

Spatial–temporal variations in primary productivity and population dynamics of skipjack tuna *Katsuwonus pelamis* in the western and central Pacific Ocean

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Abstract The western and central Pacific Ocean (WCPO) is the largest skipjack tuna *Katsuwonus pelamis* fishing ground in the world. Understanding the spatial–temporal variation of primary productivity in the WCPO is critical, as such variation might be associated with the distribution of skipjack tuna stocks. This study adopts three types of remote sensing data, i.e., sea surface temperature (SST), chlorophyll-*a* concentration and photosynthetically active radiation, and applies a vertically generalized production model to simulate the euphotic depth-integrated primary productivity (IPP) of the WCPO to elucidate the relationships between the distribution and variation in IPP and the estimated population dynamics of skipjack tuna. In addition, catch data from a Taiwanese purse seine fishing company (2003–2010) were analyzed to improve the accuracy of the model. The results suggest that (a) in the WCPO, the most of the high-IPP locations are in the eastern Pacific areas; (b) the areas in which IPP is significantly correlated with the El Niño Southern Oscillation are mainly located along the equatorial zone; and (c) there were high recruitments of skipjack in 26 and 49 months following an IPP bloom, respectively. The findings from this study reveal the correlation between primary productivity and fish resources and highlight the influence of climate variability on tuna resources.

Keywords Skipjack · Primary productivity · Recruitment · Climate variability · ENSO

Introduction

Global and regional climatic variability is associated with profound changes in marine ecosystems, which affect the quantity and quality of aquatic food supplies, and even the welfare of human society [1]. Skipjack tuna *Katsuwonus pelamis* is an important economic fish resource because of its high nutritional value; the total catch ranks third among global seafood catches [2]. It is mainly harvested from the western and central Pacific Ocean (WCPO) by seining. To ensure a sustainable supply of skipjack tuna, it is widely recognized that it is necessary to carefully monitor the skipjack tuna resources in the WCPO and to evaluate the productivity of this region of the ocean.

The equatorial Pacific cold tongue is a cold, eutrophic water mass that periodically enters the WCPO. Consequently, there is a greater production of lower trophic levels in this region, which is higher than some tropical water regions [3–5]. To the west of the cold tongue is a warm pool with relatively lower primary productivity that serves as a habitat for organisms from higher levels of the food pyramid, such as skipjack tuna and other tropical tuna [6]. In association with the occurrence of special climate events, such as El Niño and La Niña, the cold tongue and warm pool undergo successional changes and zonal movements, with profound impacts on the distribution of skipjack tuna [7]. In addition, there are a large number of islands and seamounts that are distributed throughout the WCPO, and their distribution has regional impacts on local marine ecosystems [8].

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Although skipjack tuna have an effective thermoregulatory mechanism [9], the sea temperature might still have a strong impact on this species. Other environmental variables are also important, such as ocean currents and available food sources. Ocean currents are a decisive factor in the east–west transport of food sources, determining the amount of primary productivity from the eastern Pacific Ocean that can be delivered to the WCPO. The importance of primary productivity in supporting the ecosystem can be determined by observing the trophic level of energy flow, the impact of food sources on skipjack, and skipjack spawning habitats, survival rates, recruitment, and biomass [10]. Skipjack tuna prey upon fish including herrings, anchovies, and sardines. Primary productivity provides nutrients for phytoplankton, and these fish may follow phytoplankton, or the productive area may correspond to oceanic fronts in the region, represented by ambient phytoplankton.

El Niño and La Niña climatic variations strongly impact the marine environment of the tropical Pacific Ocean and the gravity center of skipjack tuna fisheries [6]. These impacts arise from changes in ocean currents and primary productivity [6, 11]. The results of several climate models employed for the analysis of the tropical Pacific Ocean climate indicate that an “El Niño-like” climate will appear in the future, with SSTs in the central and eastern equatorial Pacific increasing more than those in the west [12]. Therefore, we urgently require an understanding of the impacts of climate variability on primary productivity and the impacts of primary productivity on skipjack tuna resources. Although this type of research is applicable to other species [13, 14], studies that explore skipjack remain rare.

