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Hydrological and trophic characteristics of tuna habitat: consequences on tuna distribution and longline catchability

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Abstract: We studied relationships between tropical tunas (albacore, *Thunnus alalunga*; bigeye, *Thunnus obesus*, and yellowfin, *Thunnus albacares*, tunas) and their biotic and abiotic environments through simultaneous acoustic observations of tunas and their prey, experimental longline catch, and oceanographic data in French Polynesia. Vertical habitat limits were estimated, based on temperature- and dissolved oxygen-at-capture data. We then studied tuna-micronekton relationships to better understand how tuna occupy the pelagic space. At a regional scale, tunas were more abundant in areas rich in prey with favourable hydrological conditions. Inside such areas, at a longline-set scale, however, the longline catches were maximal only when prey were not distributed in dense patches (except for yellowfin tuna). We interpreted this result by considering that areas with high prey abundance attract tunas, but at a small scale, if prey are patchy distributed, tunas are more inclined to feed on them rather than on longline baits. The effect of patches on yellowfin tuna catch per unit effort (CPUE) does not appear likely because this species also feeds on the mixed layer, where patch density was very low. Not only hydrological characteristics, but also prey density and prey patch characteristics, should be taken into account for interpreting longline CPUE data.

Keywords: tunas, acoustic observations, hydrological

Résumé

Nous étudions les relations liant les thons tropicaux (germon, *Thunnus alalunga*, thon obèse, *Thunnus obesus*, et thon à nageoires jaunes, *Thunnus albacares*) à leurs environnements biotique et abiotique. Pour ce faire, nous avons réalisé simultanément, en Polynésie Française, des observations acoustiques des thons et de leurs proies, des pêches à l'aide d'une palangre instrumentée et des mesures hydrologiques. Des limites d'habitat vertical des thons calculées sur la base de données de température et d'oxygène dissous sont proposées. Nous étudions ensuite les relations thons-micronecton afin de mieux comprendre la stratégie d'occupation de l'espace des thons. A une échelle régionale, les thons sont plus abondants dans des zones riches en proies avec des conditions hydrologiques favorables. Cependant, à l'intérieur de telles zones, les captures sont maximales lorsque les proies ne sont pas distribuées sous forme de patchs (sauf pour le thon à nageoires jaunes). Nous interprétons ces résultats en considérant que les zones de fortes abondances en proies attirent les thons mais, qu'à une échelle fine, si les proies sont distribuées sous la forme de patchs denses, les thons s'en nourrissent préférentiellement, au détriment des appâts de la palangre. Ces patchs ne semblent pas influencer les prises par unité d'effort (PUE) des thons à nageoires jaunes, probablement parce que cette espèce se nourrit également dans la couche homogène où la densité en patchs est très faible. Les caractéristiques hydrologiques, mais également la densité en proies et leur type de distribution, devraient donc être pris en compte pour l'interprétation des données de PUE.

Introduction

The influence of oceanographic features (mainly temperature and oxygen) on tuna distribution has been the focus of several reviews (e.g., Sharp 1978; Sund et al. 1981; Brill 1994). The distribution of tunas has also been linked to forage availability (Sund et al. 1981). These results are not surprising considering the elevated metabolic rates of tropical tunas (Olson and Boggs 1986). Studying the relations binding tunas to their biotic and abiotic environments is difficult, as it is necessary to simultaneously observe tunas, their prey, and the physico-chemical conditions. This is especially true when using fishing data, because observations are biased by accessibility and catchability. Longline catch per unit of effort (CPUE) values are not necessarily good indices of tuna distribution or abundance. Hook depths must coincide with the vertical distribution of tunas, which is not always the case (Hanamoto 1987; Boggs 1992; Hampton et al. 1998). Similarly, micronekton (i.e., tuna prey) observations or biomass estimations are known to be biased when using pelagic trawls (Power 1996). However, recent developments in acoustic survey technologies have made it possible to simultaneously observe both tunas (Bertrand et al. 1999a; Bertrand and Josse 2000; Josse and Bertrand 2000) and their prey (Marchal and Lebourges 1996; Bertrand et al. 1999b) independent of any fishing activity.

Describing a biological system requires an appropriate choice of scales of observation. This choice is difficult because the populations and the ecosystems cannot be described by a single scale (Levin 1992). We chose to describe the pelagic habitat at two scales: first, a regional scale, i.e., the northern part of the French Polynesian Exclusive Economic Zone (EEZ), and second, a finer (local) scale, i.e., the scale of a longline set. The regional scale allowed the description of the broad outlines of the biotic and abiotic conditions as well as the general relationships between members of the pelagic ecosystem. This was necessary before investigating smaller-scale relationships, in particular, fishing gear-predator-prey interactions.

Using simultaneous acoustic data (on both tunas and their prey), experimental longline data, and hydrological data collected during the ECOTAP Program (a joint scientific project between IRD, Institut de Recherche pour le Développement; IFREMER, Institut Français de

Recherche pour l'Exploitation de la MER and SRM, Service des Ressources Marines, to study the distribution and behaviour of sub-surface tunas in French Polynesia), we developed a schematic model of the relationships between adult tropical tunas, i.e., albacore tuna (*Thunnus alalunga*), bigeye tuna (*Thunnus obesus*), yellowfin tuna (*Thunnus albacares*) and their environment at regional and local scales. First, we defined a volume of suitable habitat for tunas based on temperature and dissolved oxygen conditions. We combined these results with acoustic prey observations to interpret the vertical and horizontal distributions of tunas observed from acoustics and longline experiments. At a finer scale (longline-set scale), the fishing independent observations of tunas from acoustics allowed us to determine which environmental factors most influenced longline catchability. We specifically attempted to determine if the abundance and spatial distribution of prey modified the attraction of tunas to baited longline hooks.

Material and methods

The data were collected on board the IRD R/V "ALIS" (28 m long) during experiments carried out in the French Polynesia exclusive economic zone (EEZ) between 4°S and 20°S latitude and between 134°W and 154°W longitude in the vicinity of the Society, Tuamotu, and Marquesas Archipelagos, from July 1995 to August 1997 (Fig. 1).

Instrumented longline fishing experiments

Due to the expanse of the study area and to logistic constraints, fishing sets were distributed continuously along a transect in such a way that the largest possible ocean surface could be sampled. A total of 80 000 hooks were deployed during 163 fishing operations (Fig. 1). The longline was instrumented with hook timers and time-depth recorders (Boggs 1992) to estimate both time and depth of capture using a model developed by Bach et al. (1996). The gear was generally set early in the morning (between 04:00 and 07:00) and retrieved in the afternoon (between 13:00 and 15:00). Typically, longlines were used to fish down to 500 m depth, except in the Marquesas where the presence of deoxygenated waters justified a reduction in the maximum fishing depth.

