

Original Research Article

Biodiversity in the bycatch community of Chinese tuna longline fisheries in the Pacific Ocean

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ABSTRACT

The biodiversity of the bycatch community in tuna longline fisheries has historically been under-studied. In this study, observer data from 9744 sets of Chinese tuna longline fisheries were used to estimate the biodiversity of the bycatch by applying alpha diversity measures, and their habitat preference was predicted with the Generalized Additive Model. A total of 98 bycatch species were observed, mainly consisting of bony fishes and elasmobranchs. We found that there was a similar species composition in the ALB (*Thunnus alalunga*) and BET (*Thunnus obesus*) sets that was different in abundance assemblages. Regarding the entire study area, biodiversity in the tropical Pacific was higher than that in the temperate Pacific, and it was highest in the eastern tropical Pacific. In the western Pacific, higher pelagic biodiversity was noted between 15° and 20° latitude. The species richness and diversity were largely influenced by geographical positions, sea surface temperature and fishing depth. The indicators of species richness and density performed well in identifying the hotspots of biodiversity. This study helps to understand the predator biodiversity in pelagic ecosystems and identify, for conservation purposes, critical habitats for the bycatch community in tuna longline fisheries.

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1. Introduction

Pelagic marine organisms play an important role in mediating the functioning of the global ecosystem through their influence on biomass production, elemental cycling, and atmospheric composition (Bellino et al., 2019). Growing studies suggest that biodiversity is important for the stability and functioning of the pelagic ecosystems (Duffy and Stachowicz, 2006). Pelagic fisheries alter fish community structures through the unsustainably capture of a great abundance of target and non-target species (Hall, 2000). The question of how to effectively govern fisheries to avoid the harmful impact of fishing on pelagic ecosystems largely depends on how well we understand the biodiversity in the open ocean (Sala and Knowlton, 2006).

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The Pacific Ocean has the world's largest longline fishery (Clarke et al., 2014). Tuna longline fisheries, mainly targeting albacores (ALB, *Thunnus alalunga*), bigeye (BET, *Thunnus obesus*), and yellowfin tunas (*Thunnus albacares*), have been identified as having one of the highest bycatch rates for many species. Most of the bycatch, such as billfishes, and other bony fishes, sharks, sea turtles, and marine mammals, are considered to be top predators that play a critical role in the structure and function of all marine ecosystems (Ferretti et al., 2010; Libralato et al., 2006; Morgan and Sulikowski, 2015). For example, the reduction in biomass of sharks through fishing, as well as tunas and billfishes, will trigger top-down effects that will contribute to the loss of ecosystem services and the collapse of marine ecosystems (Ferretti et al., 2010; Ward and Myers, 2005). Consequently, control rules for catch and gear are used to regulate fisheries, but they have so far proved inadequate in protecting many target and bycatch species (Game et al., 2009). tRFMOs (tuna Regional Fisheries Management Organizations) are increasingly examining their governance systems to adopt Ecology-Based Fisheries Management (EBFM) related measures (Zhou et al., 2010) that enhance management of their fisheries by encouraging them to be more compliant to mitigating impacts on target and bycatch species, their trophic relationships and habitat requirements (FAO, 2017). However, owing to poor data coverage, our understanding of the pelagic fish community of the Pacific Ocean is still limited (Worm et al., 2003; Zhu et al., 2011).

Indicators, which can provide information on the state of the ecosystem, are needed to support the implementation of an ecosystem approach to fisheries (Jennings, 2005). Alpha diversity metrics summarize the structure of an ecological community concerning its richness, evenness, or both. It is ubiquitous to summarize and compare community structure through alpha diversity because many perturbations to a community affect the alpha diversity of a community (Hurlbert, 1971). Predictions of the diversity's spatial distribution and the relationships between environmental variables such as gradients in species richness associated with latitude, longitude, temperature, and water depth, will provide insights on the change of ecosystem structure (Lezama-Ochoa et al., 2017, 2015). Conserving biodiversity hotspots has been identified as an effective means to protect many species in the terrestrial ecosystem at the same time (Marchese, 2015), and this concept has been extended to coastal marine ecosystems (Worm et al., 2003). In pelagic ecosystems, spatial protection was considered to be an effective way to reduce fishing-related threats to fishes and other organisms (Game et al., 2009). Understanding the biodiversity distributions of the bycatch community in tuna longline fisheries and their relationship with the environment can potentially lead to identifying critical conservation habitats.

Information supporting the application of EBFM in pelagic fisheries is limited. Observer programs, designed to monitor the catch and bycatch, and collect fisheries-relevant information (Gilman et al., 2014), are an important source of ecological data that underpin the application of EBFM (Gilman et al., 2017). Data from these programs are widely used in conducting stock assessments and estimating the total bycatch and the bycatch patterns of species with high ecological risks (Amande et al., 2010; Anderson et al., 2011; Huang, 2015; Huang and Liu, 2010; Peatman et al., 2018). In contrast, studies published about the biodiversity of the bycatch community are less in number. There have been some studies using tuna fishery data or observer data to predict the spatial distribution patterns of pelagic fish biodiversity and their habitat preference (Morato et al., 2010a; WCPFC, 2010; Worm, 2005; Worm et al., 2003), but only a few have been specifically focused on the bycatch community in the open oceanic pelagic ecosystems (Lezama-Ochoa et al., 2017, 2015), especially for the tuna longline fisheries (Zhu et al., 2011).

This paper aims to use the observer data to, (1) study the species diversity of the pelagic ecosystem based on the bycatch community of Chinese tuna longline fisheries in the Pacific Ocean, (2) explore the relationships among patterns with environmental variables; (3) identify the most diverse areas for future conservation issues. To address this, the indicators of bycatch density, richness, evenness, and Shannon index were measured in each fishing sets and area.