In addition to use in environmental analyses, remote sensing data can also be used to estimate primary productivity [15]. The first approach to marine primary productivity estimation was proposed by Smith and Baker [15]. In general, estimation approaches rely on satellite chlorophyll-*a* concentration data for the calculation of primary productivity [16], and a large amount of remote sensing data (including sea surface temperature and photosynthetically active radiation) is also integrated to enhance estimation accuracy. Several estimation models have been created through the integration of multiple data sets. The calculation approaches of these models may differ, but the estimation errors are limited [17]. The algorithm proposed by Behrenfeld and Falkowski [18] is the most commonly applied algorithm, and several studies have applied and optimized this algorithm by improving the accuracy of the chlorophyll-*a* normalized photosynthesis rate as a function of depth [19].

Skipjack resources are important for distant-water fishing nations and Pacific island economies, and skipjack tuna are an important source of food worldwide. To respond to the impacts of global climate change, we must

thoroughly understand the relationship between local resources and the environment. Climate variation impacts on skipjack fisheries arise from changes in ocean currents and primary productivity [6, 11]. Here we examine two hypotheses for the link between primary productivity and skipjack stock variability. First, skipjack recruitment and primary productivity are related. Second, this relationship appears delayed. We analyze the importance of each hypothesis as a cause of the variability of skipjack recruitment observed in the WCPO. Therefore, the primary objective of this study was to characterize the temporal and spatial distribution of the primary productivity. A secondary objective was to explore the relationship between climate variability and primary productivity and the role of primary productivity in the life history of skipjack.

Materials and methods

Data and study area

The study area is located in the central Pacific Ocean region, which is mainly constituted by the aforementioned warm pool and cold tongue. The surface temperature of the warm pool is high relative to that of the cold tongue, and the waters are low in nutrients, whereas the upwelling waters in the eastern Pacific supply relatively nutrient-rich, cold waters known as the cold tongue. First, we observed the origin of the cold tongue (10°S–10°N and 135°E–90°W) across the entire region of the equatorial Pacific. Then, we focused on the western and central Pacific region (10°S–10°N and 135°E–160°W) to evaluate the relationship between primary productivity and skipjack recruitment.

The remote sensing data for the monthly SST, Chl-*a* and Photosynthetically Active Radiation (PAR) were obtained from NASA OceanColor Web (<http://oceancolor.gsfc.nasa.gov/>) MODIS Satellite Imagery. These data were downloaded in HDF format and covered the area from 10°S to 10°N and 135°E to 90°W, which comprises the study area. The spatial resolution is 4 km. The daily fishery data of Taiwanese purse seiners for 2004–2014 were provided by the Overseas Fishery Development Council of the Republic of China and covered the area between 140°E and 160°W and between 15°S and 15°N. The nominal catch rates (m.t./net) data were aggregated into a grid of 0.1° longitude by 0.1° latitude. A time series of standardized recruitment data was obtained by employing an age-structured statistical model for fisheries stock assessment (MULTIFAN-CL [11]). We used the Multivariate ENSO Index (MEI) as index of climatic variability. This index illustrates the timing and magnitude of El Niño and La Niña events [20]. The study also

used the IPP time series. The analytical methods were performed as described below.

Primary production model

We used the VGPM (vertical generalized production model) to estimate IPP [18, 19]. The VGPM is expressed as follows:

$$\text{IPP} = 0.66125 \times P_{\text{opt}}^B \times \frac{\text{PAR}}{\text{PAR} + 4.1} \times D_{\text{ez}} \times \text{Chl} \times \text{DL},$$

where IPP is the euphotic-zone integrated primary production ($\text{mgC m}^{-2} \text{ day}^{-1}$); DL is the day length (h), calculated for the middle of the month at each location; P_{opt}^B is expressed by Behrenfeld and Falkowski [18] as a seventh-order polynomial function of SST; and D_{ez} is the depth (m) of the euphotic zone, which is calculated from the Chl-*a* data following Morel and Berthon [21].