Acoustic data measurements

Acoustic data were collected from diurnal rectangular surveys above the longline or from rectangular or straight surveys at night between each fishing operation. These data were collected with a SIMRAD EK500 (version 4.01) echosounder connected to a 38 kHz, split-beam, hull-mounted SIMRAD ES38B transducer (beam angle 6.9° at -3 dB), with a 1 ms pulse duration. The water column was sampled to a depth of 500 m. Acoustic and navigation data were stored on a PC using SIMRAD Subsea EP500 software. The on-axis and off-axis calibration was performed using a 60 mm copper sphere and a standard procedure (Foote et al. 1987). Acoustic measurements were recorded so as to observe both tunas by echo-counting and their prey by echo-integration.

Individual target echoes were selected using the trace-tracking procedure of the EP500. The criteria used to select individual tuna targets were described by Bertrand and Josse (2000). Direct *in situ* species recognition was not possible. A -70 dB threshold was applied on integration data. All prey echo types were coded as described by Bertrand et al. (1999b), who showed that the acoustic back-scattered energy by the surface unit (s_a) can be considered representative of micronektonic fish and squid biomass. For some analyses, the s_a was classified into three categories: low, medium, high.

Hydrological measurements

Physico-chemical measurements were carried out near the experimental longline. Temperature, salinity, and dissolved oxygen profiles were determined using a Seacat SBE 19 (Seabird Electronics, Inc.) from the surface to 600 m depth.

Large scale characterization of the pelagic habitat

Using multivariate analysis, Bertrand et al. (1999b, 2000) have defined two typologies of the study area based on hydrological and micronekton characteristics according to acoustic and pelagic trawl data. Based on hydrologic features, we divided the northern part of the Polynesian EEZ into three zones (Fig. 1). The first one (zoneH1), located south of 14°S, was characterized by a mixed layer of about fifty meters, with temperature slowly decreasing from this layer down to 500 m. The dissolved oxygen (DO) concentration was high throughout the vertical section. The second zone (zoneH2), between 9°S and 14°S, presented a 60-meter mixed layer, below which a weak thermocline was present between 170 m and 320 m and a weak oxycline (3.3 mL•L⁻¹ to 1.5 mL•L⁻¹) between 200 m and 350 m. The third zone (zoneH3), north of 9°S, presented a strong thermocline and oxycline between 100 m and 250 m with an average, minimum DO concentration of 0.8 mL•L⁻¹ (values lower than 0.1 mL•L⁻¹ were sometimes observed).

In French Polynesia the micronekton is mainly composed of a vertically migrating multispecies community dominated in weight by lanternfishes (myctophids). The mesopelagic fishes are distributed either in scattering layers with other prey species or in dense, quasi-monospecific patches (Bertrand, 1999). We described this prey community according to their overall biomass and the number of dense patches. The characterization of the micronekton distribution allowed us to divide the study area into three zones quite similar to the hydrologic ones (Fig. 1). The first micronekton zone (zoneM1), located south of 13°S, was characterized by a very low overall biomass and a small number of micronekton patches. The second zone (zoneM2), located mainly between 8°S and 13°S, corresponded to a weak convergence. This zone presented the highest overall biomass and numbers of micronekton patches. In the third zone (zoneM3), located north of the Marquesas Archipelago, the micronekton biomass was moderate in comparison to the whole study area, while micronekton patches were not numerous. It must be noted that, in the text, when the type of zone, i.e., micronektonic or hydrologic, is not indicated the results are valid for both types.

Definition of an index for the “habitat volume”

Bertrand et al. (2000) defined a volume of tuna habitat based on temperature and dissolved oxygen, which are the main hydrologic parameters used by previous workers to describe the distribution of tunas (Hanamoto 1987; Cayré and Marsac 1993; Brill 1994). For each parameter and each species, we measured a threshold value below which less than 2.5% of experimental longline catches were made (Table 1). For each observation site and each species, we then defined a habitat depth matching the shallowest depth associated with the temperature or the DO thresholds (Fig. 2). For statistical purpose we classified into four categories the vertical habitat range of the three tuna species individually and pooled. In this last case the calculation of the range of habitat takes account of the species proportion as determined by catches.

Environmental correlates with tuna distribution

We employed four methods to identify the environmental factors (a selection is presented in Table 2) that are correlated with variations in tuna CPUEs and/or of the acoustic tunas densities.

Correlation analyses

Correlation analyses using the “Desco” procedure of the SPAD 3.5 software (CISIA-CERESTA) were used to analyze the global linear effect linking tuna abundance and distribution to the environmental factors. This procedure allows characterizing continuous variables by other continuous variables using correlation, by the category of the nominal variables using mean comparisons, and by nominal variables using the Fisher statistics.

General linear models

General linear models (GLM) (SAS Institute Inc.) were used to estimate CPUEs and tunas acoustic densities from environmental parameters. Deviates were assumed normal.

Robust regressions

Descriptors retained by GLM were independently studied in order to better understand the highlighted relations, mainly in each micronektonic zone. For that purpose, we used the least trimmed squares (LTS) regression (S-PLUS 4.5 Software, MathSoft inc.) to minimize the effect of outlying points, which are almost always present in data resulting from *in situ* observations. Bias corrected confidence intervals (BC_{α} , Efron 1987) were calculated on regression parameters by bootstrapping with 1000 replications. In some cases, a robust regression was not a relevant tool because of the strong proportion of zeros in the data. The model could thus only capture the alignment of these values on the X-axis. As the number of null values was independent of $\log(s_a+1)$, they were withdrawn from analyses in these cases.

Influence of micronekton patches

Micronekton is distributed in scattering layers and dense patches. When large prey patches were observed during a survey, they contributed to the major part of the prey density, i.e., the prey density was correlated to the number and the size of prey patches. When only small patches were observed, prey density was not correlated to the number of prey patches. The structure of the prey environment, mainly the presence or absence of dense patches of myctophids, may influence the presence and/or the catch of tunas. In order to clarify this point, we measured longline CPUEs and tuna acoustic densities for each of the three categories of micronekton abundance (low, medium, high) in presence and in absence of prey patches. We also calculated the corresponding standard deviations.

Results

Tuna distribution

The relationship between the zonal distribution of tuna CPUEs (all species pooled) and acoustic densities of tunas (Table 3) was linear ($R^2 = 0.996$, $p < 0.01$). This result suggests that our experimental longline tuna CPUEs can be considered as an index of relative abundance at a regional scale. Our experimental catches can be considered less biased than commercial ones because, as far as possible, the whole range of tuna habitat was sampled.

Tuna CPUEs were significantly higher in zone 2 (in the text, when the type of zone, i.e., micronektonic or hydrologic, is not indicated the results are valid for both types) than in the two other zones (Kruskal-Wallis test, $p < 0.01$), with about 2 tunas per 100 hooks. In zone 1, tuna abundance was intermediate compared to the whole study area with 1.3 tuna per 100 hooks. Lastly, the lowest CPUEs were observed in zone 3 with 0.8 tuna per 100 hooks. The results are different if we consider CPUEs by species. Albacore tuna were caught with similar CPUEs in zones 1 and 2 and were almost absent in zone 3. Bigeye tuna CPUEs were significantly higher in zone 2 (Kruskal-Wallis test, $p < 0.01$) than in the other zones, which were not significantly

different between each other (Kruskal-Wallis test, $p > 0.05$). Yellowfin tuna CPUEs were similar in zones 2 and 3, and very low in zone 1 (Table 3).