2. Materials and methods

2.1. Study areas

The study areas were part of the tuna longline fishing ground (30°S–30°N and 150°E–100°W) in the Pacific Ocean and were divided into five sections: NP (the north temperate Pacific), SP (the south temperate Pacific), WT (the western tropical Pacific), CT (the central tropical Pacific), and ET (the eastern tropical Pacific) as shown in Fig. 1.

2.2. Data collections

The 9744 fishing sets of data were collected by observers onboarded the Chinese tuna longline vessels in the Pacific Ocean from 2012 to 2019 according to the Conservation and Management Measure for the Regional Observer Programs in the WCPFC (Dai et al., 2019). Scientific observers were first rigorously trained for collecting fishery data of tunas and other pelagic fish stocks. Next, the observers were randomly allocated to longline vessels on fishing grounds. During their trips, observers were required to record basic information about fishing operations (which included fishing/hauling time, positions, hooks between floats (HBF), length of float line and branch line, setting speed of the mainline and vessels, and target species) and catch information (which included all species captured by the sets) at the species level. More details are available in the annual report of China to the commission of WCPFC (Dai et al., 2019). Based on the target species, the sets can be divided into ALB and BET sets. The fishing time was also separated into 4 seasons: 1st season (January–March), 2nd season (April–June), 3rd season (July–September), and 4th season (October–December).

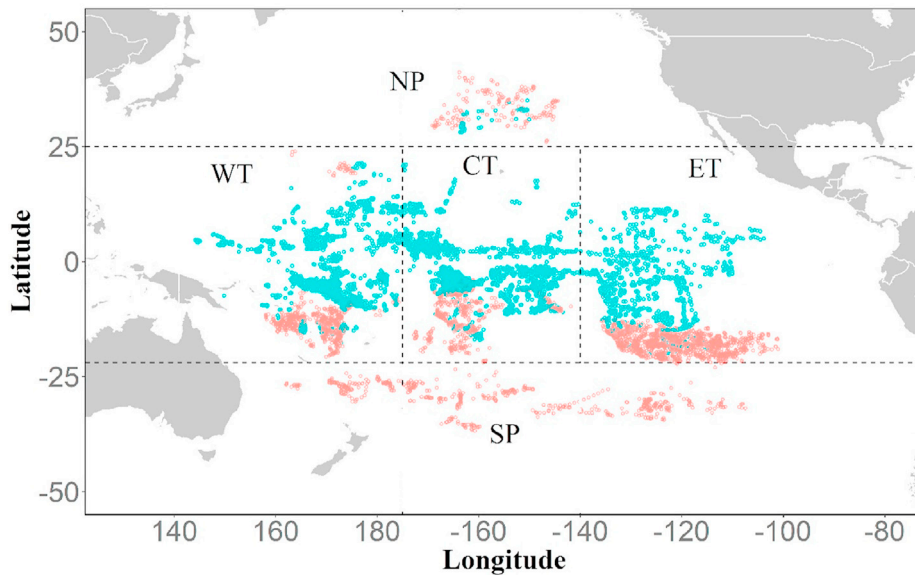


Fig. 1. Observed sets of Chinese tuna longline fishery between 2012 and 2019. The red and green dots represent the fishing sets targeting albacore and bigeye tuna, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2.3. Environmental data

The values of oceanographic variables for each fishing set were derived from NOAA's Ocean Watch Central Pacific Node (<https://oceanwatch.pifsc.noaa.gov/doc.html>). Sea surface temperature (SST, in °C) with a 5 km spatial resolution and a frequency of one day were used. The Chlorophyll-a (Chla) had a 4 km resolution with a frequency of one month. The spatial resolution for the daily Sea Level Anomaly (SLA, in cm) was 20 km.

2.4. Alpha diversity

In this study, bycatch is defined as non-target species. Therefore, species such as tunas (excluding for ALB, BET, and YFT), billfishes, other bony fishes, elasmobranchs, sea turtles, and marine mammals were included in the bycatch community (Clarke et al., 2014). Sea birds and several unidentified species were not included.

Species richness was calculated. The Chao2 non-parametric estimator (Chao, 1984) based on the incidence or frequencies of species, was also calculated to obtain the estimated total species richness. The Shannon index used to represent the diversity of the bycatch community was calculated for each set. A higher Shannon index indicates higher diversity (Shannon, 1948). J-evenness was calculated as $H/\ln(S)$, where H is the Shannon diversity index and S is the species richness (Hurlbert, 1971). The species abundance models, such as geometric, log-series, log-normal, and broken stick models, are used to describe the structure of the community (Lezama-Ochoa et al., 2017, 2015; Magurran, 2013). The data were fitted to different models and the best model is selected by AIC (Akaike's Information Criterion), which best represents the community structure (Kindt and Coe, 2005). Species density defined as the bycatch number per 1000 hooks was estimated to reflect the abundance distribution of the bycatch community.

Table 1
Summary of the total number of species and Chao2 by targets, seasons and areas.

	Sets	N	Species	Chao2
ALL		9744	98	107.8
Targets	ALB	3984	82	90.7
	BET	5760	86	93.2
Seasons	1	1762	68	100.0
	2	930	57	61.1
	3	2767	74	79.8
	4	4285	83	95.1
Areas	CT	3424	71	76.3
	ET	2690	64	80.7
	NP	237	36	44.1
	SP	600	41	45.1
	WT	2793	80	92.1