Trend analysis of primary production

After analyzing the temporal and spatial characteristics of the estimated primary productivity, we evaluated the trends in changes in primary productivity across the WCPO. We chose empirical orthogonal function (EOF) analysis because this method allows for temporal and spatial variation in several main components and includes independent variables for time and space. The EOF conceptual formula is applied as follows:

$$\text{IPP}(t) \approx \overline{\text{IPP}} + \sum_{i=1}^k \text{PC}_i(t) \times \text{eof}_i,$$

where t denotes the time step, $\overline{\text{IPP}}$ is the mean IPP, k is the number of the principal components, PC_i represents the eigenvectors of the time domain space, and eof_i is the eigenvector of the spatial domain i . The analysis was performed using the R package `clim.pact` [22].

Time-series analyses of IPP and recruitment

Based on the EOF analysis and previous studies [23, 24], we generated a time series of the major changes in first primary productivity (PC1) through EOF analysis. The change in primary productivity was synchronized to increase or decrease with the change in the amount of nutrient transfer associated with the change in the intensity of the Pacific Gyre from east to west. The values of PC1 were calculated monthly, and there was no need to average or sum the IPP data. Recruitment refers to the number of fish surviving to enter a fishery, and the recruitment values are also monthly data.

In this study, we evaluated the existence of a significant time-lagged correlation between primary productivity and

skipjack tuna recruitment. To characterize the variability in both IPP and recruitment, the monthly values were converted to an index of variability (V) according to the following:

$$V = \frac{X_i - \mu_x}{\sigma_x},$$

where X_i is the monthly value of IPP or recruitment, i refers to the i th value in the time series, μ_x is the mean of X , and σ_x is the SD of X . The converted value (V_i) is applied in the cross-correlation function (CCF) in the R software environment for the calculation of the time lag. The CCF is of key interest in time lag analyses. The CCF describes the strength of the relationship between time points in the series. For this study, the CCF was defined as follows: $\text{CCF}(\text{log}) = \text{Correlation}(\text{SKJ}_t, \text{IPP}_{t-\text{lag}})$ for $\text{lag} = 1, 2, \dots, 60$, where SKJ_t is the time series of skipjack recruitment, IPP_t is the main monthly variance of primary production, and lag is a lag of 1–60 months.

The null and alternative hypotheses for the test were as follows. H0: there is no relationship between skipjack recruitment and primary production. H1: there is a significant relationship between skipjack recruitment and primary production. We used the CCF to test for a significant relationship between skipjack recruitment and primary production at lags of ≤ 60 months according to the following steps: (1) decide on an α -level, e.g., 0.05 for a 95 % confidence interval; (2) compare the computed t value with the probability point; (3) if the absolute value of the t value is greater than the probability point, reject H0.

Results

Characterization of IPP in the WCPO

As shown in Fig. 1, more areas of high IPP in the WCPO are concentrated near the equator. The IPP decreases with an increase in latitude, and the meridional width of the zone of high IPP decreases gradually from east to west. The IPP value along the South American coast is greater than $540 \text{ mgC m}^{-2} \text{ day}^{-1}$, which indicates that the majority of the primary productivity in the study area is supplied from the Peru upwelling region in the eastern Pacific Ocean.

To understand the relationship between climate variability and the distribution of primary production in the WCPO, we used the IPP at the equator (longitude = 0) and the climate indicator to generate a figure for comparison. Figure 2 shows that the changes in primary production are related to the changes in the climate indicator (MEI). When El Niño occurs, the westward extent of the range of the high IPP region decreases. When La Niña occurs, the high-IPP region extends significantly westward toward the

