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Environmental preferences of bigeye tuna, *Thunnus obesus*, in the Indian Ocean: an application to a longline fishery

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Abstract A survey of the fishing grounds for bigeye tuna, *Thunnus obesus*, in the Indian Ocean was carried out for a better understanding of the environmental preferences of bigeye tuna in a longline fishery. Catch rates of bigeye tuna were analyzed with respect to the ranges of depth, temperature, salinity, chlorophyll-a, and dissolved oxygen. The optimum capture depth, water temperature, and dissolved oxygen range of bigeye tuna were identified as 240.0 m to 279.9 m, 12.0°C to 13.9°C, and 2.00 mg·L^{-1} to 2.99 mg·L^{-1}, respectively, in the study area of Indian Ocean. Neither salinity nor chlorophyll-a had a detectable effect on the vertical distribution of the adult bigeye tuna. The dissolved oxygen is the principal factor limiting the vertical distribution of bigeye tuna.

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Introduction

Bigeye tuna, *Thunnus obesus*, is the most valuable tropical tunas targeted by the pelagic longline fisheries, which has resulted in extensive studies of this species in all oceans. Recent studies in the Indian Ocean have focused on biological characteristics (Chantawong et al. 1999; Ye et al. 2003; Nootmorn 2004; Song and Gao 2006a); resource assessment (Nishida and Takeuchi 1999; Hsu and Liu 2000; Matsumoto 2000; Nishida et al. 2001; Ricard and Basson 2002; Fonteneau et al. 2004); and their distribution in relationship to oceanographic and habitat parameters (Mohri and Nishida 1999a, b; Feng and Xu 2004; Chen et al. 2005). Various investigators have attempted to study the habitat selection of tuna species by analyzing catch statistics and oceanographic variables averaged over time and space (Mohri and Nishida 1999a, b; Feng and Xu 2004; Chen et al. 2005).

Oceanographic variables, *e.g.* temperature, salinity, chlorophyll-a, and dissolved oxygen, are different at various water depths. Bigeye tuna are caught by longline in different water depths. In many studies of the relationships of distributions of bigeye tuna with respect to oceanographic variables (e.g. Yoshihara 1951, 1954; Suzuki et al. 1977; Nakano et al. 1997; Jiang et al. 2005), it has been assumed that the underwater shape of a deployed longline is a catenary curve. While the fishing depth of hooks (hook depth) can be inferred by assuming catenary geometry, the actual depths are modified by environmental variables that may force the longline closer to the surface (Bigelow et al. 2006). This may result in biases of 30–50% of the actual hook depth (Bigelow et al. 2006) in estimates of capture depth made using traditional catenary equations.

Temperature-Depth-Recorders (TDRs) were used to measure the actual hook depths of longline during fishing (Boggs 1992; Mohri and Nishida 1999a, b; Bertrand et al. 2002a; Bach et al. 2003; Song and Gao 2006b). An alternative to estimating hook depth is to model the hook depth based on the actual hook depth measured, the environmental variables, and the hook depth by a geometry method.

Most studies of the impacts of environmental variables on tuna distribution in the Indian Ocean have been based on mesoscale data (Mohri and Nishida 1999a, b; Romena 2001; Marsac 2002) and/or long-term-averages of observations from satellite remote sensors (Chen et al. 2005). The temporal and spatial resolutions are inadequate for both mesoscale data and long-term-averages of observations, in general, and the errors associated with catch statistics and environmental data are usually too broad to show meaningful relationships (Brill 1994).

In contrast to the studies of the relationships between bigeye tuna and environmental variables on large spatial and temporal scales, several studies have focused on preferences exhibited by individual fish. Distributions by size of bigeye tuna with respect to depth, temperature, and time of day, have been based on studies using acoustic telemetry (Josse et al. 1998; Dagorn et al. 2000a; Bach et al. 2003), and archival tags (Schaefer and Fuller 2002; Musyl et al. 2003). Most of these studies have shown that bigeye tuna usually exhibit a diurnal vertical movement pattern, descending to about 300–500 m with regular returns to the surface layer during the day, but occupy only the surface layer at night. Physiological studies (Holland et al. 1990, 1992; Brill 1994) suggest that bigeye tuna excursions into the uniform-temperature surface layer are made to warm the muscles and/or to repay oxygen debts. Bach et al. (2003) suggested that instrumented longlines can be used to study the vertical behavior of pelagic species. Only a limited number of studies (Bach et al. 2003) investigated distributions of bigeye tuna with respect to at-sea measurements of dissolved oxygen concentrations.

This study evaluates the relationship between environmental variables and catch rates of bigeye tuna in the Indian Ocean. Catch rate, defined as catch-per-unit-effort (CPUE; Cooke 1984), is the quantity of fish caught in number with one standard unit of fishing effort; e.g. number of fish taken per 1,000 hooks (FAO 1998). CPUE is often used as an index of fish biomass (or abundance) in longline fisheries (FAO 1998). In this study, the data were obtained during two experimental longline fishing trips on two different Chinese longliners that used commercial fishing gear from September to December 2005.

The results derived in this study can improve the accuracy of estimation of optimal-capture depth, temperature, salinity, chlorophyll-a, and dissolved oxygen of bigeye tuna because the method for estimating hook depth was improved and because all the data were collected at sea. Improved estimation should lead to more informed choices of environmental variables considered in CPUE standardizations. The results of environmental preferences of bigeye tuna derived in this study may be also used to compare with those derived based on catenary depth, remote sensing data, oceanographic data sets, which may be subject to large errors, or tagging data, for validation.

Materials and methods

Fishing vessels and fishing gear

Data were collected from operations on two longliners Huayuanyu No.18 and, Huayuanyu No.19. The vessels had the identical specifications, with overall length of 26.12 m; registered beam of 6.05 m; registered depth of 2.70 m; gross tonnage of 150 t; net tonnage of 45 t; and main engine power of 407 kW. Both were equipped with super spools and chilled sea water systems.

The longline gear consisted of 3.6 mm diameter, 100 km monofilament main line; 360 mm diameter hard plastic floats; 5 mm diameter, 22 m nylon float line; and 16 m branch lines ending in either a ring hook or a circle hook. Two configurations of fishing gear were used in the study, conventional and experimental gear (Beverley et al. 2004). The conventional gear configuration was used as the control group. The conventional gear was assembled as one type of gear with no messenger weight (Table 1). The experimental gears were assembled as 16 types of gear with four groups of messenger weight (0.5 kg, 1.0 kg, 1.5 kg and 2.5 kg in water). The configuration and designs of experimental gear are shown in Table 1 and the figures indicated in Beverley et al. (2004).

In general, the gear deployment started between 03:00 and 06:00 local time, and lasted for about 5 h. Gear retrieval generally started between 12:00 and 15:00, and lasted for 12 h. Soak-times for individual hooks ranged from about 6 h to 16 h. In general, the number of hooks remained in the water during day (all of the hooks) were greater than during night (about three-fourths), and the soak-times of the fishing gear remained longer in the water during day (12 h) than during night (9 h). Fishing capacity (the number of hooks×the soak-times) during day was about twice as that during night. During gear deployment, the vessel speed was about 4.3 $m \cdot s^{-1}$, line shooter speed was 6.2–7.0 $m \cdot s^{-1}$, and the time interval between deploying the fore and after branch lines was about 7.8 s. The length of the main line between two branch lines was 43.5 m, and there were 25 hooks between successive floats (HBF). Each vessel used 100 circle hooks, 400 experimental hooks, and 200 to 1,500 ring hooks per set. The total hooks per set ranged from 700 to 2,200 hooks.

Fishing vessels were targeting bigeye tuna, and bycatch included yellowfin tuna, *Thunnus albacares*, swordfish, *Xiphias gladius*, albacore, *Thunnus alalunga*, and billfishes, Istiophoridae. Fishing activity was restricted principally to 0°47′N to 10°16′N and 61°40′E to 70°40′E (Fig. 1). The sampling sites are shown in Fig. 1. The vessel operations were conducted from 15 September to 12 December 2005, with each boat fishing for 54 days.