By weighting the CPUEs by the volume of corresponding potential habitat, we transform an index of abundance into an index of density (expressed in a number of fish per 100 hooks per 100 m of habitat) (Table 4). The distributions then appear different. These densities were proportionally lower in zone 1 for each of the three species. Bigeye tuna were captured with identical CPUEs per unit of volume in zones 2 and 3. Yellowfin tuna density was highest in zone 3, whereas, albacore tuna presented the highest CPUEs with respect to the volume of habitat in zone 2.

Environmental correlates with tuna distribution

Correlation analyses

Results of the correlation analysis can be synthesized as follows. At a total study area scale, tuna CPUE were positively correlated with zone 2 where micronekton abundance was maximum. At a zone scale, tuna CPUEs (all species together and for each species) were positively correlated with the abundance of micronekton and the presence of patches in zoneM1 and zoneM3. In zoneM2, where prey abundance was maximal, tuna acoustic densities and CPUEs were also maximal. However inside this zone, albacore and bigeye tuna CPUEs were negatively correlated with the micronekton abundance (negative correlations also between albacore tuna CPUEs and the presence of patches), while the correlation was positive for yellowfin tuna CPUEs.

GLM

Models were fitted to tuna acoustic densities and CPUEs for all tuna pooled and individually for yellowfin and albacore tunas (Table 5). No model could be fitted for bigeye tuna. In all cases, the best models were additive with interaction between the diurnal acoustic back-scattering energy (s_a) and either the micronektonic zone (ZoneM) or the range of the albacore vertical habitat (RALB). The categories of the albacore vertical habitat followed the latitudinal evolution of the habitat volume: RALB1 (0-290 m) located north of 9°S, RALB2 (0-340 m) located between 9°S and 12°30'S, RALB3 (0-410 m) located between 12°30' and 15°30'S, RALB4 (>410 m) located south of 15°30'S.

The fitting of the analysis of variance model led to estimates of tuna acoustic densities or the tuna CPUEs (Y):

$$E(Y_{i,j,k}) = \mu_{i,j} = \mu + \alpha_{i,j},$$

where i is the micronektonic zone or the class of habitat range; j , the acoustic back-scattering energy (s_a); and k the number of observations corresponding of the (i, j) combination. The term μ is the general mean of the population and α the interaction term. We used least-square mean fitting to estimate the CPUEs or the tuna acoustic density for each class of variable (Fig. 3).

Results can be synthesized as follows: in zoneM1 and zoneM2, observed tuna acoustic densities appeared maximal when the micronekton abundance was medium. The whole tuna CPUEs decreased as micronekton biomass increased in zoneM2, and less markedly in zoneM1. These results were driven by the albacore data, the most commonly caught species in these zones. Conversely, the CPUE of all tunas increased with the micronekton biomass in zoneM3 where yellowfin tuna represent 50% of catches. These results highlight both zone and species effects.

Robust regressions

The results of the variance analysis show that the best models are additive models with interaction between acoustic back-scattering energy (s_a) and the micronektonic zone for bigeye and yellowfin tunas or the range of habitat for albacore tuna. Robust regressions were computed between the tuna acoustic densities or the CPUEs and the micronekton abundance (s_a). These regressions were adjusted by zone and for the whole study area when species were considered separately. The observation of the CPUEs or scatterplots of acoustic density of tunas according to the s_a and the first attempts at adjustment showed that the relationship between the two types of data was not linear; a logarithmic curve better fit the data. A logarithmic transformation of the explanatory variable ($\log(x+1)$) was thus made to approach a linear relation.

The results of the robust regressions did not highlight relations between the tuna acoustic densities and the diurnal micronekton abundance (s_a) (Table 6). The expectancy of the tuna acoustic density at a given site was the arithmetic mean of abundance in the zone, with no effect of the s_a . In zoneM3, the robust regression was not fully relevant because of the strong proportion of null values. The CPUEs of all tunas were negatively correlated with the diurnal micronekton abundance in zoneM1 and zoneM2. This result is doubtful in zoneM1 as each species considered individually did not show such correlation (Table 6). Total albacore tuna CPUEs were negatively correlated with the micronekton abundance. This trend was significant for habitat range 2 (zone 2) and not significant for the range 3 (which presents few observations, zones 1-2) and was not observed for range 4 (zone 1). In the areas where albacore tuna were present, CPUEs and micronekton abundances were negatively correlated especially where micronekton was very abundant. The LTS regressions are of poor relevance with bigeye tuna CPUE data because of the numerous zero values. Nevertheless, in zone 2, the robust regression displayed a clear negative slope. Yellowfin tuna was the only species not presenting any negative correlation but a positive trend (but non significant) in each case.

Influence of micronekton patches

Results (Table 7) show that the coefficients of variation of CPUEs between samplings are very high. This result is not surprising taking into account the low number of samples and the nature of the data (the catch of one tuna may notably change the results). Thus, these results are only additional information to reinforce the previous analyses.

In the absence of micronekton patches, for example, when prey were in scattering layers only, tuna acoustic densities were positively correlated with the density of micronekton, while a opposite trend was mainly observed when prey were distributed in patches. However, this last trend was much less marked than the one observed for tuna CPUEs. In the absence of micronekton patches, CPUEs did not show any clear relationship with the overall micronekton density. It should nevertheless be noted that the highest tuna CPUEs were associated with high densities of micronekton distributed in scattering layers while the trend was opposite when micronekton was patchy in distribution. It is important to recall that during the day, if patches were present and of significant size, they contributed to the majority of the total micronekton density. So when patches were present, the value of s_a was correlated with the size and the number of patches. Very high tuna CPUEs were thus observed when micronekton was distributed in scattering layers whereas the CPUEs were low in the presence of large dense patches. These results also applied at the species level to bigeye and albacore tunas, even if, in the absence of prey patches, the maximum CPUEs were not associated with the strongest micronekton densities. Conversely, yellowfin tuna present a different pattern; CPUEs did not tend to decrease in the presence of micronekton patches.

Discussion

Habitat limits of tropical tunas

Longline catches rely on the behaviour of fishes to be attracted by the longline baits, and might represent biased observations of the fishes' vertical distribution. Considering also that longline data represent fish depth at only one instant in time, they should be considered with caution, but they should not be rejected as they also provide large samples of indirect observations (indirect as the fish have to behave to be caught, then to be observed) that can provide reliable trends. Such a large database thus represents valuable information on tuna vertical distribution. We already know that bigeye tuna tracked with sonic transmitters in French Polynesia (Josse et al. 1998; Dagorn et al. 2000) moved in hydrological conditions consistent with the proposed level values, as shown by a comparative study (Bach et al., 2002). More direct observations of vertical movements through electronic tags should be developed, especially for yellowfin and albacore tunas.