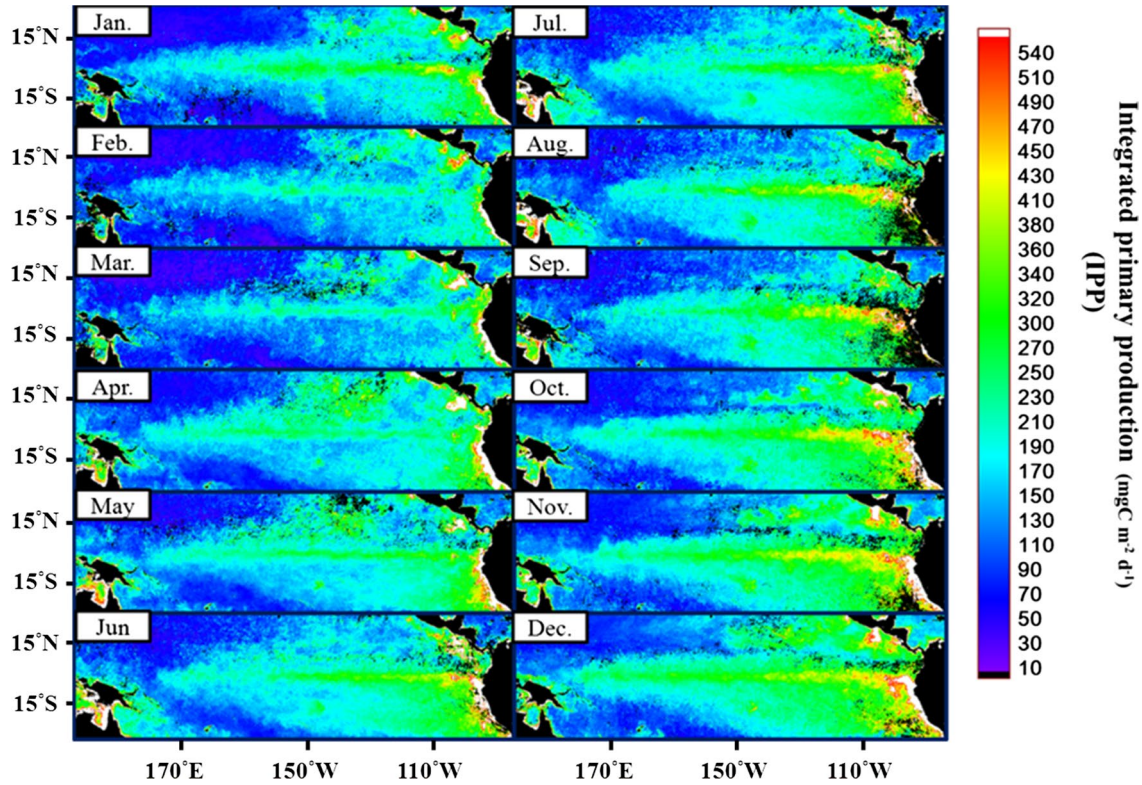


Fig. 1 2000–2011 Mean monthly IPP for the Pacific Ocean

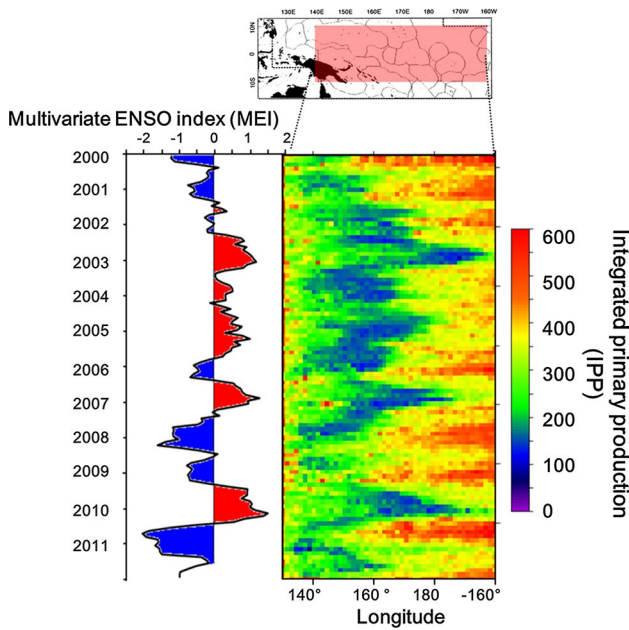


Fig. 2 Comparison between integrated primary production and climate indicators of the equatorial Pacific Ocean. *Left* the temporal change in the Multivariate ENSO Index (MEI); the *red regions* represent El Niño years, and the *blue regions* represent La Niña years. *Right* the time series for the longitudinal distribution of primary production integrated across the major longitudinal operating range (130°E to 160°W) of Taiwan tuna purse seiners in the western and central Pacific Ocean (colour figure online)