Instrumentation

The environmental sampling instruments included autonomous profiling data loggers (APDLs) (XR-620), TDR (2050) (RBR Co., Ottawa, Canada), and conductivity-temperature-depth (CTD) recorders (SBE37SM) (SeaBird Co., Bellevue, USA). Each boat was equipped with seven TDRs. The measurement range of temperature, conductivity, dissolved oxygen, and chlorophyll-a of APDL are 5°C to 35°C, 0 $mS \cdot cm^{-1}$ to 2 $mS \cdot cm^{-1}$, 0% to 150%, 0.02 $\mu g \cdot L^{-1}$ to 150 $\mu g \cdot L^{-1}$, respectively. The precision of the data is 0.002°C, 0.0003 $mS \cdot cm^{-1}$, 1% of dissolved oxygen measurement range, and less than 2% of chlorophyll-a

Table 1 Configuration of the conventional and experimental gears

Gear	Type[a]	Messenger weight (kg)[b]	Weight (g) of barrel swivel[c]	Weight (g) of sinker[d]	Luminous sleeve
Conventional	1	/	10	/	/
Experimental	1	0.5	75	18.75	yes
	2	0.5	60	18.75	yes
	3	0.5	45	11.25	no
	4	0.5	10	11.25	no
	5	1.0	75	18.75	no
	6	1.0	60	18.75	no
	7	1.0	45	11.25	yes
	8	1.0	10	11.25	yes
	9	1.5	75	11.25	yes
	10	1.5	60	11.25	yes
	11	1.5	45	18.75	no
	12	1.5	10	18.75	no
	13	2.5	75	11.25	no
	14	2.5	60	11.25	no
	15	2.5	45	18.75	yes
	16	2.5	10	18.75	yes

[a] For the experimental gear, types 1 to 8 used by Hua Yuan Yu No. 19, types 9 to 16 by Hua Yuan Yu No. 18, [b] The messenger weight was made of cement and sand, [c] The barrel swivel connected the first part and the second part of the branch line. This is a swivel made of the lead and shaped like a barrel to prevent entanglement with the branch lines, [d] The lead sinker was moored in the wire and above the hook to weight the hook

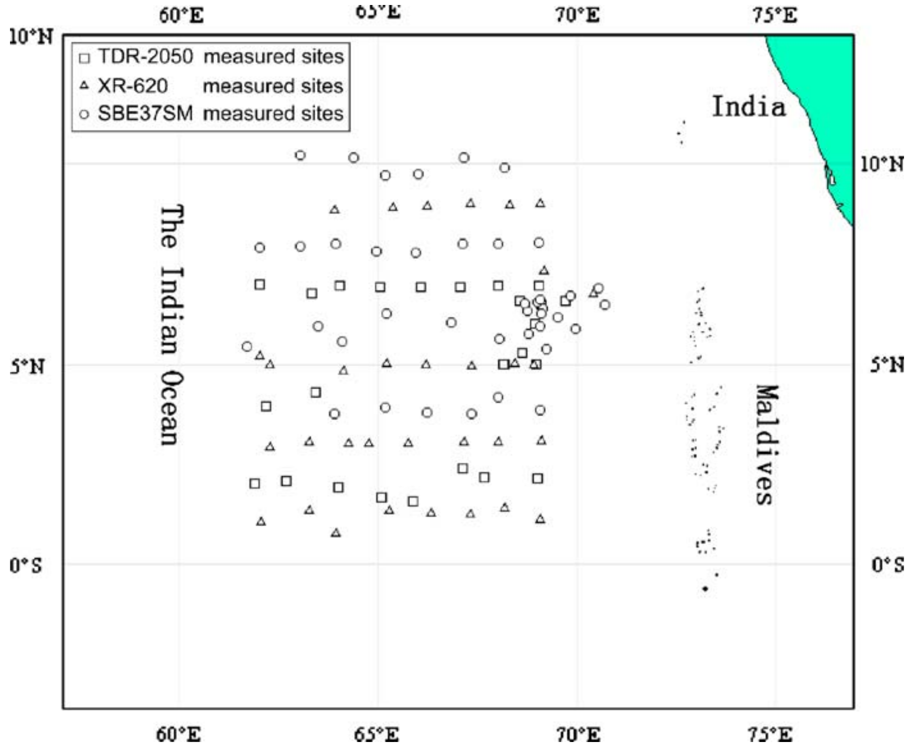

Fig. 1 The study area, bounded by 0º47′N, 10º16′ N, 61º40′E, and 70º40′E; locations where TDR-2050, XR-620, and SBE37SM were used (at 25, 33, and 38 sampling sites, respectively)

measurement range, respectively. Depth measurement error of the TDR was within ±0.05% in depths of 10–740 m, and temperature was measured to ±0.002°C. The conductivity was measured to 0.0003 s·m^{-1} with the CTD (SBE37SM), and the temperature was measured to ±0.002°C. All of these measurement errors were cited from the manufacturer's literature. These instruments were new and bought at the starting of this study in 2005. All of them were calibrated in the factories before the use. They were stable after the calibration for one year. Considering the accuracies of data from varied instruments and requirements of the study, the data of depth, temperature, and catch rate were processed to one effective decimal place, salinity and dissolved oxygen to two decimal places, and chlorophyll-a to three decimal places, respectively.

Investigational methods

A total of 80 sites for sampling, based on the traditional bigeye tuna fishing grounds of the Indian Ocean, were selected, but the actual sampling sites were slightly different from the planned ones due to logistical problems. Water temperature, salinity, dissolved oxygen, and chlorophyll-a vertical profiles were measured at 66, 52, 13, and 13 sites, respectively. Water temperature, salinity, dissolved oxygen, and chlorophyll-a vertical profiles changed with latitude over the study area and were shown in Fig. 2. These environmental variables were measured at all sites using APDL (XR-620), CTD (SBE37SM) or TDR (2050) after the gear was deployed. The greatest depth at which the environmental variables were measured was limited by the maximum length (500 m) of the wires that were used to lower the instruments. Temperatures, salinities, and values of chlorophyll-a at levels beyond the maximum depth that the instrument could reach were estimated from vertical profiles by extrapolating trend lines.

The following operational data were also collected: deployment position, time of day, vessel speed, course, line shooter speed, number of hooks between floats, time intervals between successive hooks, total number of hooks, times at which retrieval of the lines were initiated and completed, codes of the hooks at which the fish were caught, number of bigeye tuna hooked per day, and positions at which bigeye tuna were hooked.

Analytical methods

Two sets of fishing gear, conventional and experimental, and two hook types, ring hook and circle

