal populations influenced by climatic variability (Berryman and Lima 2006, Lima and Berryman 2006).

Although our approach did not denied the relevance of more complex models (e.g. standard age-structured stock assessment models) to disentangle the effect of different climatic variables on specific processes (e.g. catchability,

growth, survival), it shows that very simple models can offer reasonable explanations and accurate predictions of tuna populations provided they are based on population dynamic theory (Royama 1992, Berryman 1999, Turchin 2003). Our simple logistic models were able to show an important predictive capability despite that age-structure and spatial-structure were not considered. We think that this result is very important since most of the available information of animal abundance in nature do not include information on age, sex, or spatial structure. Moreover, using simple logistic models and including climatic perturbations, we were able to predict independent data quite adequately despite the high variability inherent in the skipjack tuna CPUE data. Using the western skipjack tuna stock as an example, we have demonstrated that a first step toward considering ecological effects in management approaches is the use of population dynamic theory and the explicit inclusion of the combined role of intra-population processes and environmental variables.

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