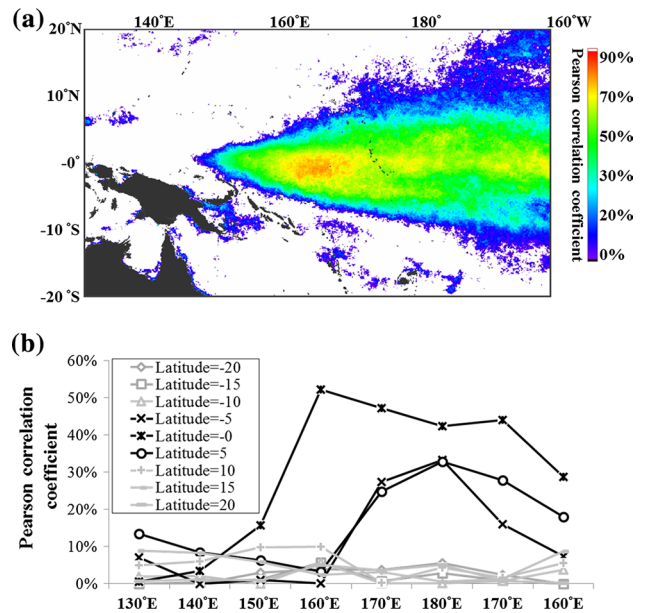


Fig. 3 Spatial distribution of the time-averaged correlation coefficient between IPP and MEI for the period from 2001–2011. **a** Spatial distribution of the Pearson correlation coefficient between IPP and MEI across the WCPO. **b** The areas of high IPP are located near the equator between longitudes of 160°E and 170°E

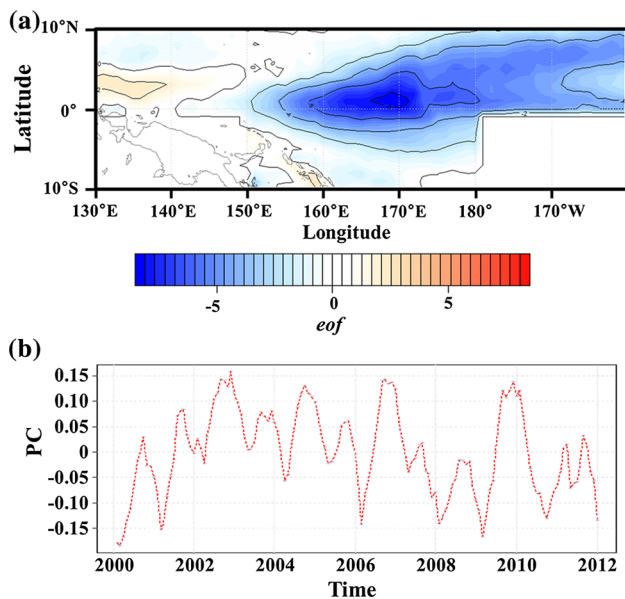


Fig. 4 The spatial pattern and time series of the EOF analysis. **a** The spatial pattern of the first principal component. **b** The time series of the first principal component

western Pacific Ocean. Figure 3 presents the correlation coefficients between IPP and MEL. The higher IPP values are concentrated at the equator between the longitudes of 160°E and 170°E (Fig. 3a). If we compare values across latitudes, the correlation coefficient is highest at latitude 0 (Fig. 3b), and the strength of the correlation decreases with increasing latitude.

The first modes of the EOF analysis performed on the IPP for the period 2000/01–2012/12 are shown in Fig. 4. The modes explain 58 % of the variance in the data, and show the well-documented IPP variation in spatial structure that centers in the equatorial Pacific and extends into the WCPO (Fig. 4a). PC1 shows how this variance evolves temporally (Fig. 4b) and serves as an indicator of cold tongue strength. Therefore, we determined that the value of PC1 is a feature vector of time for IPP in the WCPO. Following this procedure, we determined the monthly variance of primary productivity.