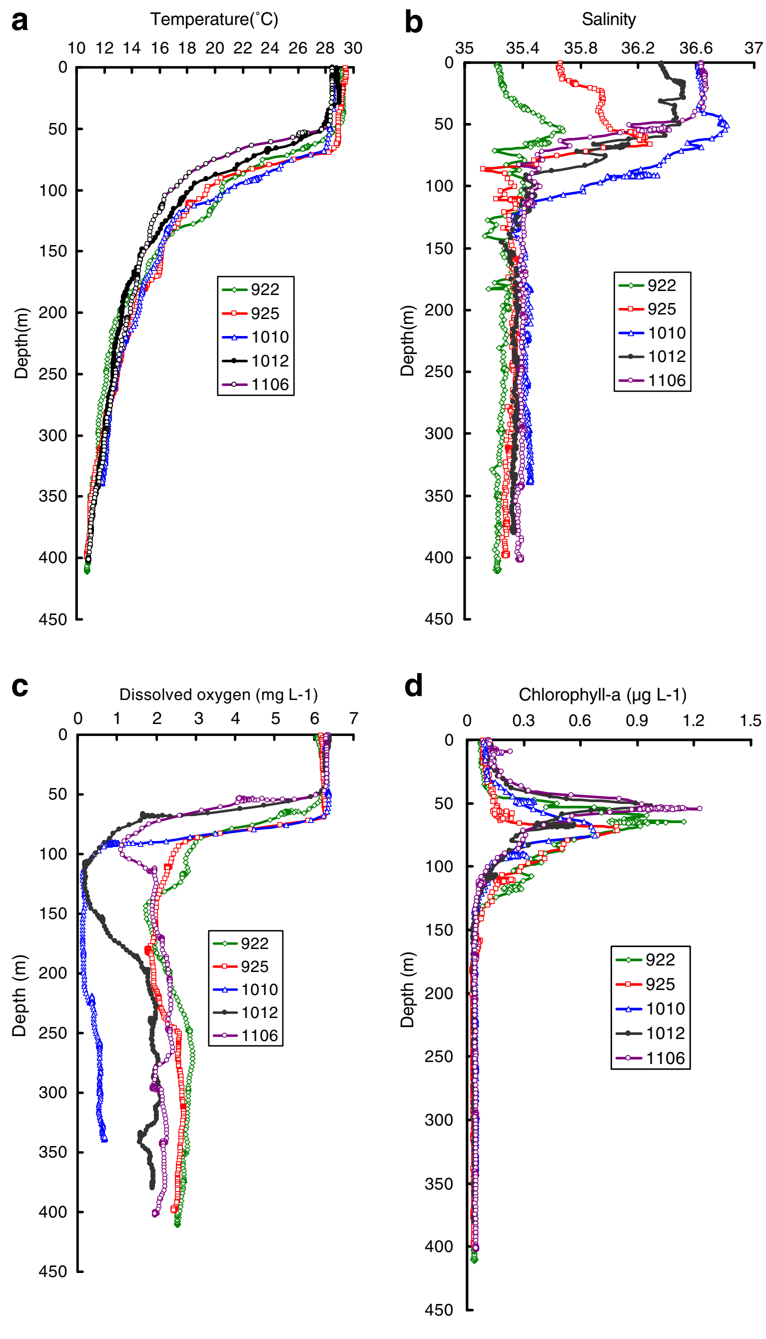

Fig. 2 Water temperature (**a**), salinity(**b**), dissolved oxygen(**c**), and chlorophyll-a (**d**) vertical profiles changed with latitudes over the study area (922:22 Sep. 2005, 1°25′N, 68°10′E; 925: 25 Sep. 2005, 3°07′N, 69°05′E; 1,010: 10 Oct. 2005, 9°02′N, 69°04′E; 1,012: 12 Oct. 2005, 7°22′N, 69°09′E; 1,106: 6 Nov. 2005, 5°02′N, 68°53′E)

hook, were used in the study. The catch rates of bigeye tuna for the conventional and experimental gears were compared using the Student t-test (paired-samples test; Cai and Yue 2004) to determine whether there were significant differences. The catch rate of bigeye tuna by the ring and circle hooks were also compared at three different drifting speeds (0.00–0.20 $m\cdot s^{-1}$, 0.21–0.40 $m\cdot s^{-1}$, and 0.41–0.76 $m\cdot s^{-1}$) using the one way ANOVA (Cai and Yue 2004) to determine whether there were significant differences.

Current shear between the surface and the thermocline has been hypothesized as the paramount factor in preventing longline gear from obtaining the predicted depths (Boggs 1992; Mizuno et al. 1998, 1999).

Additionally, shoaling dynamics are dependent on the direction of the environmental forcing in relation to the longline (Bigelow et al. 2006), who modeled the relationship between the actual and theoretical hook depths by the catenary curve, wind force, current shear, and current speed (derived from Ocean Global Circulation Model (OGCM)), using the general linear and general additive modeling. Song and Gao (2006b) analyzed the relationship between the actual and calculated hook depths and environmental variables, using stepwise regression method.

To determine the relationship between actual and calculated hook depths and environmental variables, the depths for 519 hooks of conventional (248 hooks) and experimental gears (271 hooks) were measured by TDR. For the conventional gear, the hook depths were calculated by the catenary curve equation (Saito 1992). When we calculated the hook depth of the experimental gear, we made the following assumptions in this study: (1) the depth from the sea surface to the connected site, where the mainline was connected to the messenger weight, as the adjusted float line; (2) the length of the adjusted float line equals to the length of original float line plus the mainline length from the connected site, where the original float line was connected to the mainline, to another connected site, where the mainline was connected to the messenger weight; and (3) the gear configuration below the connected site, where the mainline was connected to the messenger weight, as the catenary geometry and the calculation method followed the catenary geometry (Saito 1992) for this part. The relationships between the measured and calculated hook depths and the environmental data were quantified by the use of stepwise regression method (Song and Gao 2006b) for estimating the depths of the hooks for which the depths were measured or not measured.

For the conventional fishing gear, it was assumed that the hook depth was influenced mainly by gear drift velocity (denoted as V_g) over the ground, wind speed (V_w), measured by anemoscope, wind direction (C_w), measured by compass, angle of attack (Q_w) between the prevailing course in deploying the gear and direction that the fishing gear was drifting, and angle (γ) between the direction of the wind and the prevailing course in deploying the gear (Song and Gao 2006b). The longline fishing gear drift speed and angle of attack were the combined indices influenced by current shear at different depths, wind speed, and wind direction at different positions. The actual hook depths changed continuously within certain ranges. For the experimental fishing gear, the weight of messenger in the water was included as an additional variable in the model.

For the conventional fishing gear, the following equation was used to quantify the relationship between theoretical depths (D_T) and average hook depths measured by TDRs $\left(\overline{D}\right)$,

$$\overline{D} = b_0 + b_1 D_T + b_2 V_w^2 + b_3 V_g^2 + b_4 \sin\gamma + b_5 \sin Q_w \tag{1}$$

where $b_0, b_1, b_2, \ldots\ldots b_5$ were the respective parameters. This regression model was fitted to the observed data, using the least-squares method. The resultant regression model was estimated as

$$\overline{D} = 0.30 + 0.67 D_T + 1.03 V_w^2 + 47.21 \sin Q_W \tag{2}$$

and R=0.84, n=248, F=187.1, and P<0.0001. The terms V_g, and $\sin\gamma$ were deleted because they were not significant. To predict the depths of hooks for the conventional fishing gear, we can use Eq. 2 by inputting theoretical hook depth D_T, and the environmental data V_w, and $\sin Q_W$.

For the experimental fishing gear, the following equation was used to fit the relationship between the theoretical depths (D_T) and average hook depths measured by TDRs $\left(\overline{D}\right)$,

$$\overline{D} = b_0 + b_1 D_T + b_2 V_w^2 + b_3 V_g^2 + b_4 \sin\gamma + b_5 \sin Q_w + b_6 W \tag{3}$$

where $b_0, b_1, b_2, \ldots\ldots b_6$ were the respective parameters and W was the weight of the messenger in the water. The model was estimated as

$$\overline{D} = 96.53 + 0.69 D_T - 17.03 W - 19.73 V_g^2 \tag{4}$$

and R=0.66, n=271, F= 68.4, and P<0.0001. The terms V_w,$\sin\gamma$, and $\sin Q_w$ were deleted because they were not significant. For both of the models, $\overline{D}$ was defined as the predicted hook depth. To predict the depths of hooks for the experimental fishing gear, we can use Eq. 4 by inputting theoretical hook depth D_T, the weight of the messenger in the water W, and the environmental data V_g.

To determine the life stage of the bigeye tuna in this study, 413 of the 624 hooked fish from the tip of the snout to the fork of the tail (fork length) were measured. The lengths ranged from 88 cm to 190 cm. Most of the bigeye tuna were adult fish. In addition, we measured temperature at the depth of catch for 242 fish (a sample coverage of 38.8%), salinities for 147 fish (a sample coverage of 23. 6%), and chlorophyll-a and dissolved oxygen values for 77 fish (a sample coverage of 12.3%).