By definition, the limit values calculated for the temperature and DO are not lethal limits as some fish were caught beyond those levels. They also do not correspond to “comfort limits” *sensu stricto*. For instance, bigeye tuna are able to forage in very deep waters where they tolerate very low temperatures and sometimes low DO concentrations. Archival tagging shows that bigeye tuna can temporarily dive deeper than 1000 m at a temperature of 3 °C, (J. Hampton, Secretariat of the Pacific Community, BP D5, 98848 Nouméa Cedex, Nouvelle Calédonie, personal communication). In such conditions, bigeye tuna need to make brief upward excursions (Holland et al. 1992; Dagorn et al. 2000) to increase muscle temperature (Holland et al. 1992). These deep waters might, therefore, not correspond to physiologically comfortable areas for bigeye tuna, but they occupy these waters for foraging activities. In fact, inside limits, tunas are likely to adopt depths where prey are present rather than depths of preferred temperature or DO. We consider that the vertical extent of tuna habitat is limited by the parameter that first goes over its threshold: temperature, DO, or prey biomass. Therefore, the threshold values proposed here can be considered as vertical habitat limits. These limits are in agreement with those proposed in the literature (Sharp 1978; Holland et al. 1990; Brill 1994) for bigeye and albacore tunas. However, our temperature-at-capture data for yellowfin tuna show contrasting results to those observed in previous studies. Several ultrasonic tagging experiments (Holland et al. 1990; Block et al. 1997; Brill et al. 1999) have shown that during the daytime, yellowfin tuna usually swim within or immediately below the mixed layer, in warm water usually between 17.5 °C and 26 °C. In fact, yellowfin tuna have been observed diving into very cold waters beneath the thermocline (as cold as 7 °C, Block et al. 1997), but those dives were not numerous and were usually very short in duration, and we do not know the reasons for those dives. In contrast, our data show that more than 80 individuals (45% of our database) were caught at temperatures below 17.5 °C (with a minimum of 10 °C), which is very cold for this species. More than the absolute water temperature, the temperature gradient (Cayré and Marsac 1993) is a key factor which determines the vertical swimming behaviour of this species. Comparing vertical movements of small yellowfin tuna tracked in the northern extreme of their range in the eastern Pacific (Block et al. 1997), and large individuals tracked near the Hawaiian islands, Brill et al. (1999) found similar time-at-temperature distributions for the two groups when temperature was expressed relative to the surface-layer temperatures, despite very different environments. All fish spent the majority of their time in water temperatures no lower than 8 °C below the surface layer temperature. Surprisingly, in our study, 100 individuals (56% of our database) were caught at depths where the water temperature was more than 8 °C below the mixed layer temperature (with a maximum of 18.6 °C difference).

Our data lead to two possible interpretations that we express as questions: (1) Do deep longlines attract yellowfin tuna to deeper and colder waters, modifying their natural vertical distribution? Are yellowfin more inclined to bite longline hooks when making some rapid dives to depth with marginal temperature and DO levels than when swimming in more comfortable conditions? (2) Do yellowfin tuna exhibit deeper and cooler vertical distributions in offshore areas of French Polynesia than those observed in other oceanic areas?

The first interpretation is not in accordance with previous comparisons between ultrasonic telemetry data and longline catch data. Ultrasonic telemetry and depth-of-capture data near the main Hawaiian islands showed similar depth distributions for yellowfin tuna (Holland et al. 1990; Boggs 1992; Brill et al. 1999), while Bach et al. (2002) found similar results for bigeye tuna in French Polynesia. However, by setting the gear deeper than the assumed preferred depth stratum for yellowfin tuna, our longline experiments might have provided biased results of yellowfin tuna depth distribution as individuals might have been attracted by deep baits. The second interpretation might also be valid as all the ultrasonic telemetry data on yellowfin tuna in tropical waters have been collected in coastal areas. Our knowledge of yellowfin tuna vertical dynamics might only correspond to an inshore behaviour, while yellowfin tuna in some offshore waters might exhibit a different vertical swimming behaviour notably because of different prey communities. For instance, it should be noted that in French Polynesia, yellowfin tuna feed on the mixed layer and on deeper sound scattering layer (SSL), as shown by stomach content analyses (Bertrand 1999), which also explains the high variance of our depth-of-capture data. Further ultrasonic telemetry experiments on yellowfin tuna in offshore areas are therefore clearly needed to clarify the moment-to-moment vertical movements they use to exploit those two layers, and therefore their depth and temperature distributions.

Tuna catches and environment

As stated above, vertical and horizontal limits of tuna habitat depend on the trophic and hydrologic conditions. In the study area, catches of albacore tuna were highest, followed by bigeye tuna. CPUEs and acoustic tuna densities were higher in zone 2 where the hydrologic conditions did not prevent the tunas (mainly albacore and bigeye tuna) from exploiting abundant deep prey. North of the Marquesas Islands, in zone 3, tuna abundance was lower. This may be a function of the very low occurrence of albacore tuna. Despite a rather low prey biomass, tuna abundance in zone 1 was fairly high compared to what would be expected based on analysis of commercial-catch data (Fonteneau 1997).

Albacore distribution

Catch rates of albacore tuna were very low in zone 3. Low albacore abundance close to the equator is typical, as those from the northern and southern hemispheres are assumed to come from two distinct populations with very limited exchanges (Sund et al. 1981; Kimura et al. 1997). It appears that the hydrological conditions (i.e., the vertical range of habitat) close to the equator prevent them from occupying such areas. The CPUEs were quite similar in zones 1 and 2, while the prey environments were different: zone 1 had a large vertical range of habitat with scattered prey, while in zone 2, the vertical range of habitat was lower but prey were much more abundant and distributed in dense patches. The dense patches in zone 2 are likely to concentrate albacore tuna.

Bigeye tuna

Bigeye tuna is the most tolerant species with respect to hydrological constraints. In zone 1, bigeye tuna were located in deep strata presumably to forage on SSL organisms (Dagorn et al.

2000). In zone 3, where the micronekton density was moderate, CPUEs were slightly higher than in zone 1. Perhaps this is due to more hooks being concentrated in the waters occupied by this species in zone 3, while in zone 1, mainly the deep hooks caught this species. Bigeye tuna CPUEs were significantly higher in zone 2 where the micronekton was abundant.

Commercial catch analyses (Fonteneau 1997) show very low bigeye tuna catch rates in zone 1, contrary to our experimental catches. As Hanamoto (1987) showed, commercial longline catches reflect the real distribution of tunas only in areas where the fishing depths overlaps habitat depth. A biomass of bigeye tuna is located south of the classical fishing ground but is only accessible to longlines set deeper than the classic “deep” ones. It could correspond to a “cryptic” biomass as defined by Fonteneau et al. (1998).