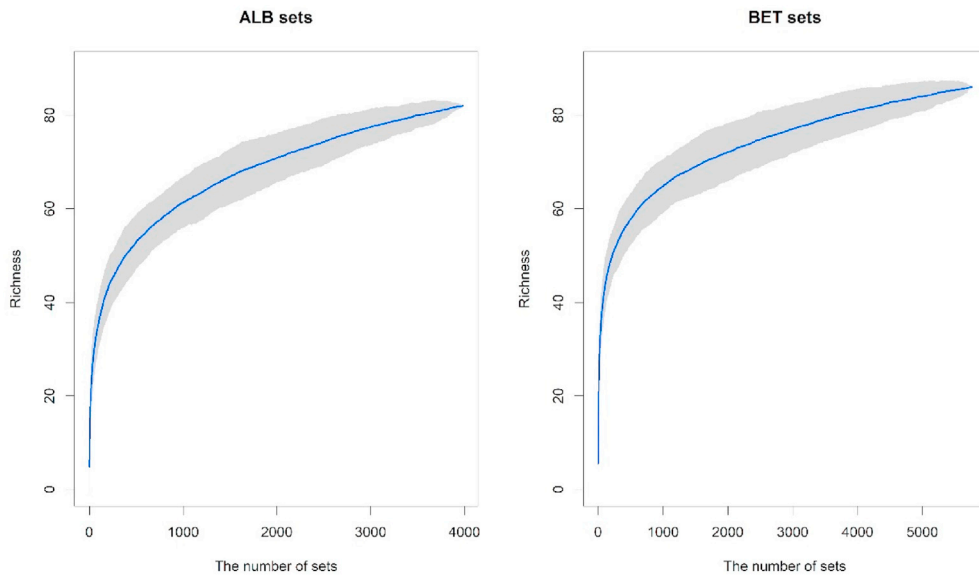


Fig. 2. Species accumulation curve by set. The shaded area corresponds to the standard deviation.

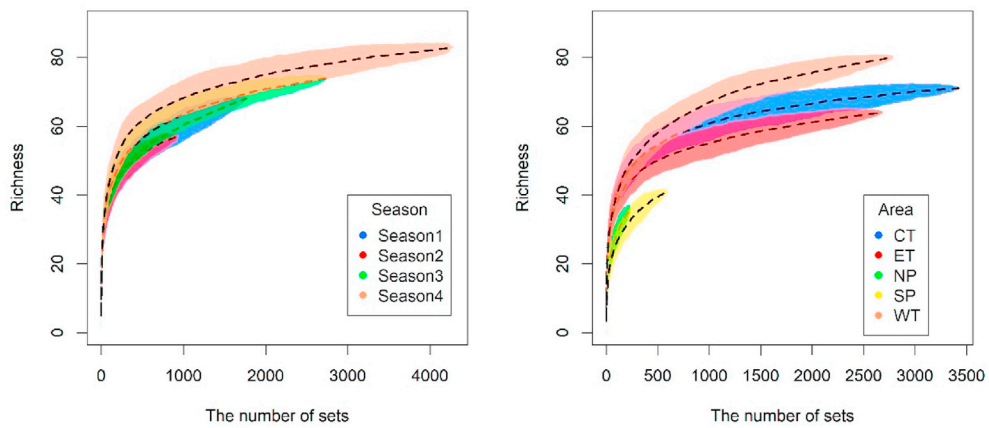


Fig. 3. Species accumulation curve by seasons and areas. The shaded area corresponds to the standard deviation.

2.5. General additive models (GAM)

GAM was used to quantify the statistical relationship between the species richness or the Shannon index and environmental and spatial variables (Lezama-Ochoa et al., 2017). The variables built into the model include sea surface temperature (SST), Chlorophyll *a* (Chla), sea level anomaly (SLA), seasons, longitude, latitude, hooks between floats (HBF), and target species (Worm, 2005; Worm et al., 2003). HBF in tuna longline fisheries is often used to indicate the fishing depth (Peatman et al., 2018).

$$\text{Index} \sim s(\text{Longitude, Latitude}) + s(\text{SST}) + s(\text{SLA}) + s(\text{Chla}) + s(\text{HBF}) + \text{factor}(\text{Seasons}) + \text{factor}(\text{Target})$$

Where the index is the species richness and Shannon index of each set, and where *s* is spline smoother.

After all variables were included initially in the GAM, the most significant single term was selected and included as one of the main effects in the final models, based on correlation analysis (<0.6) and chi-square statistical significance ($\alpha = 0.05$) (Lezama-Ochoa et al., 2017).

All analyses were carried out in R software using mainly “vegan”, “BiodiversityR”, “maps” and “mgcv” packages of R-3.5.3 free software (Team, 2013).