In this study, the following assumptions were made: (1) the fish swimming inhabiting at a depth were influenced by the combined effects of local environmental variables (temperature, salinity, chlorophyll-a, dissolved oxygen, *etc.*) and preys; (2) temperature, salinity, chlorophyll-a, and dissolved oxygen influenced the bigeye tuna distribution, and indicated the environmental conditions that are suitable for bigeye tuna; and (3) bigeye tuna hooked were caught on stationary gear during daytime.

Equation 2 or 4 was used for estimating the depths of all hooked fish for which hook codes were identified. The temperature, salinity, chlorophyll-a, and dissolved oxygen were calculated for hooked bigeye tuna for which hook codes were identified from temperature, salinity, chlorophyll-a, and dissolved oxygen vertical profiles measured by APDL, CTD, or TDR, respectively, based on the estimated hook depths. The number of hooked fish for which the environment profiles were not measured or the hook codes were not recorded were prorated to the different ranges of various environment variables based on the percentages of N_{Sij} versus N_{Si}, where N_{Sij} and N_{Si} was defined as the number of fish in different ranges of various environmental variables and the number of fish for various environmental variables respectively. To understand the habitat selection of bigeye tuna, the hooked bigeye tuna were grouped into various environmental variable ranges in the defined intervals from the respective starting point to the final point, based on various environmental variables measured at the depths at which bigeye tuna were hooked (Table 2).

The data processing procedures are shown in Fig. 3, and the following Eqs. 5–12 were used to calculate the CPUEs of bigeye tuna in various environment variable ranges by the use of frequency statistic method (Song and Gao 2006b).

$$P_{ij} = N_{Sij} / N_{Si} \quad (5)$$

$$P_{Hij} = H_{Sij} / H_{Si} \quad (6)$$

$$P'_{Hij} = H'_{Sij} \Big/ H'_{Si} \quad (7)$$

$$N_{ij} = P_{ij} \times N \quad (8)$$

$$H_{ij} = P_{Hij} \times H \quad (9)$$

$$H'_{ij} = P'_{Hij} \times H' \quad (10)$$

$$H_{Tij} = \sum_{k-1}^{n} H_{ij} + \sum_{k-1}^{m} H'_{ij} \quad (11)$$

where, k indicates operating days, n is for conventional hooks, m is for experimental hooks. The symbols and variables in the equations stand for indicated in Fig. 3.

$$CPUE_{ij} = N_{ij} / H_{Tij} \quad (12)$$

Each range of depth, temperature, salinity, chlorophyll-a, and dissolved oxygen to identify how

Table 2 Ranges of depth, temperature, salinity, chlorophyll-a, and dissolved oxygen for the hooked bigeye tuna with “interval” of observation

Environmental variables	Starting point	Final point	Interval	Total ranges
Depth	40.0 m	399.9 m	20 m	18
Temperature	10.0°C	28.9°C	1°C	19
Salinity	33.80	36.79	0.1	20
Chlorophyll-a	0.030 μg·L^{-1}	0.099 μg·L^{-1}	0.010 μg·L^{-1}	8
Dissolved oxygen	0.5 mg·L^{-1}	3.99 mg·L^{-1}	0.5 mg·L^{-1}	7

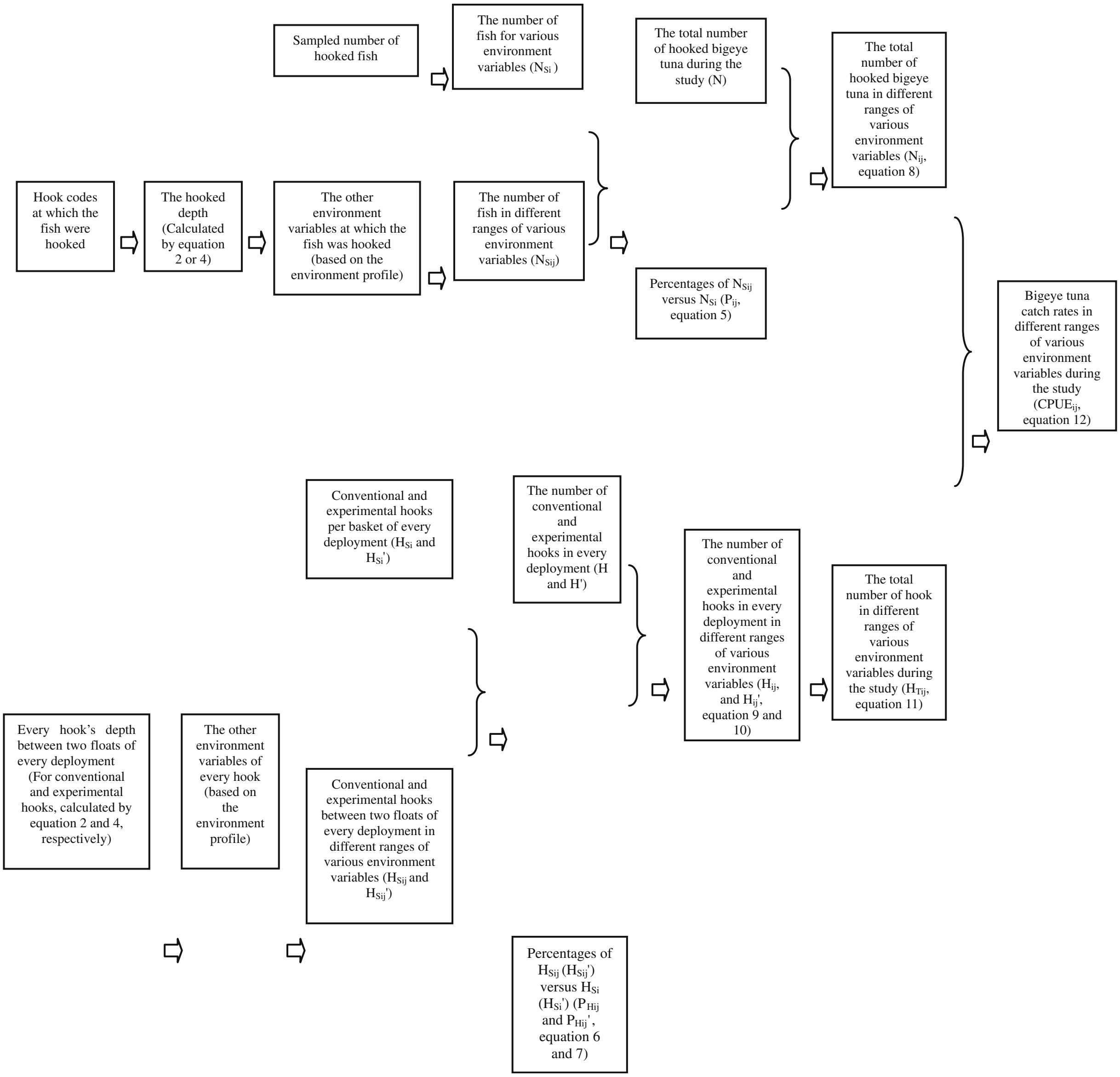

Fig. 3 The diagram of data processing procedures. N_{Sij}, H_{Sij} and H_{Sij}' are calculated using the frequency statistic method. Subscript "s" indicates "sample" and "i" indicates various environmental variables. For example, "depth (i=1)" or "water temperature (i=2)" or "salinity (i=3)" or "chlorophyll-a (i=4)" or "dissolved oxygen (i=5)". "j" is the ranges of various environmental variables (see Tab. 2)

they were correlated with the CPUEs (calculated in Eq. 12), number of bigeye tuna hooked (calculated in Eq. 8), and hooks (calculated in Eq. 11) were analyzed using hierarchical cluster analysis following the method of Ward by the using of DPS software (Tang and Feng 2002). The data were standardized to a mean of zero and a standard deviation of one before the cluster analysis. The distance used in the cluster analysis was the Euclidean distance.