In the same way, Fréon and Misund (1999) showed that bigeye tuna catches are high in areas where deep waters are deoxygenated, “as if this species was taking advantage of its physiological capabilities for limiting competition with other tuna species”. Although this assumption is consistent, it is necessary to be careful when using solely commercial catches to describe tuna distribution. The presence of hypoxic deep waters can lead bigeye tuna to be shallower and more accessible to fishing gears (purse seine and longline) and increases the CPUE. In zone 3 where an oxycline (and a thermocline) is present, bigeye tuna are distributed in a depth stratum which coincides with the depth of the “deep” commercial longlines (i.e., about 250 m). This may explain why most longliners catch bigeye tuna in this area. Conversely, where no oxygen gradients are present (in zone 1 for instance), during the day bigeye tuna are distributed deeper than the depth strata sampled by the “deep” commercial longlines. Strong DO gradients cause the apparent abundance of bigeye to appear higher than in areas with weak oxycline. Consequently, sampling the whole tuna habitat range allows better understanding of tuna spatial occupation and calls into question the role imputed to the oxygen gradients. Therefore high bigeye tuna catches in areas where deep waters are deoxygenated are probably due more to an increase in bigeye accessibility to the fishing gear than to the total bigeye abundance.

Yellowfin tuna

Yellowfin tuna catches were deeper than expected, considering our knowledge of this species (see the previous section on habitat limits). Yellowfin tuna are less tolerant to low temperatures and low DO concentrations than bigeye tuna, which explains why catches of this species were shallower than those of bigeye tuna regardless of the zone. It also should be noted that the theoretical vertical range of yellowfin tuna habitat is greater than that for albacore in zones 2 and 3 because of a higher tolerance of this species for low DO concentrations. Yellowfin tuna CPUEs were always positively correlated to the micronekton abundance. Despite a lower prey abundance in zone 3 than in zone 2, CPUEs were similar in those two zones. The overall micronekton richness of zone 2 contributed to increase the presence of yellowfin tuna in the zone. The lower micronekton abundance, found in zone 3 was compensated by the fact that more prey were distributed toward the surface, being more accessible to yellowfin tuna.

Environment and tuna catchability

Tunas and micronekton abundances were maximal in zone 2. Inside this zone, however, albacore and bigeye tuna CPUEs were negatively correlated with prey abundance. Thus, relationships differ according to the scale of observations. This apparent contradiction results from the effect of catchability.

Catchability is a key parameter for abundance estimates. Until present, tuna catchability was principally studied in the horizontal plane, and related to abiotic parameters (Maury et al.

2001). Several studies (Hanamoto 1987; Brill 1994; Hampton et al. 1998) pointed out that bigeye tuna catchability increases with the use of deep longlines, as observed in our work. These studies related catchability to hydrological factors. Few investigators have studied the influence of both the range of habitat and prey availability. Podesta et al. (1993) indicated that swordfish (*Xiphias gladius*) catchability with a longline increases close to thermal fronts, but that CPUE variability cannot be interpreted and must be a function of unmeasured parameters. These authors considered the frontal zone to be areas where prey were abundant, but they did not consider the patchiness of the prey community. Prey distribution is likely to play an important role in the distribution of a fish, its feeding behaviour, and consequently its catchability by a longline.

To analyze the factors influencing tuna catchability according to the species and the environmental conditions, we compared the influence of the environmental parameters on the tuna acoustic densities as well as on the longline catches. It should be noted that each method alone did not always give definitive results due to the low number of observations and the strong occurrence of null values. However, the results of the various methods were sufficiently similar to validate our conclusions.

Tuna acoustic densities

Acoustic surveys allowed us to observe the presence of tunas independently of catchability. Results did not show clear relationships between tuna acoustic densities and the micronekton abundance inside each zone. Bertrand and Josse (2000) assumed that tuna acoustic counting was negatively biased in presence of micronekton patches. Such bias can partly explain our results, and we can therefore assume that the density of tunas was under-estimated when dense prey patches were present. The lack of a trend could also be linked to the complex pattern of interactions between predators and prey. Predators tend to congregate where prey are abundant. On the other hand, mobile prey tend to avoid areas of high predator density as stated by Rose and Leggett (1990). These authors showed that at large scales, predator and prey densities are positively correlated. As the scale decreases and approaches the aggregation scale, the strength of the correlation decreases and becomes non significant. Finally at scales smaller than this dimension, predator and prey densities are negatively correlated. Our results agree with this scheme, as we observed a positive correlation between prey and tuna abundances at the scale of the study area and no correlation at the scale of the acoustic survey. Swartzman et al. (1999) indicated that correlation between zooplanktivorous fishes and their prey was more linked to the patch density than to total prey biomass. They observed a spatial correlation even at a small scale. However, they noted that in the case of piscivorous fish, the proximity between predators and prey may be more difficult to demonstrate at small scales than for planktivorous fish because fish are more mobile than zooplankton.

Tunas

Despite having highest CPUEs in zone 2, albacore and bigeye tuna CPUEs calculated at a set scale showed a negative correlation with prey abundance and/or the presence of prey patches. This negative relation was not observed in the other zones. The difference could come from albacore and bigeye tunas displaying different motivations to attack the longline baits when they are inside or outside of dense prey patches. (Fig. 4-a and 4-b). These tunas are likely to be attracted by prey patches during the daytime to feed on them. However, in zone 1, where prey patches are small and not very dense, they can still be inclined to attack baits, as large immobile bait might still represent a good target compared to mobile and disperse live prey. On the other hand, large, dense patches, like those found in zone 2, their motivation to attack baits might be reduced because they focus on very dense prey, with increased foraging success. Such results are

in agreement with Swartzman et al. (1999), who highlighted the importance of the prey distribution with respect to the total biomass of prey. As assumed by Bertrand (1999), it is likely that tunas in a low state of repletion (i.e., hungry) attack the longline baits, while those inside dense prey patches might be quickly satiated and soon cease searching for food. This suggests that above a certain threshold of prey density, a dense prey patch leads to lower catchability: tunas are present in the area but are not motivated to attack the baited hooks.

Yellowfin tuna (Fig. 4-c) showed trends similar to the two other species in zones 1 and 3, but differed from them in zone 2 as the correlation between CPUEs and prey abundances remained positive, even at a small scale. Yellowfin tuna feed on organisms of the mixed layer as well as on organisms of deeper SSL, while albacore and bigeye tunas mainly feed on the deep SSL, and not in the mixed layer. We can therefore assume that, as for albacore and bigeye tunas, yellowfin tuna might be less attracted by longline baits when feeding in very dense prey patches in deep waters of zone 2. However, a large proportion of yellowfin tuna also forage in the mixed layer, where the prey density is lower, which limit the possible competition between prey and baits. Therefore, because yellowfin tuna feed on two different depth strata with different prey densities, the competition between prey and baits in deep patches of zone 2 is probably not sufficient to decrease the yellowfin tuna CPUEs, as for the other species.