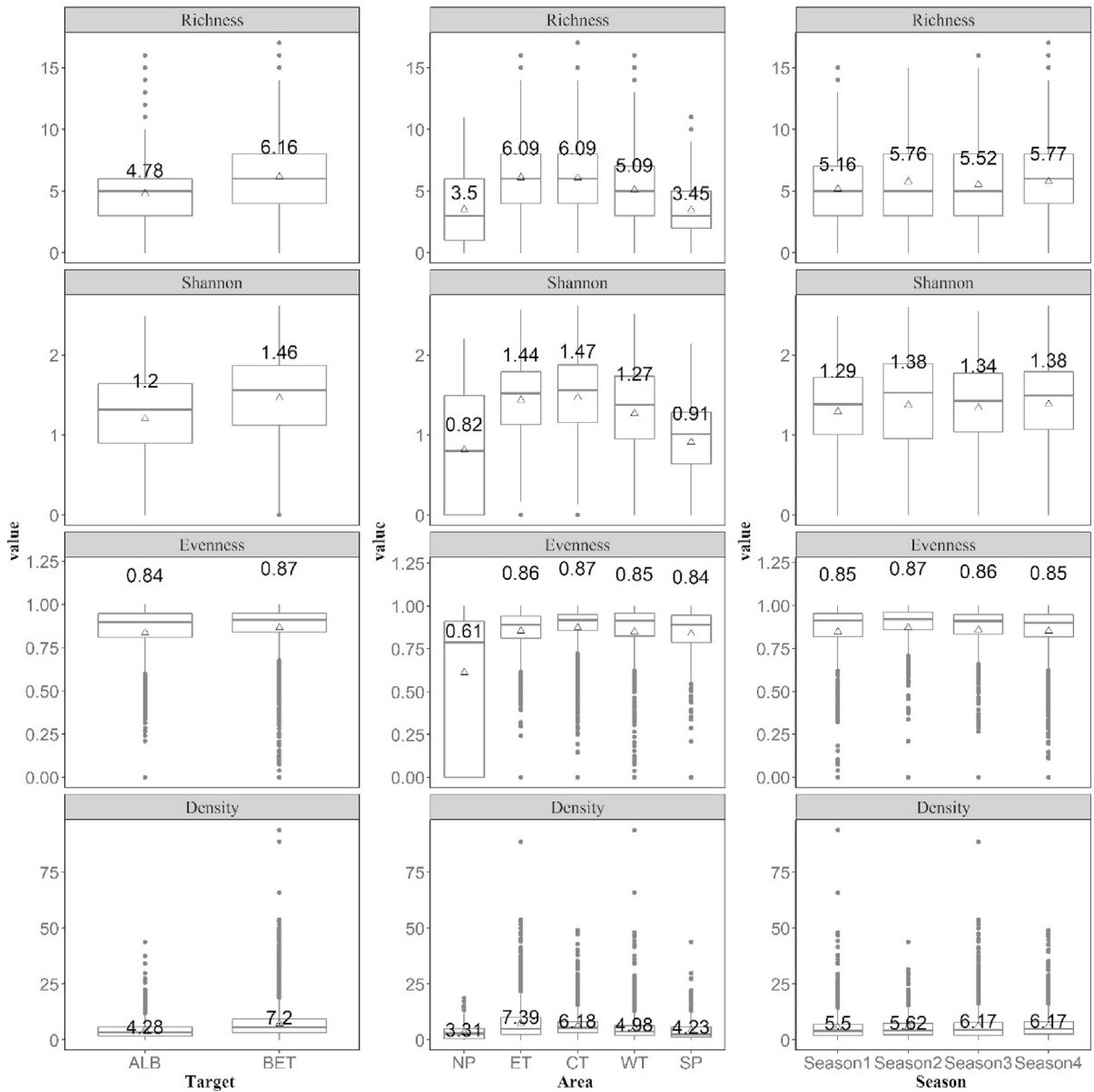


Fig. 4. The species richness, Shannon diversity index, and evenness of bycatch community in Chinese tuna longline fisheries by targets, areas, and seasons (The values in the plot are means).

3. Results

3.1. Alpha diversity

The species richness and Chao2 estimators of each fishing set, area, and season is summarized in [Table 1](#). A total of 98 bycatch species were observed on 9744 sets. The total bycatch of the BET sets was higher (86) than that of the ALB sets (82), which means most bycatch species can be captured by both fishing sets. The species accumulation curves of both BET sets nearly reached the asymptote (93). In the ALB fleets, it was not reached (91). These findings indicate that almost all species caught by the BET sets can be observed under the current sample size, but more samples should be collected to encounter all species in ALB sets ([Table 1](#) and [Fig. 2](#)). Species richness was highest in season 1, followed by season 4 (95.1), season 3 (79.8), season 2 (61.1). Areas from most to least species richness were ordered as follows WT (92.1)>ET (80.7)>CT (76.3)>SP (45.1)>NP (44.1). This means the tropical Pacific had higher species richness than the temperate Pacific. Chao2 non-parametric estimators show that the asymptote was not reached in seasons of 1 and 4 and the areas of ET and WT ([Table 1](#) and [Fig. 3](#)).