Results

In most cases, the hook depths measured with TDRs were less than those calculated by catenary geometry (Fig. 4) and the actual hook depths varied with the fishing condition. The average hook depths of the experimental gear were deeper than those of the conventional gear while the catenary theoretical hook depth was the same (Fig. 4).

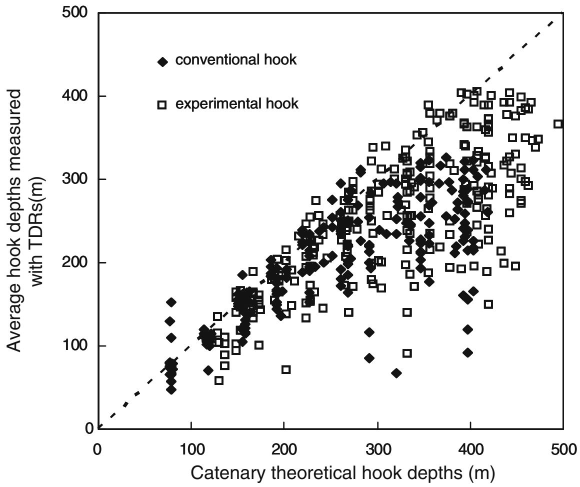

Fig. 4 A comparison of hook depths calculated from the catenary equation and average hook depths measured with TDR. The horizontal axis is catenary theoretical hook depths, and the vertical axis is average hook depth measured with TDRs. The diamonds and squares indicate conventional and experimental hooks, respectively. The dashed line indicates the loci at which the catenary and measured hook depths are equal

According to the paired sample t-test, there were no significant differences (P=0.64, n=94) between the conventional gears (3.81±4.81) and experimental gears (3.54±4.67) in the catch rates of bigeye tuna (Table 3). According to one way ANOVA, there were no significant differences (α=0.05) in the catch rate of bigeye tuna between the ring hooks and circle hooks at three different gear drift velocity (Table 4).

The CPUEs of bigeye tuna in various environment variable ranges were shown in Fig. 5. The group numbers, the group intervals, and the greatest catch rates were different for the various environmental variables (Fig. 5). Thus, catch rates could only be compared for the same environmental variable. The different criteria were used to define "the high level of catch rate" for various environmental variables, based on the above reasons and the expert's experience. Based on Fig. 5, the criteria to define "the high level of catch rate," the range of environmental variables to produce the high or highest catch rate and the highest catch rate for the various environmental variables were indicated in Table 5. The results of the hierarchical cluster analysis were summarized in Fig. 6.

For water depth, temperature, salinity, chlorophyll-a, and dissolved oxygen (Fig. 6a–e), the criteria used to group the environmental variable were the Euclidean distance equal to 1.04. We defined the bottom group in the vertical axis (Fig. 6a–e), which was the closest group to the horizontal axis, based on the strongest correlation to the catch rate of bigeye tuna, number of bigeye tuna hooked, and hooks, as "closely correlated environmental variable group" and the bottom environmental variable class in the vertical axis, which was the closest class to the horizontal axis, as the "most strongly correlated environmental variable range." The analysis suggested that the range of water depth, temperature, salinity, chlorophyll-a, and dissolved oxygen with which bigeye tuna often swam in was 220.0–279.9 m for depth, 12.0–13.9°C for water temperature, 35.10–35.49 for salinity, 0.040–0.049 $\mu g{\cdot}L^{-1}$ for chlorophyll-a, and 2.00–2.99 $mg{\cdot}L{-}^{1}$ for dissolved oxygen. The range of water depth, temperature, salinity, chlorophyll-a, and dissolved oxygen with which bigeye tuna swam in optimally was 260.0 m to 279.9 m, 13.0°C to 13.9°C, 35.40 to 35. 49, 0.040 $\mu g{\cdot}L^{-1}$ to 0.049 $\mu g{\cdot}L^{-1}$ and 2.50 $mg{\cdot}L^{-1}$ to 2.99 $mg{\cdot}L{-}^{1}$, and the corresponding CPUEs were 3.0, 5.8, 6.4, 5.7, and 3.8 individuals per 1,000 hooks, respectively (Fig. 5).

Discussions

The catch rates of bigeye tuna by the conventional, experimental gears were not significantly different. We employed one-way analysis of variance to compare the catch rates of bigeye tuna by ring hooks and circle hooks and found no significant differences (α=0.05). The data for conventional gears, experimental gears, ring hooks, and circle hooks can be

Table 3 The result of paired two samples t-test for catch rates of bigeye tuna between the conventional gear and experimental gear

Catch rate (individuals/1,000 hooks)	Conventional gear	Experimental gear
Mean	3.81	3.54
Std. deviation	4.81	4.67
Observations	94	94
df	93	93
t Stat	0.46	
$P(T<=t)$ 2-tailed	0.64	

Table 4 One way ANOVA for catch rate of bigeye tuna

Drifting speed ($m \cdot s^{-1}$)		df	Sum of Sq	Mean Sq	F	Sig.	F(0.05)
0.00–0.20	Between	1	12.28	12.28	0.22	0.64	4.02
	Within	54	2,987.09	55.32			
	Total	55	2,999.37				
0.21–0.40	Between	1	7.73	7.73	0.42	0.52	4.08
	Within	40	728.72	18.22			
	Total	41	736.46				
0.41–0.76	Between	1	84.26	84.26	1.83	0.18	4.00
	Within	60	2,759.22	45.99			
	Total	61	2,843.48				

combined like this study to analyze the catch rates of bigeye tuna under various environmental variables.

In most cases, the hook depths measured with TDRs were less than those calculated by catenary geometry (Fig. 4), which is consistent with the findings of Boggs (1992) and Bigelow et al. (2006). Data obtained with TDRs tend to be more useful for the analysis about the habitat selection of bigeye tuna. The accuracy of the analysis on the environmental preferences of bigeye tuna can be improved by the use of the predicted hook depths calculated in Eq. 2 or 4.

The habitat selection of bigeye tuna is constrained by many factors, e.g. physiological (Holland et al. 1990, 1992; Brill et al. 1994), biotic (Dagorn et al. 2000b; Marcinek et al. 2001), and abiotic oceanographic variables (Hanamoto 1987; Mohri and Nishida 1999a; Feng 2003; Jiang et al. 2005; Song and Gao 2006b). Maintaining elevated metabolic rates characteristics (Brill 1996) requires that bigeye tuna maintain elevated muscle temperatures, which may explain bigeye tuna regular upward excursions into the warm surface layer (Musyl et al. 2003). Dagorn et al. (2000b) and Marcinek et al. (2001) concluded that tuna movements coincide with those of prey organisms, such as squid, cephalopoda, euphausids, euphausiacea, and mesopelagic fishes, which undertake extensive diurnal vertical migrations. Josse et al. (1998) and Musyl et al. (2003) suggested that excursion of bigeye tuna mirrored the daily vertical movement of the sound scattering layer (SSL). Bertrand et al. (2002a) suggested that prey distribution was likely to play an important role in the distribution of a fish, its feeding behavior, and consequently, its catchability by longline gear. Tunas are more likely to be captured by longline if the availability of forage is relatively low (Bard 2001; Bertrand et al. 2002a, b). Comparisons of the optimum range of various environment variables between this study and the other studies for the bigeye tuna are shown in Table 6. The study areas of this paper, Mohri and Nishida (1999a), Feng (2003), Jiang et al. (2005), and Song and Gao (2006b), are in the Indian Ocean, and the other studies are in the Pacific Ocean (Table 6). The discussion of this study focuses mainly on the relationship between the habitat of the bigeye tuna and the ambient oceanographic variables.