In conclusion, the simultaneous observations of the biotic and abiotic pelagic habitat and tunas provided new insights into the characteristics of the tuna/environment relationships. For each tuna species, a range of vertical habitat was defined depending on the vertical hydrological characteristics. Combined with the observations of prey, especially their accessibility by each species, we could better understand the strategy used by each species to occupy the pelagic environment. We highlighted the importance of the scale of observations and the role of prey in studying tuna catchability with a longline. On a regional scale, tuna CPUE and prey abundance appeared to be positively correlated. On a finer scale, i.e., at a longline-set scale, it seems that above a certain threshold of prey patch density, tunas might prefer to feed on prey rather than on dispersed baits, and might become satiated, reducing their motivation toward baits. Longline catch rates are thus higher in areas of high-prey density (zone 2), but at a small scale inside such areas, very dense patches might reduce the catchability of albacore and bigeye tunas. As yellowfin tuna also forage on the scattered prey in the superficial layers, the competition between prey in deep, dense patches and baits does not affect the CPUE of this species as it does for the other species in zone 2. Prey patch characteristics should therefore be taken into account for resource management and when interpreting longline CPUEs.

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Table 1. Average weight of tuna caught by experimental longline; temperature and dissolved oxygen concentrations below which less than 2.5% of the fish were caught. Standard deviation (sd) or sample size (n) are in parentheses.

Species	Average weight (kg)	T °C	O ₂ (mL•L ⁻¹)
Bigeye	31.4 (sd = 14.8)	8 (n = 271)	0.6 (n = 251)

Albacore	20.7 (sd = 3.2)	10 (n = 511)	1.5 (n = 475)
Yellowfin	29.1 (sd = 12.5)	10.5 (n = 191)	1.0 (n = 174)

Table 2. Descriptors of the environment used in the analyses (N: categorical variable, C: continuous variable), s_a (acoustic back scattering energy by surface unit), RALB range of albacore vertical habitat, RBET range of bigeye vertical habitat, RYFT range of yellowfin vertical habitat, RTUNA range of pooled tunas vertical habitat.

Variable code	Description	Type
Lat	Latitude	C
ZoneM	Belonging to one of the three micronektonic zones	N
ZoneH	Belonging to one of the three hydrological zones	N
SAT	Presence / absence of micronekton patches	N
RALB, RBET, RYFT, RTUNA	Category of hydrological habitat range for the three tuna species individually and pooled	N
Salog	$\log(s_a + 1)$ total diurnal	C
SaNlog	$\log(s_a + 1)$ total nocturnal	C
S_a	Category of s_a diurnal	N
S_{aN}	Category of s_a nocturnal	N

Table 3. Catch per unit effort (in number of fish per 100 hooks) of tuna caught using instrumented longlines related to the hydrologic zone (first number) and micronekton zone (second number) and of acoustic densities of tuna (number of fish per square kilometre) corresponding to the micronektonic zone.

Zone	Acoustic densities	All tunas	Albacore	Bigeye	Yellowfin
Total	1.33	1.40	0.73	0.39	0.28
Zone 1	1.33	1.25 / 1.38	0.90 / 1.00	0.26 / 0.30	0.09 / 0.09
Zone 2	1.87	2.05 / 1.94	1.05 / 0.88	0.60 / 0.58	0.40 / 0.48
Zone 3	0.69	0.84 / 0.84	0.02 / 0.03	0.36 / 0.38	0.45 / 0.43

Table 4. Density indices (catch per unit effort over the habitat range) of tuna caught by the instrumented longline (in number of fish per 100 hooks per 100 m depth) by hydrologic zone. Parentheses indicate mean depth of habitat (m).

Zone	Bigeye	Albacore	Yellowfin
ZoneH1	0.05 (503)	0.21 (428)	0.02 (413)
ZoneH2	0.13 (451)	0.35 (301)	0.12 (332)
ZoneH3	0.13 (263)	0.01 (223)	0.18 (251)

Table 5. Goodness-of-fit parameters of the analysis of variance model fitted for tuna catch per unit effort (CPUE) and tuna acoustic density. s_a , acoustic back-scattering energy; ZoneM, micronektonic zone; RALB, range of albacore's vertical habitat; n, total number of observations; df, degrees of freedom; *, $P < 0.05$; **, $P < 0.01$.

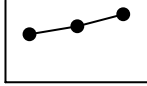
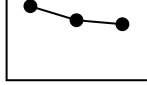

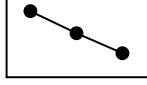
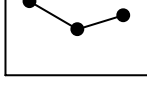
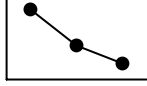

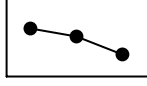
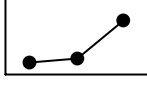

CPUE or tuna density	Tested effect	df	R ²	P level
Tuna acoustic density (n = 93)	ZoneM* s_a	8	0.20	*
All tuna (n = 121)	ZoneM* s_a	8	0.18	**
Albacore (n = 125)	RALB* s_a	10	0.44	**
Yellowfin (n = 125)	ZoneM* s_a	8	0.24	**

Table 6. Sign of the slope of the robust regression between the tuna acoustic densities and catch per unit effort (CPUE) according to the $\log(s_a \text{ diurnal} + 1)$ for the whole study area, and by micronektonic zone. In the case of albacore, CPUEs are represented according to the range of albacore vertical habitat (RALB) categories 2, 3 and 4. 0: non significant slope; (-): slope significantly negative. The shaded boxes are those for which the strong proportion of null values makes the robust regression less relevant.

CPUE or tuna abundance	Total	ZoneM1	ZoneM2	ZoneM3
Tuna acoustic density		0	0	0
All tuna		(-)	(-)	0
Bigeye	0	0	(-)	0
Yellowfin	0		0	0

CPUE	Total	RALB2	RALB3	RALB4
Albacore	(-)	(-)	0	0

Table 7. Tuna acoustic densities and catch per unit effort (CPUE) for all tunas and by species (ALB, albacore; BET, bigeye and YFT, yellowfin), according to the category of the diurnal s_a and of the presence or the absence of micronekton patches (SAT) (coefficient of variation, cv in %). The trend of the relation binding the tuna densities or CPUE with the diurnal s_a is also represented.