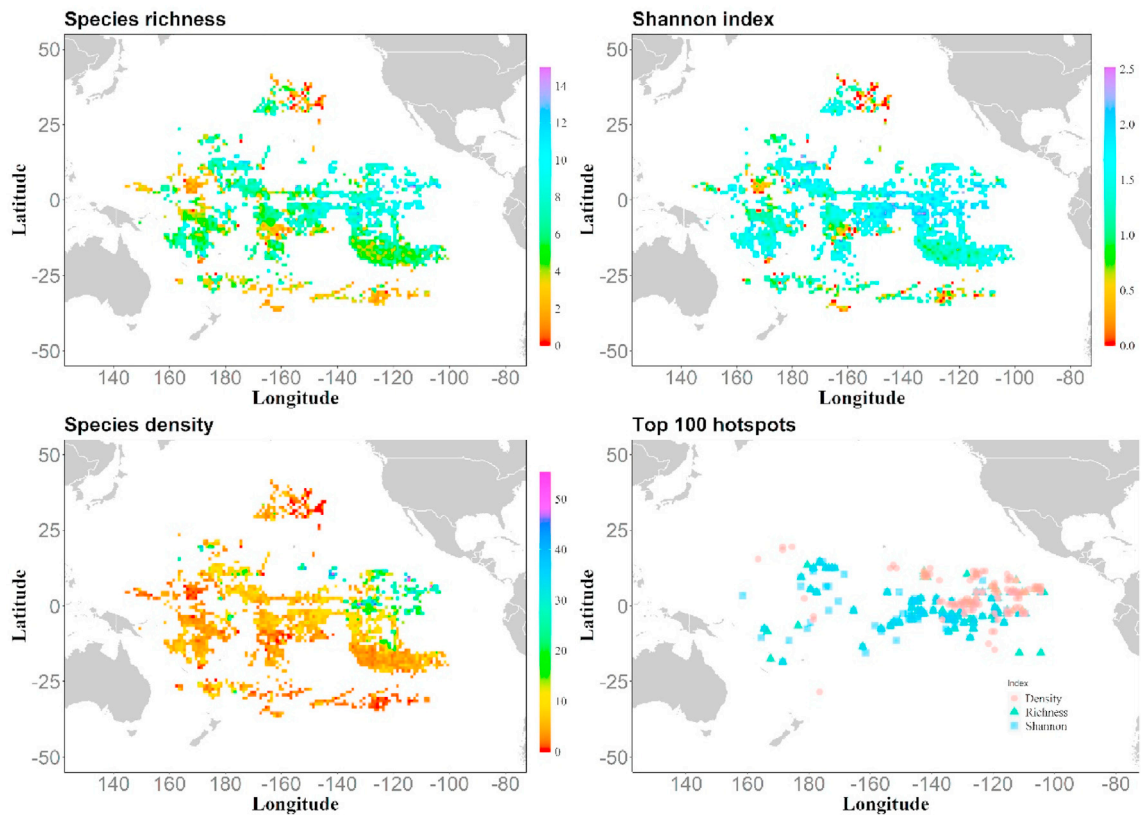


Fig. 5. The observed distributions of species richness, Shannon index, and bycatch community density by the Chinese tuna longline fishery in 2012 and 2019 ($1^\circ \times 1^\circ$), as well as the largest 100 hotspots for each index.

Table 2
Species abundance in BET and ALB sets.

Rank	BET sets			ALB sets		
	Species	Abundance	Proportion	Species	Abundance	Proportion
1	<i>Dasyatis violacea</i>	9385	10%	<i>Alepisaurus ferox</i>	9651	19%
2	<i>Prionace glauca</i>	8564	9%	<i>Katsuwonus pelamis</i>	9091	18%
3	<i>Katsuwonus pelamis</i>	8335	9%	<i>Acanthocybium solandri</i>	6617	13%
4	<i>Xiphias gladius</i>	7562	8%	<i>Lepidocybium flavobrunneum</i>	5260	10%
5	<i>Alepisaurus ferox</i>	7363	8%	<i>Dasyatis violacea</i>	3101	6%
6	<i>Lepidocybium flavobrunneum</i>	7315	8%	<i>Tetrapturus angustirostris</i>	3091	6%
7	<i>Carcharhinus falciformis</i>	5866	6%	<i>Lampris guttatus</i>	2951	6%
8	<i>Gempylus serpens</i>	4540	5%	<i>Coryphaena hippurus</i>	1803	4%
9	<i>Taractichthys longipinnis</i>	4440	5%	<i>Prionace glauca</i>	1361	3%
10	<i>Makaira nigricans</i>	3486	4%	<i>Brama</i>	1016	2%

The values of species richness, Shannon index, J-evenness, and species density for each group are shown in Fig. 4. Generally, the diversity of the bycatch community in the BET sets was higher than that in the ALB sets. The highest values occurred in ET and CT, followed by WT, SP, and NP. The most diverse bycatch was found in season 4 and season 2.

We estimated the mean values for species richness, Shannon index, and species density in each cell (1° by 1°) to show the spatial distribution of biodiversity. The largest 100 cells of each index were then chosen to represent the hotspots of biodiversity. Most hotspots appeared in the eastern tropical Pacific. (Fig. 5).

The first ten most abundant species (shown in Table 2) accounted for 86% of the total bycatch in the ALB sets and 71% of the total bycatch in the BET sets. The most abundant species were *Dasyatis violacea* (10%) and *Prionace glauca* (9%) in the BET sets, and *Alepisaurus ferox* (19%) and *Katsuwonus pelamis* (18%) in the ALB sets (Table 2).

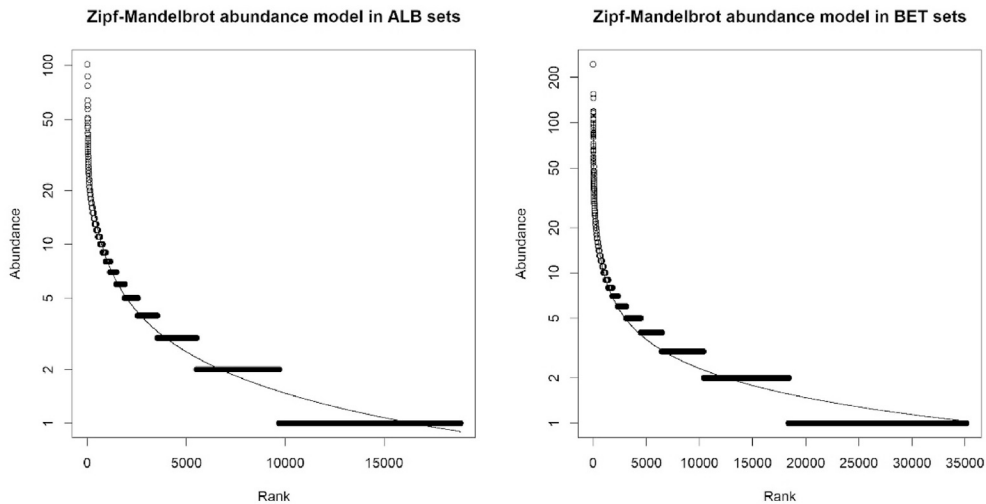


Fig. 6. Models selected to fit log-rank abundance curves in BET and ALB sets.

The bycatch community in both the ALB and the BET sets followed a Zipf-Mandelbrot distribution based on the lowest AIC values (Supplementary Material Table 1). Slopes in the curve of the ALB sets were steeper than those in the BET sets, where the curve reached larger values on the x-axis (Fig. 6).

3.2. Statistical relationship between biodiversity and environmental variables

The Quasi-Poisson family with the link function of log was selected for species richness and the Gaussian family with the identity link function was used for the Shannon index (Table 3). All factors were included in the final model as explanatory variables spatial variables (latitude-longitude interaction), temporal variables (seasons), target species, and environmental variables (SST, Chla, and SLA). The estimated parameters for species richness and p -values are listed in Table 3 and Fig. 7.