For the optimum swimming depth, although the study areas and data sources used are different, the results of this study are, in general, consistent with those of Mohri and Nishida (1999a), and Schaefer and Fuller (2002). The daytime SSL depths (300–400 m) in the eastern equatorial Pacific Ocean (Fiedler et al. 1998) were suggested to be similar to those for parts of the Indian Ocean. The results of this study are different, however, from those of Hanamoto (1987), Jiang et al. (2005), and Song and Gao (2006b) due to the fact that the greatest depths of their hooks were less than the greatest depth of this study. Additionally, during this investigation, the number of hooks remained in the water during day (all of the hooks) were greater than during night (about three-fourths). The soak-times of the fishing gear remained longer in the water during day (12 h) than during night (9 h). Fishing capacity (the number of hooks × the soak-times) during day was about twice as that during night. As a result, the optimum swimming depth derived from these data is deeper than that suggested by the studies of Hanamoto (1987), Jiang et al. (2005), and Song and Gao (2006b). The results of this

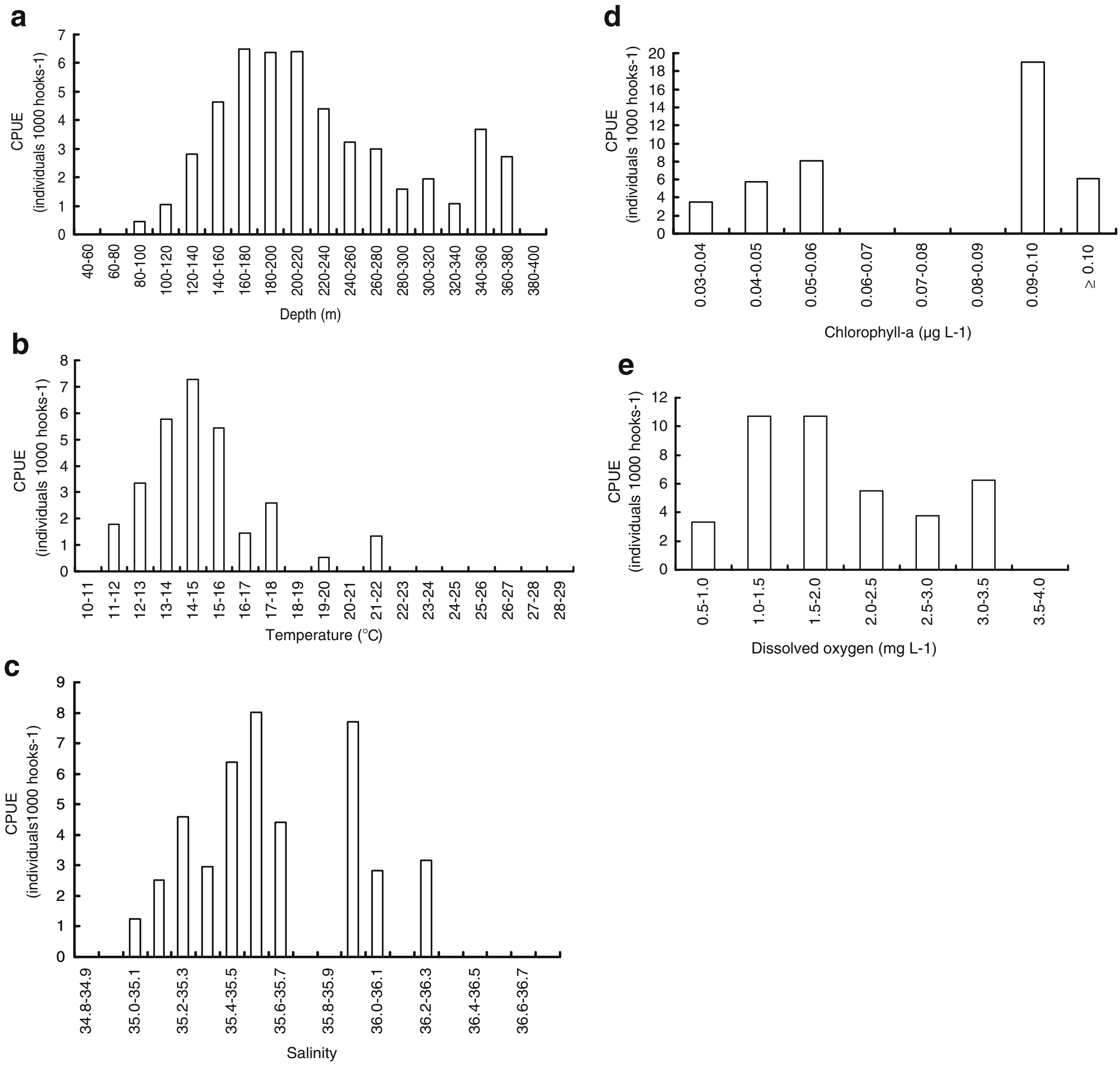

Fig. 5 Catch rates of bigeye tuna (individuals per 1,000 hooks) at different ranges of **a** depth, **b** temperature, **c** salinity, **d** chlorophyll-a, and **e** dissolved oxygen

study also differ from those of Boggs (1992), Holland et al. (1990, 1992), and Musyl et al. (2003). This could be the result of the greater depths of the SSL during the daytime in the vicinity of Hawaii (≥400 m) (Fiedler et al. 1998; Josse et al. 1998) or French Polynesia (≥500 m, but sometimes around 300 m) (Bach et al. 2003) or the possibility that sub adult fish cannot dive as deeply as can adult fish. Musyl et al. (2003) found that there were strong correlations between fish size and average depth during the daytime, but not during night. We suggest that the optimum capture depth range of bigeye tuna is 240.0–279.9 m during daytime in the Indian Ocean.

The results of this study for optimum water temperature are generally consistent with those of Hanamoto (1987), Mohri and Nishida (1999a), Schaefer and Fuller (2002), and Jiang et al. (2005). The hook depths of Hanamoto (1987) and Jiang et al. (2005) match the optimum water temperature suggested by Mohri and Nishida (1999a), Schaefer and Fuller (2002), and this study. The results of this study, however, differ from those of Boggs (1992), Holland

Table 5 The criteria to define "the high level of catch rate," the range of environmental variables that produces the high or highest catch rate and the highest catch rate for various environmental variables, based on Fig. 5

Environmental variables	High level of catch rate		Highest catch rate	
	Criteria (individuals per 1,000 hooks)	Range of environmental variables	Value (individuals per 1,000 hooks)	Range of environmental variables
Depth	>6.4	160.0–219.9 m	6.5	160.0–179.9 m
Temperature	>5.4	13.0–15.9°C	7.3	14.0–14.9°C
Salinity	>6.4	35.40–35.59, 35.90–35.99	8.0	35.50–35.59
Chlorophyll-a	>5.7	0.040–0.059, 0.090–0.099, above 0.10 $\mu g{\cdot}L^{-1}$	19.0	0.090–0.099 $\mu g{\cdot}L^{-1}$
Dissolved Oxygen	>5.5	1.00–2.49, 3.00–3.49 $mg{\cdot}L^{-1}$	10.7	1.00–1.49 $mg{\cdot}L^{-1}$

et al. (1990, 1992), Bertrand et al. (2002a), Bach et al. (2003), Musyl et al.(2003), and Song and Gao (2006b) for the same reason as we explained for the optimum swimming depth. We suggest that the optimum water temperature range of bigeye tuna is 12.0°C to 13.9°C in the Indian Ocean.

Feng (2003) suggested that salinity is quite stable, not varying much among areas or season, and that no relationship between the distribution of bigeye tuna and salinity is apparent in the Indian Ocean. The data in Table 6 indicate that the optimum salinity range of bigeye tuna is extensive (34.00 to 35.79), suggesting that salinity has little influence on the distribution of bigeye tuna.