	SAT	s_a1	s_a2	s_a3	Trend
Tuna acoustic density	Absent	1.18 (n: 50, cv: 88)	1.38 (n: 37, cv: 128)	1.64 (n: 13, cv: 81)	
	Present	1.80 (n: 4, cv: 143)	1.46 (n: 15, cv: 77)	1.35 (n: 6, cv: 41)	
CPUE Tuna	Absent	1.64 (n: 51, cv: 84)	1.22 (n: 36, cv: 85)	2.05 (n: 13, cv: 83)	
	Present	2.44 (n: 4, cv: 60)	1.59 (n: 15, cv: 39)	0.90 (n: 12, cv: 76)	
CPUE ALB	Absent	0.91 (n: 51, cv: 105)	0.56 (n: 36, cv: 124)	0.74 (n: 13, cv: 89)	
	Present	1.71 (n: 4, cv: 92)	0.83 (n: 15, cv: 75)	0.38 (n: 12, cv: 99)	
CPUE BET	Absent	0.52 (n: 51, cv: 139)	0.36 (n: 36, cv: 123)	0.33 (n: 13, cv: 85)	
	Present	0.59 (n: 4, cv: 121)	0.50 (n: 15, cv: 100)	0.27 (n: 12, cv: 109)	
CPUE YFT	Absent	0.21 (n: 51, cv: 154)	0.31 (n: 36, cv: 183)	0.98 (n: 13, cv: 202)	
	Present	0.10 (n: 4, cv: 115)	0.25 (n: 15, cv: 98)	0.24 (n: 12, cv: 121)	

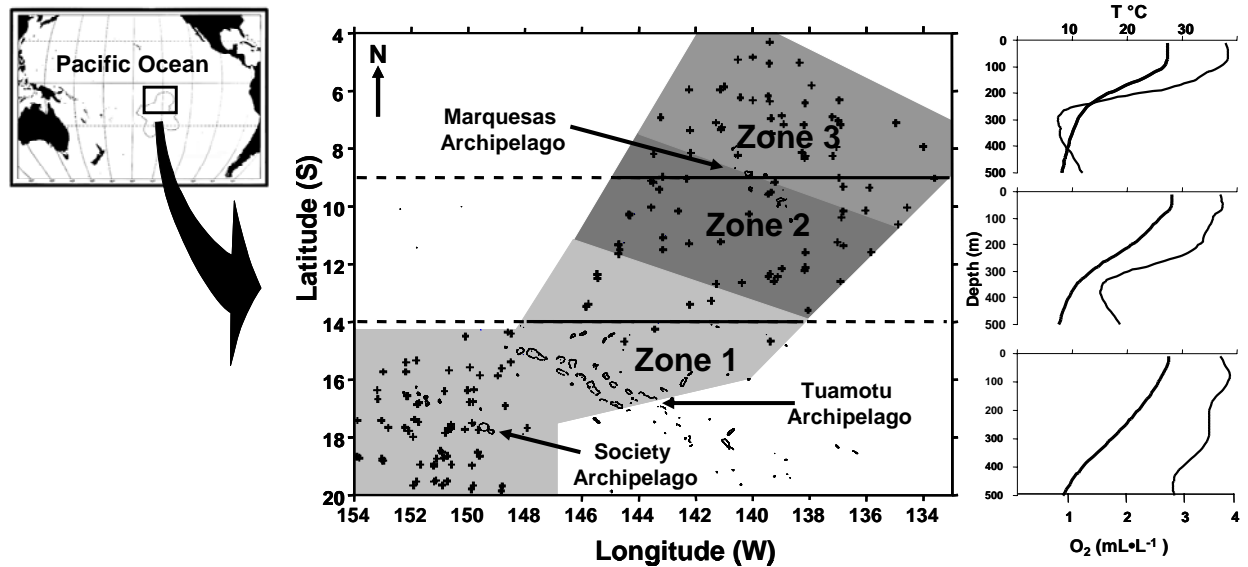


Fig. 1. Position of longline and hydrological stations (crosses) and zones defined from habitat characterisation of hydrologic features (horizontal lines) and micronekton distribution (shaded areas) (from Bertrand et al. 1999b, 2000). Mean temperature (T, bold line) and dissolved oxygen (thin line) profiles calculated by ten metres strata are plotted for each zone hydrological zone.

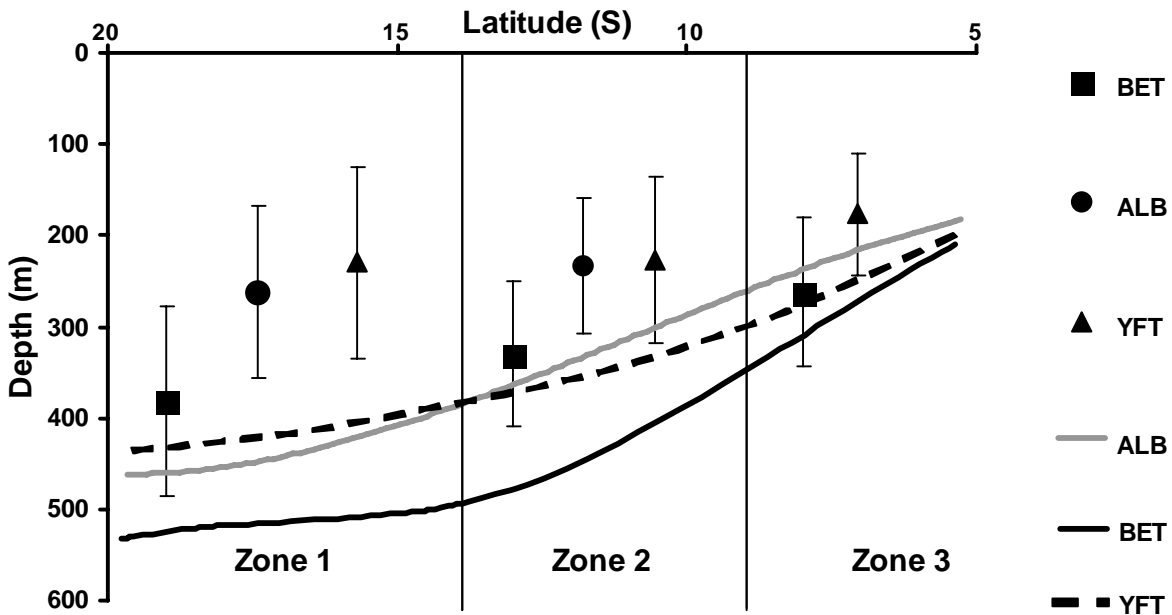


Fig. 2. Latitudinal display of the theoretical habitat limits for bigeye *Thunnus obesus* (BET), albacore *Thunnus alalunga* (ALB) and yellowfin *Thunnus albacores* (YFT) tuna. The limits of the three hydrological zones are indicated and the mean depth of catches (with standard error) are also plotted species by species for each zone (except for albacore in Zone 3 as only 5 fish were caught).