The correlations between the variables (Fig. 2) and the distribution of residuals (Figs. 3 and 4) are provided in the Supplementary Material. The Normal Q-Q plot shows a normal distribution as well as the relationship between fitted and response values. The good distribution of residuals indicates that the areas of high diversity can be identified correctly through the models.

The model explained 28.9% of the total deviance with an R^2 of 0.292 for species richness. The individual contribution of the variables is shown in Table 3. The most significant explanatory variables for the species richness was area (23.5%), followed by HBF (12.2%), SST (11.4%), Chla (6.6%), Target (4.8%), SLA (0.9%) and Season (0.5%). For the Shannon index, 28.6% of the total deviance with an R^2 of 0.281 was explained by the model. The most significant explanatory variables for the Shannon index was area (17.2%), followed by SST (10.3%), HBF (9.6%), Chla (4.8%), Target (3.3%), SLA (0.6%) and Season (0.3%).

The results show that species richness and Shannon index had similar responses for the variables in GAMs. Biodiversity peaked in the eastern tropical Pacific region. In local areas, two potential biodiversity hotspots were found between 15° and 20° latitude in the western Pacific Ocean. Observed diversity was higher in the BET sets than in the ALB sets. Diversity was higher in season 2. In general, bycatch communities preferred habitats with warm waters (24–27 °C), high Chla (>0.2). The most diversity season was season 2. Diversity was highest when the HBF was around 20 and 34 (Figs. 7 and 8).

4. Discussion

Our study estimated the diversity of the bycatch community using the data collected by observer programs for Chinese tuna longline fisheries in the Pacific Ocean. We found that the ALB and BET sets represented different bycatch assemblages. The diversity was highest in the eastern tropical Pacific waters and largely related to the geographical positions and environmental conditions in the fishing grounds, as well as the fishing depth. Species richness and density were recommended as indicators in identifying the hotspots of biodiversity.

4.1. Biodiversity in ALB and BET sets

The preferred fishing grounds are different between ALB and BET fisheries as shown in Fig. 1. The bycatch from these two fishing sets might show different assemblage patterns influenced by the geographical and environmental conditions of their respective fishing grounds. Our study finds that the species composition was similar between ALB and BET sets. It seemed to be normal in pelagic tuna longline fisheries because the two sets often share the same type of fishing gears and baits (Huang,

Table 3
Summary results for the optimal GAMs selected for species richness index and Shannon diversity index.

	Species richness			Shannon index		
Family	Quasi-Poisson			Gaussian		
Link function	Log			Identity		
Adjusted R2	0.292			0.281		
Deviance explained	28.90%			28.60%		
	Estimate	p-value	% Deviance	Estimate	p-value	% Deviance
Latitude*longitude	28.600	<0.001	23.5%	28.455	<0.001	17.2%
SST	8.917	<0.001	11.4%	8.875	<0.001	10.3%
Chla	6.774	<0.001	6.6%	6.079	<0.001	4.8%
SLA	6.212	<0.001	0.9%	4.975	<0.001	0.6%
HBF	8.434	<0.001	12.2%	7.241	<0.001	9.6%
Season	—	—	0.5%	—	—	0.3%
Target	—	—	4.8%	—	—	3.3%

Individual contribution of each variable (%Deviance) running the model separately.