The distribution of chlorophyll-a might not directly affect the distribution of adult bigeye tuna, as chlorophyll-a is several steps below adult bigeye tuna in the food chain. The relationship between the distribution of adult bigeye tuna and the chlorophyll-a should be studied in the future.

For the optimum dissolved oxygen, the result of this study (2.00–2.99 $mg{\cdot}L^{-1}$) is generally consistent with the results of Boggs (1992). During this investigation, when the dissolved oxygen level is 0.07–0.85 $mg{\cdot}L^{-1}$ (at depths of 140–320 m), no bigeye tuna were caught. This study suggests that dissolved oxygen is a more important constraint on the vertical distribution of bigeye tuna when it is less than 0.85 $mg{\cdot}L^{-1}$ (bigeye tuna physiological threshold requirements) and that the optimum dissolved oxygen range of bigeye tuna is 2.00 $mg{\cdot}L^{-1}$ to 2.99 $mg{\cdot}L^{-1}$ in the Indian Ocean. In general, we suggest that the depth, water temperature, and dissolved oxygen should be included in the CPUE standardizations to estimate the relative abundance of bigeye tuna.

The assumption, i.e., the bigeye tuna hooked were caught on stationary gear, is reasonable. All the bigeye tuna hooked on moving or stationary gear are included in this study. In the study of Boggs (1992), the number of hooks per set were very limited (128 to 600 hooks) and the retrieving time (when the hooks are moving) was longer because of the use of the hook timer. This study used more hooks per set (700 to 2,200 hooks), let the gear stay in the water longer (>10 h), and retrieved it more rapidly than was the case in the study of Boggs (1992). In this study, the moving time of the hooks was shorter than in that of Boggs (1992). The percentage of bigeye tuna caught on moving hooks in the study of Boggs (1992) was less than 12%, and the error in this study resulting from combining data for moving and stationary hooks is so low that it can be ignored. Thus, the results of the analysis of environmental preferences of bigeye tuna are likely to be reliable.

The depths at which the fish were hooked are influenced by all environmental variables. In fact, this study uses the hooking depths to determine how a fish selected each environmental variable. All environmental variables in each depth range (or each study site) should be analyzed together, using, for example, generalized linear model, quantile regression, or principal component analysis to identify which environmental variable played the major role in the habitat selection of bigeye tuna. The results of this study should be included in such a comprehensive study. In addition, other factors, such as availability of food, currents, the Indian Ocean Dipole (IOD), and monsoons may also need to be considered in studying the habitat selection of larger individuals.

In this study, there are minor biases in the relationship between CPUE and oceanographic vari-

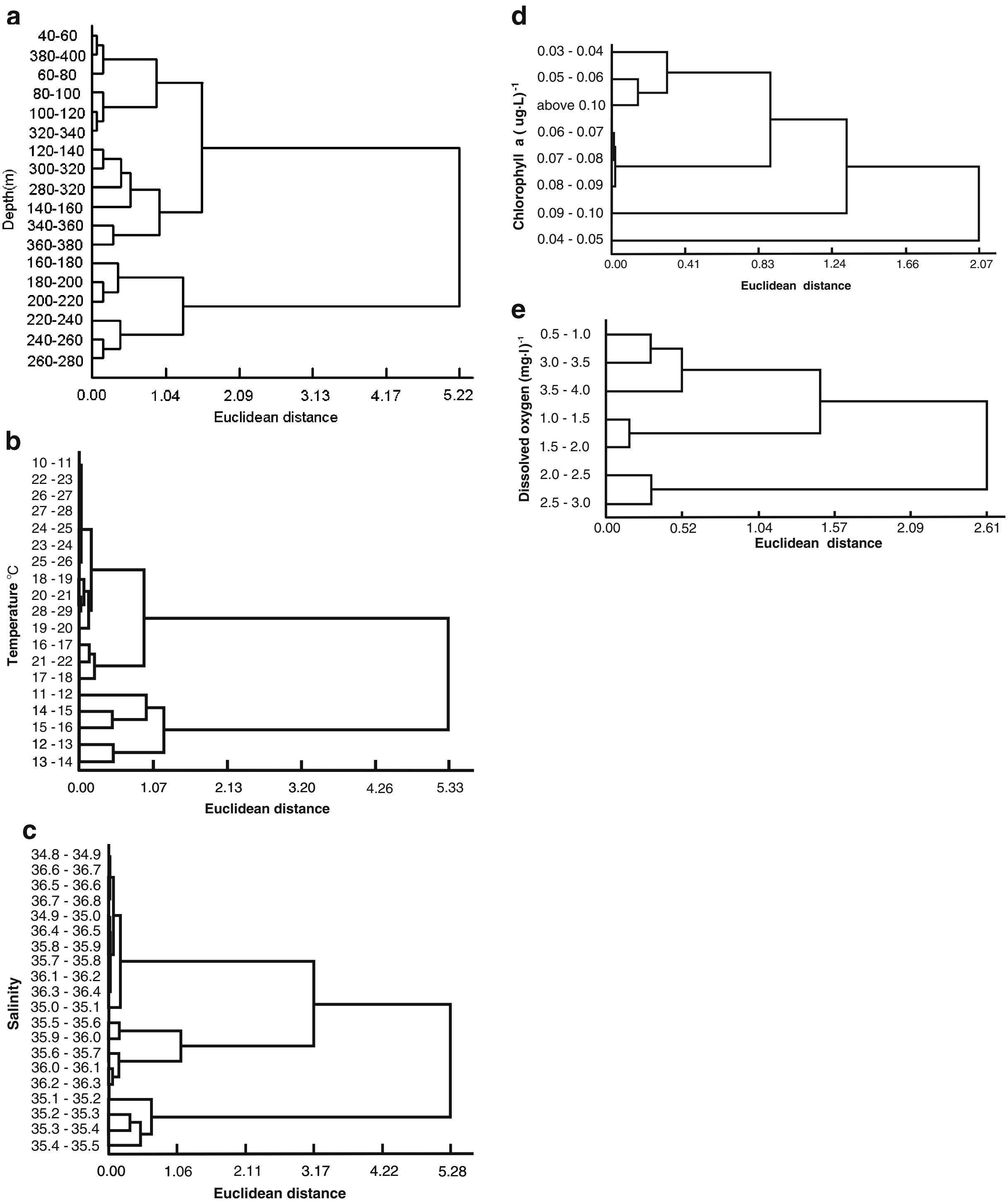

Fig. 6 Results of cluster analyses of catch rates of bigeye tuna and ranges of **a** depth, **b** temperature, **c** salinity, **d** chlorophyll-a, and **e** dissolved oxygen

Table 6 Comparisons of the optimum range of various environment variables between this study and the other studies (HBF: Hooks between successive floats)

Items	In this study		In other studies					
	Closely correlated to catch rate	Most strongly correlated to catch rate	Authors	Relatively high catch rate or concentration range	Hightest catch rate or highest concentration range	Data source	Data processing method	Study area
Depth (m)	240.0–279.9	260.0–279.9	Hanamoto (1987)	/	100.0–250.0	Japanese research vessels' data of 1977–1982, 1,400 hydrographic stations data of 1929–1981	Theoretical depth, quantitative analysis	Pacific Ocean
			Holland et al. (1990, 1992)	200.0–240.0	/	Ultrasonic tracking data of subadult fish (daytime)	/	Hawaii waters
			Boggs (1992)	200.0–400.0	360.0–400.0	Observed oceanography data	TDR data, adjusting the catenary depth by reducing 27%, quantitative analysis	Hawaii waters
			Mohri and Nishida (1999a)	161.0–280.0	261.0–280.0	Japanese longline data of 1967–1991, 11HBF	Theoretical depth combined with actual measured depth, quantitative analysis	Indian Ocean
			Schaefer and Fuller (2002)	10.0–50.0 (night) 150.0–300.0 (daytime)	200.0–300.0 (daytime)	Archival tagging data (unassociated type-1 behavior)	Statistic	Eastern Equatorial Pacific Ocean
			Musyl et al. (2003)	300.0–500.0 (daytime)	400.0–500.0 (daytime)	Archival tagging data (unassociated fish), observed environmental data	Statistic	Hawaii waters
			Jiang et al. (2005)	160.0–239.9	200.0–219.9	Chinese deep-frozen longliner, 18 HBF	Theoretical depth , quantitative analysis	Indian Ocean
			Song and Gao (2006b)	50.0–209.9	70.0–89.9	Chinese longliner with super spool and chill sea water systems, 25 HBF	Predicted hook depth, quantitative analysis	Maldives waters
				63.0–203.0 (capture depth)	63.0–134.0 (dominating depth)		Predicted hook depth, from sampled dead and stiffness fish, quantitative analysis	
Temperature (°C)	12.0–13.9	13.0–13.9	Hanamoto (1987)	10.0–15.0	11.0–14.0	Japanese research vessels' data of 1977–1982, 1,400 hydrographic stations data of 1929–1981	Theoretical depth, quantitative analysis	Pacific Ocean