The relationship between the variation in IPP and skipjack tuna resource recruitment

To understand the cross-correlation relationship between skipjack tuna recruitment and IPP, cross-correlation techniques were employed to measure the length of the time delay between the two signals. Figure 5 presents the correlation analysis for skipjack tuna recruitment as a function of its time lag from IPP. There are two periods of time lags in IPP that have significant positive correlations with skipjack tuna recruitment. In the first period, the magnitudes

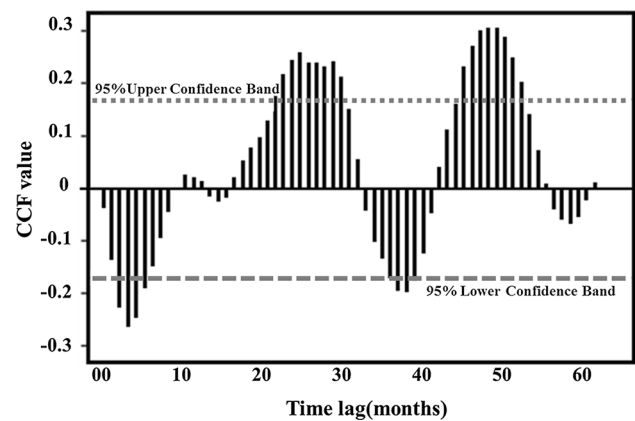


Fig. 5 Cross-correlation function between skipjack tuna recruitment and IPP. The x axis represents the lag in months

of the correlations are more variable; only seven correlations are significant ($p < 0.05$), and there is no obvious central tendency. Compared to the first period, the change in the magnitude of the correlation is smoother throughout the second period. During this period, the correlations are relatively stronger than in the first period, and eight values are significant ($p < 0.05$). This period includes three consecutive periods of negative correlations, with a continuous change. The first period that is characterized by a significant correlation has 3-monthly time lags with correlations that are greater than those of the other two periods. The second period has 2-monthly time lags that are significant, and the lengths are slightly shorter than those of the first period. The results of the third period indicate that none of the monthly time lags were significant. We list the significant correlations in Table 1, including the significant positive correlations ($p < 0.05$) for the monthly time lags during the two major periods of time-lagged correlation. One period encompasses the time lag from 24 to 30 months, and the other period encompasses the time lag from 46 to 53 months. There are also two main periods characterized by significant negative correlations: one period is the time lag from 3 to 6 months, and the other period is the time lag from 39 to 40 months. The highest correlations for those four periods are 26, 49, 4, and 39, respectively.

Finally, we selected the month with the highest skipjack catch during the study period as the object being observed, defined the gravity center of catches $\pm 5^\circ$ longitude and latitude as a core area, and assessed the process state of our hypotheses. Figure 6a shows the relationship between IPP and the distribution of fishing catches in the month with the highest total catch (May 2014). The core area was located in the region 165°E–175°E longitude and 8°N–2°S latitude. We found that IPP in the core area was lower than in surrounding regions, with IPP values mainly being distributed between 220 and 150 $\text{mgC m}^{-2} \text{day}^{-1}$. Figure 6b–e shows

Table 1 Significant time-lags of the cross-correlation function

| Significant positive correlation | | | Significant negative correlation | | |
|----------------------------------|-------------|----------------|----------------------------------|--------------|----------------|
| Lag (months) | <i>R</i> | <i>P</i> value | Lag (months) | <i>R</i> | <i>P</i> value |
| 24 | 0.16 | <0.05 | 3 | −0.23 | <0.05 |
| 25 | 0.22 | <0.05 | 4 | −0.26 | <0.05 |
| 26 | 0.24 | <0.05 | 5 | −0.25 | <0.05 |
| 27 | 0.22 | <0.05 | 6 | −0.19 | <0.05 |
| 28 | 0.21 | <0.05 | 39 | −0.20 | <0.05 |
| 29 | 0.22 | <0.05 | 40 | −0.19 | <0.05 |
| 30 | 0.19 | <0.05 | | | |
| 46 | 0.21 | <0.05 | | | |
| 47 | 0.25 | <0.05 | | | |
| 48 | 0.27 | <0.05 | | | |
| 49 | 0.28 | <0.05 | | | |
| 50 | 0.28 | <0.05 | | | |
| 51 | 0.26 | <0.05 | | | |
| 52 | 0.23 | <0.05 | | | |
| 53 | 0.18 | <0.05 | | | |