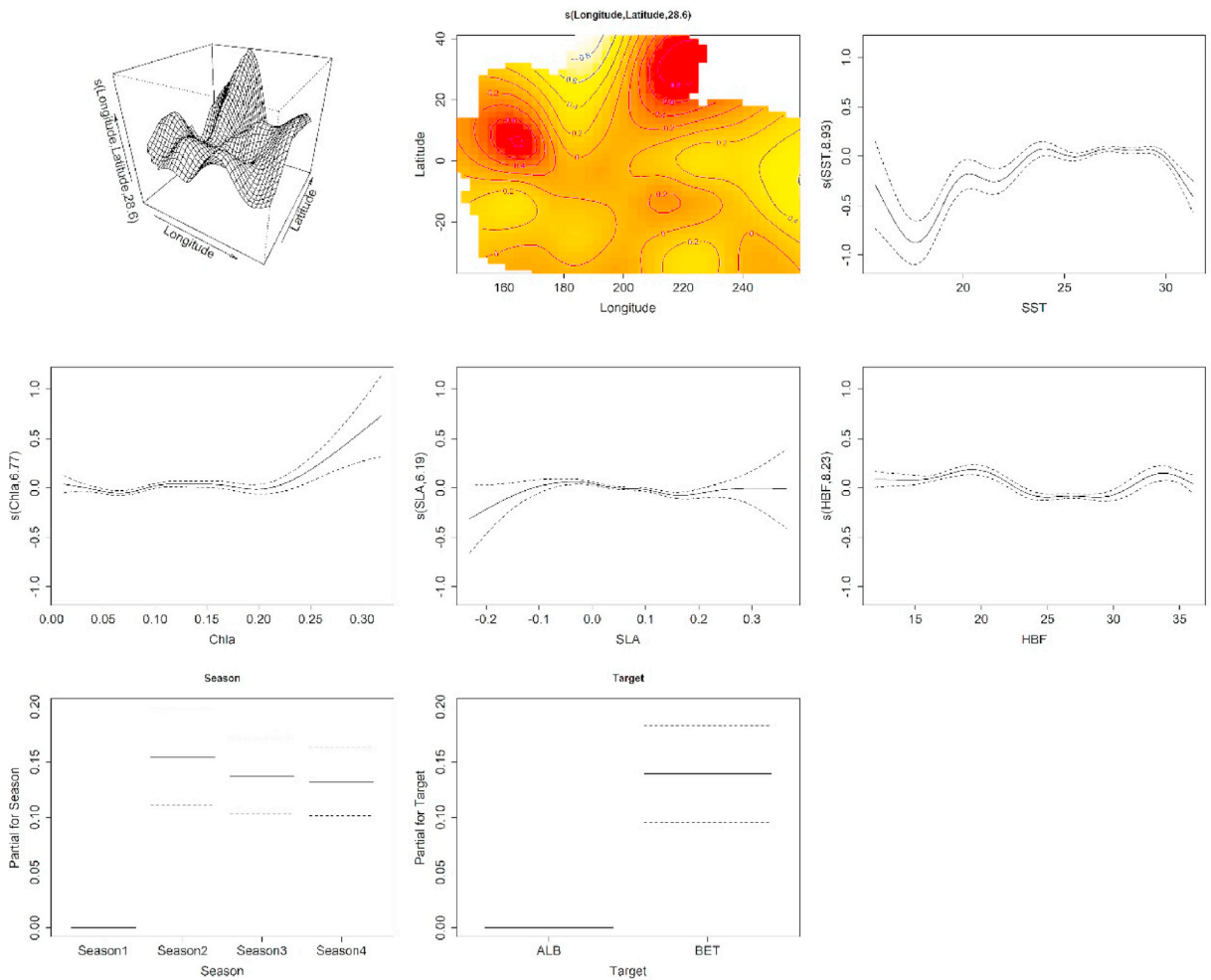


Fig. 7. Response curves of significant variables of GAM; The y-axis is the normalized effect of the variables on species richness. Dashed lines represent 95% confidence intervals.

2015), both of which can influence the fisheries' selectivity for species (Gilman et al., 2018). In addition, most of the bycatches are highly migratory and distributed across large geographic areas (Clarke et al., 2014). However, the diversity and density in the BET sets were higher than those in the ALB sets. This indicates that both sets were different in abundance assemblages. The log-rank abundance curve shows that the bycatch abundance in the BET sets was relatively evenly distributed among

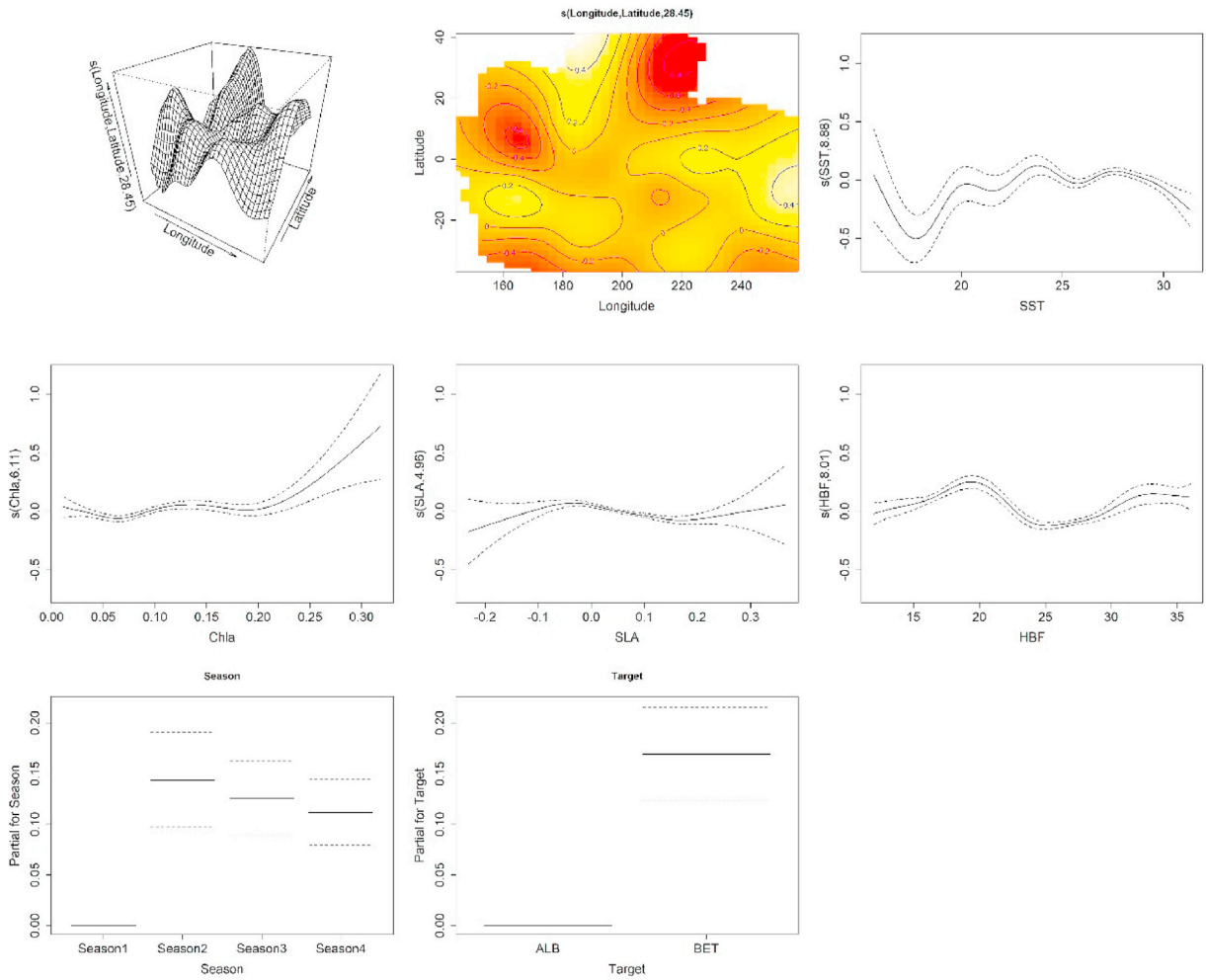


Fig. 8. Response curves of significant variables of GAM; The y-axis is the normalized effect of the variables on the Shannon index. The x-axis is the observed values. Dashed lines represent 95% confidence intervals.

species. On the contrary, the bycatch community in the ALB sets was formed by a few dominant species as well as many other occasionally captured species (Magurran, 2013). Therefore, the combination of observer data from both fishing sets can well-reflect spatial assemblage patterns of the bycatch community in tuna longline fisheries.