			Boggs (1992)	/	8.0–10.0	Observed oceanography data	TDR data, adjusting the catenary depth by reducing 27%, quantitative analysis	Hawaii waters
			Holland et al. (1990, 1992)	14.0–17.0	/	Ultrasonic tracking data of subadult fish (daytime)	/	Hawaii waters
			Mohri and Nishida (1999a)	10.0–16.0	11.0–13.0	Japanese longliner (data of 1967–1991), 11HBF, Depth specific oceanographic observation data for 1906–1989	Theoretical depth combined with actual measured depth, quantitative analysis	Indian Ocean
			Bertrand et al. (2002a)	8 .0 (threshold value)		Simultaneous acoustic observation data, experimental longline, and oceanographic data	Correlation analyses, general linear models, robust regressions, and influence of micronekton patches	French Polynesia waters
			Schaefer and Fuller (2002)	13.0–16.0 (daytime)	13.0–14.0 (daytime)	Archival tagging data (unassociated type-1 behavior)	Statistic	Eastern Equatorial Pacific Ocean
			Bach et al. (2003)	10.0–14.0	10.0–12.0	Acoustic telemetry data, monitored longline data, observed environmental data	Statistic	French Polynesia waters
			Musyl et al. (2003)	7.0–10.0 (daytime)	7.0–8.0 (daytime)	Archival tagging data (unassociated fish), observed environmental data	Statistic	Hawaii waters
			Jiang et al. (2005)	12.0–15.9	12.0–12.9	Chinese deep-frozen longliner, 18 HBF	Theoretical depth, quantitative analysis	Indian Ocean
			Song and Gao (2006b)	13.0–29.9	27.0–27.9	Chinese longliner with super spool and chill sea water systems, 25 HBF	Predicted hook depth, quantitative analysis	Maldives waters
				14.0–27.0 (capture temperature)	16.0–27.0 (dominated temperature)		Predicted hook depth, from sampled dead and stiffness fish, quantitative analysis	
Salinity	35.20–35.49	35.40–35.49	Feng (2003)	34.50–35.40	/	Japanese longline data of 1975–1997, data of World Ocean Atlas 98 (1° square grid)	Qualitative analysis by GIS, vertical weighted averages for the depth	Indian Ocean
			Hanamoto (1987)	34.50–35.50	/	Japanese research vessels' data of 1977–1982, 1,400 hydrographic stations data of 1929–1981	Theoretical depth, quantitative analysis	South Pacific Ocean
				34.00–34.70				North Pacific Ocean

Table 6 (continued)

Items	In this study		In other studies					
	Closely correlated to catch rate	Most strongly correlated to catch rate	Authors	Relatively high catch rate or concentration range	Hightest catch rate or highest concentration range	Data source	Data processing method	Study area
				34.70–35.20				Equatorial Pacific Ocean
			Song and Gao (2006b)	35.00–35.79	35.70–35.79	Chinese longliner with super spool and chill sea water systems, 25 HBF	Predicted hook depth, quantitative analysis	Maldives waters
				34.94–35.42 (capture salinity)	35.30–35.42 (dominated salinity)		Predicted hook depth, from sampled dead and stiffness fish, quantitative analysis	
Chlorophyll-a (μg L^{-1})	0.040–0.049 and 0.090–0.099	0.040–0.049	Feng (2003)	0.020–0.160	/	Japanese longline data of 1975–1997, data of World Ocean Atlas 98 (1° square grid)	Qualitative analysis by GIS, surface Chlorophyll-a	Indian Ocean
Dissolved oxygen (mg L^{-1})	2.00–2.99	2.50–2.99	Hanamoto (1987)	1.30 (minimum level)		Japanese research vessels' data of 1977–1982,1,400 hydrographic stations data of 1929–1981	Theoretical depth, quantitative analysis	Pacific Ocean
			Boggs (1992)	2.00–6.00	2.00–3.00	Observed oceanography data	TDR data, adjusting the catenary depth by reducing 27%, quantitative analysis	Hawaii waters
			Mohri (1998)	1.30 (minimum level)		Japanese longline data of 1967–1991, 11HBF, Depth specific oceanographic observation data for 1906–1989	Theoretical depth combined with actual measured depth , quantitative analysis	Indian Ocean
			Bertrand et al. (2002a)	0.80 (threshold value)		Simultaneous acoustic observation data, experimental longline, and oceanographic data	Correlation analyses, general linear models, robust regressions ,and influence of micronekton patches	French Polynesia waters
			Bach et al. (2003)	3.64–4.94	3.64–4.16	Acoustic telemetry data, monitored longline data, observed environmental data	Statistic	French Polynesia waters

ables due to uneven sampling. The fluctuation of water temperature, salinity, and chlorophyll-a over the latitudes were not very large when the depth was deeper than 120 m (Fig. 2). Most fish were caught in the depth ranges of 140 m to 280 m, and there were few fish to be caught shallower than 120 m. For the dissolved oxygen, there was no fish caught at the latitude around 9°N, few fish were caught in the north of 7°N; and most fish were caught at the latitude range of 1°N–7°N. The fluctuation of the dissolved oxygen over the latitudes 1°N–7°N were not very large when the depth was deeper than 120 m (Fig. 2).

In this study, spatial and temporal coverage are limited as almost all other studies in fisheries. However, we believe that the marine environmental variables and fisheries will change greatly over the larger spatial and temporal coverage, and pooling larger spatial and temporal data to study the environmental preferences of fish might miss some key characteristics. We think studies with current spatial and temporal coverage and the fine scale data are also necessary for us to better understand the environmental preferences of bigeye tuna.

We used fisheries data (vertical distribution of bigeye tuna CPUE) to study the environmental preferences of bigeye tuna while the others used tagging data in similar studies. We do not think we should replace one type of data with another because they have their respective advantages and disadvantages. Bach et al. (2003) suggested that longlines monitored by TDRs are superior in some ways to acoustic telemetry or archival tagging because longline monitoring can sample a large number of individuals of different sizes and species in different environmental conditions. They also suggested that the vertical distributions of the catches were good indicator of the natural depth distributions of the fish if the entire depth ranges of the various species were within the range of depths fished by longline gear. However, studies of the habitat of bigeye tuna based on the commercial data alone might produce misleading results because the fish occur at depths greater than those reached by the deepest hooks of commercial longlines. Bigeye tuna in the open ocean swim within the mixed layer above the thermocline during night (Holland et al. 1990; Dagorn et al. 2000a; Schaefer and Fuller 2002). In this study, there were only a few hooks that fished at depths less than 100 m below the surface, so the habitat selection of bigeye tuna between the surface and 100 m could not be ascertained. Data of the occurrence of bigeye tuna between the surface and 100 m could be obtained by experimental longline fishing in this depth range and by tagging with archival or pop-up tags.

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