Note the significant positive correlations between two major periods: one period encompasses the lag from 24 to 30 months, and the other period encompasses the lag from 46 to 53 months. There are also two main periods that have significant negative correlations: one period is the lag from 3 to 6 months, and the other period is the lag from 39 to 40 months. These bold words reflected the highest correlations for those four periods

the spatial distribution of IPP at 4, 26, 39, and 49 months before May 2014. In Fig. 6c and e, most of the IPP values are above $400 \text{ mgC m}^{-2} \text{ day}^{-1}$, with many IPP values close to $500 \text{ mgC m}^{-2} \text{ day}^{-1}$ being observed in core area. In contrast, in Fig. 6b and d, the highest IPP values are lower than those presented in Fig. 6c and e in the core area. Most of the IPP values range from 300 to $330 \text{ mgC m}^{-2} \text{ day}^{-1}$, although the IPP of small areas can be higher than $400 \text{ mgC m}^{-2} \text{ day}^{-1}$. These phenomena are highly consistent with our hypotheses.

Discussion

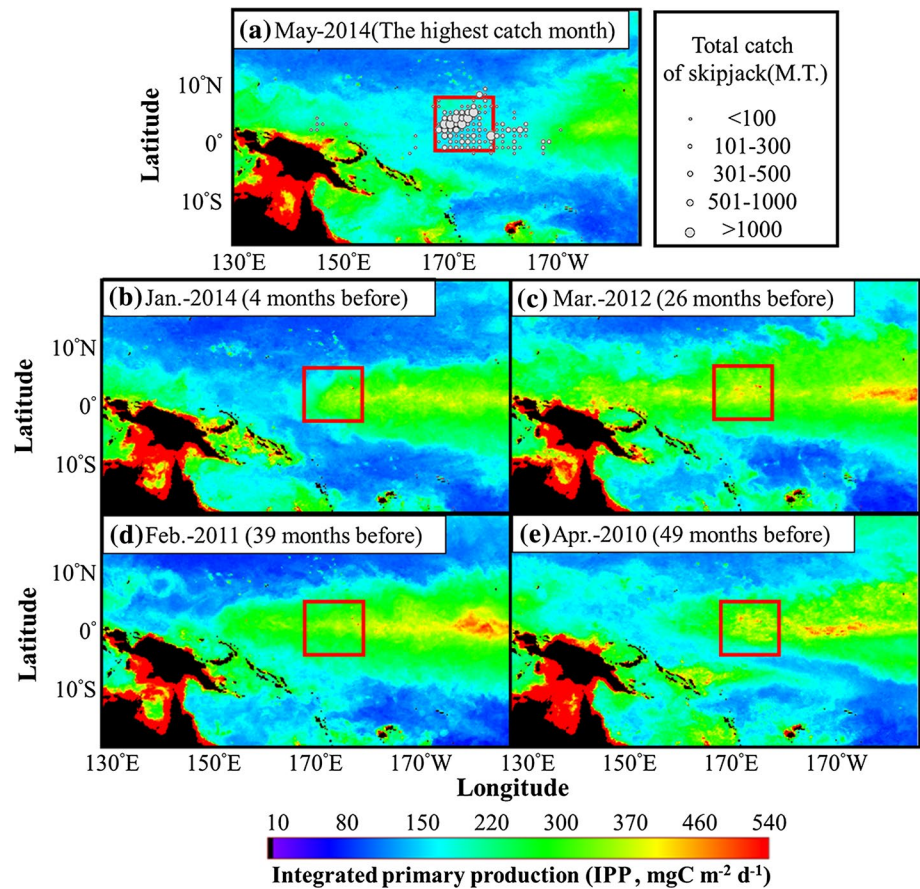
The results of this study confirm that the high IPP in the WCPO is concentrated near the equator. In addition, the IPP decreases with an increase in latitude, and the meridional width of the zone of high IPP decreases gradually from east to west. A comparison of the climate index and IPP suggest that changes in IPP occur in phase with changes in ENSO. The results of this study confirm the relationship between primary productivity and skipjack tuna and the time-delayed characteristics of this relationship. Moreover, we determined the connection between skipjack life history and the time-delayed effects of IPP. These results suggest that the 26- and

49-month periods before increased recruitment are the periods during which fish are growing to reproductive maturity.