4.2. Biodiversity hotspots

Conserving biodiversity hotspots has been demonstrated to yield significant conservation benefits (Marchese, 2015). Regarding the entire study area, biodiversity in the bycatch community peaked in the eastern tropical Pacific (Fig. 5). The tropical area had higher biodiversity than the temperate area, which matched the general trends of the latitudinal decline of biodiversity on the greater global scale (Hillebrand, 2004). In the local area, a relatively high pelagic biodiversity has been noted in the southwestern Pacific, an observation that supports the previous hypothesis that the high predator’s diversity was often at the region of intermediate latitudes in the western Pacific (Morato et al., 2010a; WCPFC, 2010; Worm et al., 2003). On the other hand, in the central and eastern Pacific, biodiversity in tropical latitudes was higher than that within intermediate latitudes (Fig. 5).

The aggregation of organisms in ocean ecosystems depends substantially on the hydrography, geography, and circulation of specific areas, thus determining the main factors influencing its distribution is difficult (Lezama-Ochoa et al., 2017). Warm waters (~25 °C) with sufficient oxygen concentrations (>2 ml l⁻¹), in combination with mesoscale oceanographic gradients often result in the formation of optimal feeding habitats, which are suited for attracting numerous species (Worm, 2005). In this study, GAM analyses show that geographical positions, SST, and Chla were the most important environmental variables in predicating biodiversity (Table 3). Biodiversity was found to be highest in the eastern Pacific Ocean, which is characterized by

warm sea surface temperature (24–27 °C), high Chlorophyll *a* (>0.2) and sea surface height (>0.15) (Supplementary Material Fig. 1). The biodiversity hotspots in the western Pacific were located in areas near the island, seamounts, and shelf breaks. Oceanographically, these features are characterized by increased turbulence, mixing, and mesoscale eddies, which can enhance local production by transporting nutrients into the euphotic zone (Oschlies and Garcon, 1998; Wolanski and Hamner, 1988). In addition, these features also tend to concentrate food supply and have been shown to provide key feeding areas for pelagic species (Morato et al., 2010a, 2010b).

In addition to oceanographic features that influence whether the bycatch community aggregates to a particular area, the deployment of longline gear may also have a large effect on the number of bycatch interactions (Bigelow and Maunder, 2007), which might ultimately influence biodiversity estimates. For example, the shallow sets can have larger proportions of bycatch than the deep sets (Harley et al., 2018), and also show different bycatch compositions (Peatman et al., 2018). Whether the hooks are set in shallow (<100) or deep (>100 m) water can have different effects on the shark species (Gilman et al., 2008). Global ocean mapping of the distributions of all shark species, tunas and billfishes have shown that species richness peaks at mid-latitudes (Wiesner et al., 2012; Worm, 2005). However, in this study, the bycatch community of Chinese tuna longline fisheries, which mainly consisted of bony fishes and elasmobranchs, showed the highest biodiversity in low-latitudes (Fig. 5). Obvious spatial differences in HBF indicate that the bycatch in the central and eastern Equatorial Pacific came from relative shallow waters, and from relatively deep waters in other areas (Supplementary Materials Fig. 1). Therefore, there may be bias in reflecting the spatial distribution pattern of predator diversity in pelagic ecosystems due to the different fishing depth. More data are needed to further analyze the vertical distribution of biodiversity in the bycatch community.

4.3. Ecosystem monitoring and protecting

The nature of threats from pelagic fisheries on the structure and functioning of the pelagic ecosystems is still unclear. Current fisheries governing strategies and monitoring programs are expressing increasing concern over the fish community and ecosystems (Gilman et al., 2014). Establishing and monitoring indicators can be an effective way to detect variation in vulnerable pelagic ecosystems or fish communities (FAO, 2017; Jennings, 2005). In this sense, our study indicates that species richness and density could be used to identify diversity hotspots in the bycatch community of tuna longline fisheries (Fig. 5).

Chao2 indicators can efficiently estimate the species richness and also allowed us to preliminarily evaluate the efficiency of the current sample size in estimating the total species richness of the bycatch community (Lezama-Ochoa et al., 2015). Fisheries monitoring is an effective way of governing bycatch and collecting ecological data. Owing to the high cost, observer coverage rates of 5% is already a compromise in many tuna longline fisheries (Gilman et al., 2014). However, low coverage rates will reduce the accuracy of many indicators, such as total bycatch estimators (Amande et al., 2012; Babcock and Pikitch, 2003). Regarding biodiversity estimates, our results show that the current sample size may be insufficient in several areas (ET and WT) and seasons (Season 1 and Season 4). The insufficient observer coverage rate may cause great uncertainty in the estimates of spatial-temporal change of bycatch biodiversity. For that reason, observer programs should be designed to permit comprehensive spatial and temporal monitoring of pelagic ecosystems in the Pacific Ocean through the establishment of indicators for the pelagic community (Gilman et al., 2017; Nicol et al., 2013).

5. Conclusion

In conclusion, our study aims to understand the spatial distribution patterns of the predator's biodiversity in the pelagic ecosystem. The biodiversity of the bycatch community in pelagic tuna longline fisheries can be well studied by using observer data from tuna longline fisheries. Maintaining high diversity may also be critical for the sustainability of fishing and thus has many conservation benefits (Worm et al., 2003). By identifying diversity hotspots in the bycatch community and predicting their habitat preferences, monitoring and protection programs centering around pelagic ecosystems in the Pacific Ocean great benefit.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2020.e01276>.

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