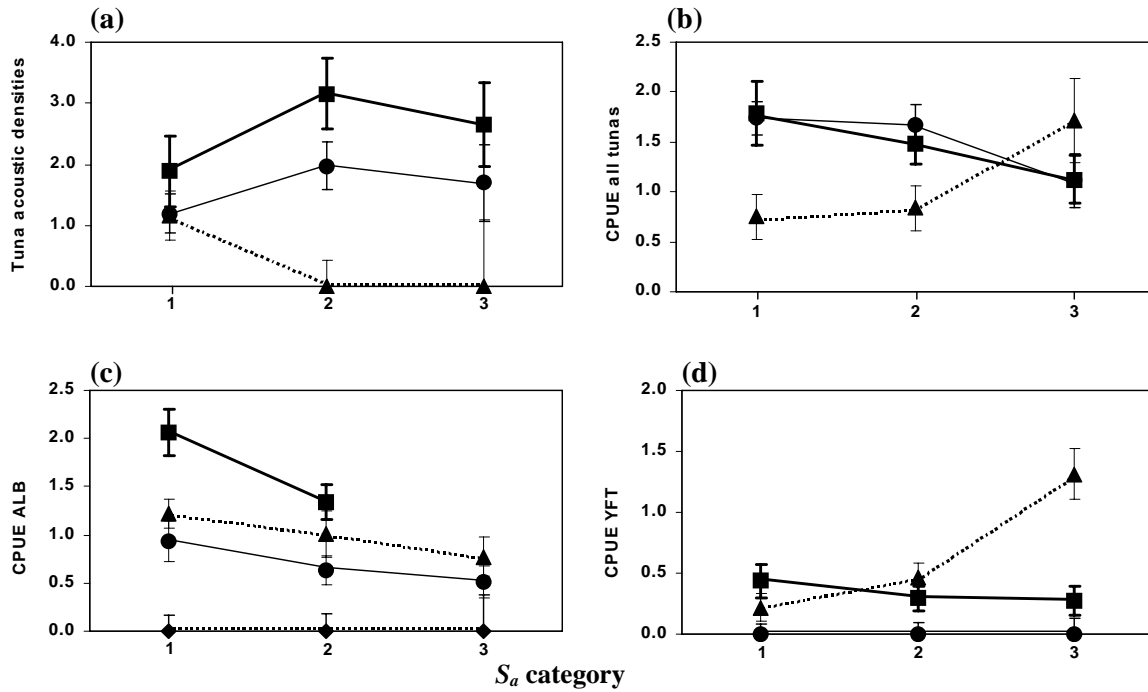


Fig. 3. Catch per unit effort (in number per 100 hooks) least-square mean evolution of tuna acoustic densities (a), all tunas (b), albacore *Thunnus alalunga* (c) and yellowfin tuna *Thunnus albacores* (c) (in number per km²) according to the categories of the acoustic back-scattering energy (S_a) by micronektonic zone: ZoneM1 (solid circles), ZoneM2 (solid squares), ZoneM3 (solid triangles) or by hydrological habitat range for albacore (c): RALB1 (solid lozenges), RALB2 (solid circles), RALB3 (solid squares), RALB4 (solid triangles). The standard deviation is plotted for each value.

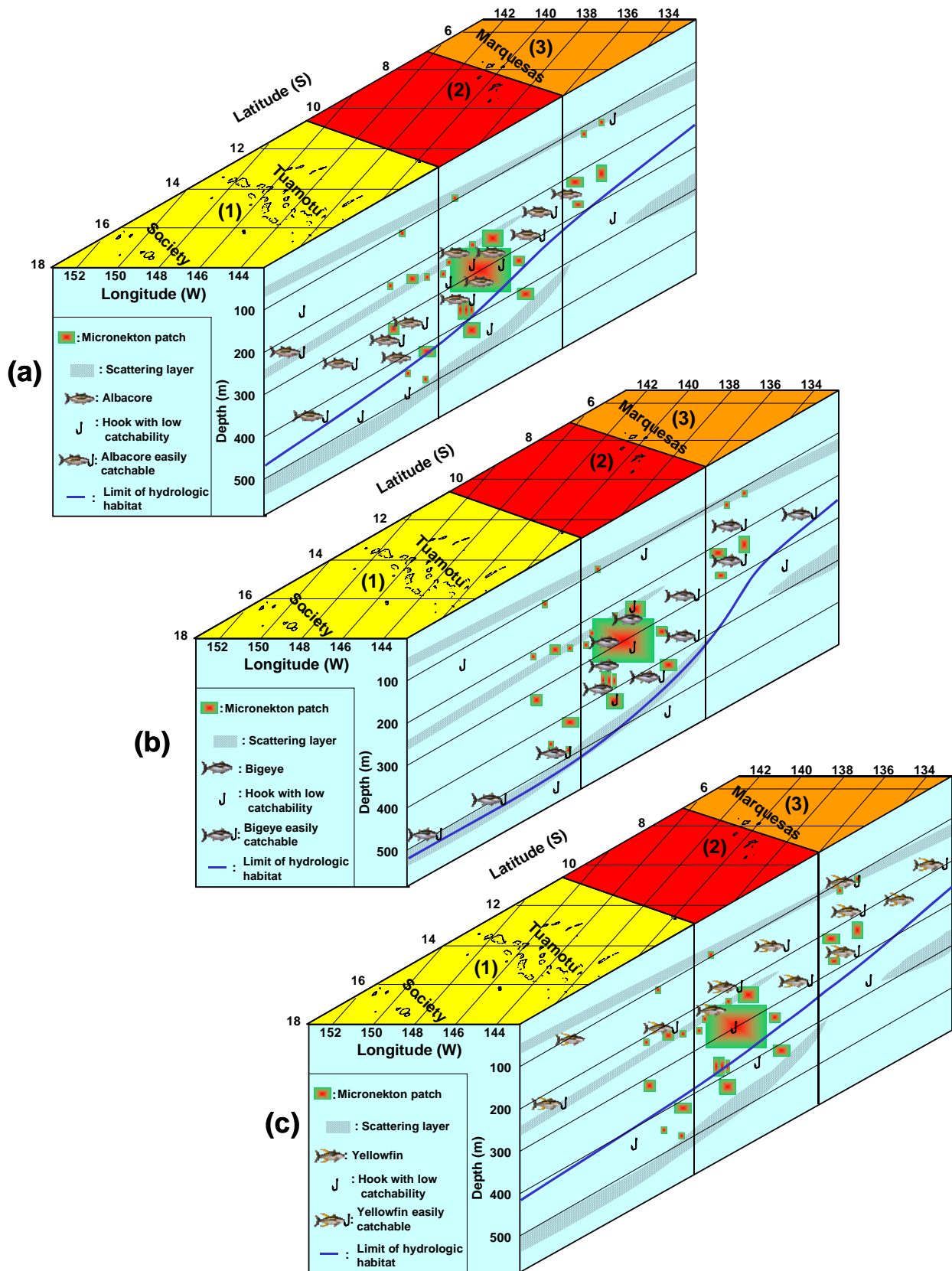


Fig. 4. Schematic representation of the distribution and catchability of (a) albacore *Thunnus alalunga*, (b) bigeye *Thunnus obesus* and (c) yellowfin tuna *Thunnus albacares* in French Polynesia.