Previous research on the life history of skipjack tuna has demonstrated that skipjack tuna in the WCPO are produced by year-round spawning [25]. After fertilization, the eggs require 20 days for incubation. After hatching, a period of approximately 1 month is required for larval fish to grow into young fish. Approximately 15–18 months are then required before recruitment into the fishing grounds as catchable-size skipjack, and the breeding stage occurs at 20–23 months [26, 27]. From the proposed schematic diagram of the life history of skipjack tuna, the 24th–26th month before an increase in recruitment corresponds to the incubation period of the parent fish at the time of the first spawning. That is, if there is high primary productivity, there will be a peak catch 26 months later. After the peak catch, the remaining fish will join the spawning stock and reproduce another strong spawning class. Another peak in recruitment occurs after another 26 months, which is 49 months after the initial period of high primary productivity. This time period overlaps with the egg-hatching period of the previous generation, which confirms the dominant-year class created by the initial period of high primary productivity. This phenomenon occurs not only in skipjack tuna but also in other pelagic fish [28, 29]. Other studies have also determined that high primary productivity is favorable to nursery and feeding conditions [30, 31].

A negative correlation between skipjack recruitment and time lags of 4 and 39 months were observed; considering the life history of skipjack tuna, this time corresponds to the period when skipjack tuna enter the “harvestable size period” from the young-fish period. The natural mortality of this life stage is approximately 0.7, which is the period of highest natural mortality during the life cycle of skipjack tuna [27]. This high mortality rate might be attributed to the increase in primary productivity resulting in an increase in skipjack tuna predators in the WCPO, with predation further leading to future decreases in recruitment. Another possibility is that the species in this stage are in a resource density-independent period; hence, when the primary productivity is high, the survival rate of young fish increases. However, with an increase in the number of fish, young fish enter a density-dependent period during which the fish are subjected to conditions of a limited food supply for the number of fish present. The rate of growth will decrease and the death rate will increase when the amount of available food no longer fulfills the demands of the large number of skipjack [32], leading to a decrease in recruitment. It is also possible that young skipjack and available food organisms are abundant during this period. The primary productivity declines because of increased biological requirements [33]. Thus, high primary productivity has a positive influence on the skipjack spawning and nursery stages. Skipjack

Fig. 6 IPP and the core area (denoted by the red box) of fishing catches in **a** the month with the highest total catch (May 2014), **b** the 6 months before, **c** the 26 months before, **d** the 40 months before, and **e** the 49 months before (colour figure online)



stocks are significantly reduced during high primary productivity periods, likely because a large number of young fish survive, resulting in a density-dependent phenomenon.

Marine primary productivity supports the entire operation of the marine ecosystem and impacts global biogeochemical cycles and the climate. Previous studies have reported that the climate anomalies of the past 10 years will result in the production of ± 2 giga tons of carbon in the global ocean; in this regard, the impact of ENSO is the highest in the central Pacific Ocean [34]. In addition, an increasing number of studies have verified that climate variability has a considerable impact on marine fishery resources [35–39], especially on pelagic species (such as tuna). The impact of ENSO on the habitat, distribution, and abundance of tuna in the WCPO has been discussed in several previous studies [6, 8, 40, 41]. The present study attempts to evaluate this relationship by connecting recruitment, primary productivity and climate variability in addition to verifying the impact of climate variability on fish resources. The results indicate that primary productivity has a variable relationship with tuna resources depending on climate variability.

In the present study, the relationship between skipjack tuna resources and primary productivity has been

elucidated. However, the greatest influence on the variation in primary productivity in the WCPO is attributed to ENSO climate variability. Conversely, spatially, there is substantial variation in the effect of El Niño. From the correlation analysis of IPP and MEI, we observed a strong correlation at the equator and a decrease in the correlation with an increase in latitude. The equatorial region is also the area of the most concentrated fishing effort and highest catches. However, the evaluated study area is substantially wider than this area. Therefore, such differences in space and time merit further study, and their effects on spawning migrations, feeding migrations, habitat, movements, and natural mortality effects also require further clarification [42].

Measurements of fish stocks and the IPP can be used to investigate the relationship between fish stocks and primary productivity. We demonstrate that primary productivity not only attracts skipjack tuna to habitats but will also affect the amount of resources and catch rates of the WCPO after a period of time. Further research is needed to test this hypothesis, including direct studies of the foraging behavior of skipjack and predator and prey species, and an understanding of the food chain is essential to a broader

understanding of the structure and function of ecosystems in the WCPO as a whole.

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