



## Biodiversity and Habitat Characteristics of the Bycatch Assemblages in Fish Aggregating Devices (FADs) and School Sets in the Eastern Pacific Ocean

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Lezama-Ochoa N, Murua H, Hall M, Román M, Ruiz J, Vogel N, Caballero A and Sancristobal I (2017) Biodiversity and Habitat Characteristics of the Bycatch Assemblages in Fish Aggregating Devices (FADs) and School Sets in the Eastern Pacific Ocean. Front. Mar. Sci. 4:265. doi: 10.3389/fmars.2017.00265 This study examined diversity and habitat characteristics for bycatch assemblages in two different types of fishing (drifting fish aggregating devices sets and sets made on school of tunas) in the eastern Pacific Ocean (20°S–30°N and 70°–150°W) between 2005 and 2011 using biodiversity metrics and Generalized Additive Models. Bycatch information was based on data collected by onboard observers covering more than 80% of the purse seine fishing trips. Our results suggest that diversity and habitat characteristics of the bycatch assemblages differ depending of the fishing mode. Thus, diversity was mostly explained by area and set type; being higher in fish aggregating devices (FAD) sets than School sets. Concretely, diversity seems to be directly related with the equatorial upwelling and the front system in FAD sets and with the Costa Rica Dome and the coastal upwelling of Panama induced by wind jets in School sets. Among environmental variables, temperature and chlorophyll were the most important predictors to describe the diversity of the bycatch assemblages and their habitat, which could be helpful for the development of an Ecosystem Approach to Fishery Management (EAFM).

Keywords: bycatch, species diversity, purse seine, eastern Pacific Ocean, ecosystem approach to fishery management

#### INTRODUCTION

Fishing is one of the recognized causes of marine biodiversity loss (Worm et al., 2006), especially when fishing activity alters the diversity, composition, biomass and productivity of the species inhabiting the marine ecosystem by changing and reducing their habitats (Dayton et al., 1995).

Various Regional Fishery Management Organizations have implemented measures to regulate and reduce catches of overfished single species (Cullis-Suzuki and Pauly, 2010). However, to date fisheries management has been generally focused on the protection of a single target species with a substantial economic cost included without addressing the impact on the ecosystems (Link, 2010). The implementation of the Ecosystem Approach to Fishery Management (EAFM), which takes into account that fisheries are embedded and integrated with the environment and cannot be managed in isolation (Garcia, 2003), is a recent approach to fisheries management. In short, the objective of the EAFM is to reduce the mortality of the most vulnerable fished species and maintain the biodiversity in the marine ecosystem (Pikitch et al., 2004). However, the patterns and trends of species diversity in the pelagic ocean are not well-known due to the complexity of the marine ecosystem (Irigoien et al., 2004; Worm et al., 2005). In addition, it is difficult to find good techniques which describe, analyze and model the biodiversity of these species under the impact of the fishing exploitation. Many different types of indicators have been developed to reflect a variety of characteristics of species in simple terms; being species diversity one of the most basic but important indicators (Smeets et al., 1999; Zhu et al., 2011). Describing the spatial-temporal variability of species diversity can provide important information to facilitate the implementation of EAFM (Greenstreet and Rogers, 2006).

The tropical tuna purse seine fishery targeting skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*) and bigeye (*Thunnus obesus*) (Arrizabalaga et al., 2012) is one of the most important fisheries for the tuna cannery industry. In the eastern Pacific Ocean, this fishery uses three fishing techniques to capture tropical tuna: sets on tuna schools associated with dolphins, sets on unassociated schools of tunas (Free or School sets), and sets on floating objects [encountered natural objects or objects deployed by the fishers, called fish-aggregating devices (FADs)] (see a recent review Hall and Roman, 2013).

Bycatch, defined as "the part of the capture which is formed by non-target species" (Hall et al., 2000), whether retained and sold or discarded, has become one of the most important issues in fishery management. The worldwide increase of FAD sets during the 1990s has led to higher bycatches (Hall and Roman, 2013), with an associated impact on the population of some particular species, such as sharks or billfishes, which are more vulnerable due to their life histories. Thus, little is known about the differences of the bycatch species assemblages in the purse seine fishery in both fishing modes. Some literature has been published about the biology and habitat characteristics of the tuna and bycatch species in the eastern Pacific Ocean (Olson et al., 2010, 2014; Scott et al., 2012; Duffy et al., 2015). Moreover, tropical tuna purse seine fishery observer data has been used recently to study bycatch species diversity and community structure in the Atlantic and Indian Oceans in different type of sets (Torres-Irineo et al., 2014; Lezama-Ochoa et al., 2015); but not yet in the eastern Pacific Ocean. Understanding the habitat and diversity patterns of these species in the eastern tropical Pacific is essential for the development of future manage strategies to mitigate the effect of purse seiner in the bycatch communities.

The main objectives of this work were to (1) study the structure and species diversity of the tropical tuna purse seiner bycatch assemblages using biodiversity metrics in FAD and School fishing mode and (2) investigate the geographical and habitat characteristics of the bycatch species in the eastern Pacific Ocean. We hypothesize that the diversity patterns of bycatch assemblages could vary according to fishing modes (FAD vs. School sets, as FADs could attract and provide shelter for several

species) and specific oceanographic characteristics of the eastern Pacific Ocean.

#### MATERIALS

#### **Study Area**

The study area encompasses the eastern Pacific Ocean between 20°S-30°N and 70°-150°W. The main surface currents in the eastern Pacific Ocean are the North Equatorial Current (NEC), the North Equatorial Counter Current (NECC), the South Equatorial Current (SEC), and the California and Peru currents (see Supplementary Material Figure 1). Both (NEC and SEC) equatorial currents converge in the Intertropical convergence Zone (ITCZ). An equatorial upwelling takes place along longitudinal gradient characterized by cold waters and high concentrations of nutrients (Kessler, 2006). These surface currents are mainly forced by the wind regime, which follows a seasonal cycle (Fiedler, 1992). California and Peru-Chile currents are eastern boundary currents (Fiedler, 1992), with high productivity associated with coastal upwelling and forming some of the most important fishing areas characterized by cool and low- salinity waters. In addition, some oceanographic processes, such as the Equatorial Front system at north of equator, the Costa Rica Dome and the coastal upwelling generated by wind jets around Central America concentrate high amount of nutrients and influence the abundance and distribution of marine organisms (Fiedler and Talley, 2006).

#### **Data Collection**

Bycatch data were collected by the Inter-American Tropical Tuna Commission observer program (2005–2011) conducted in large purse seine vessels (> 363 t carrying capacity). Since 1996 the observer coverage of the trips in large vessels, combining IATTC and national observer programs, has been larger than 90% for FAD sets. In the case of School sets, the coverage has been larger than 85% since 2008 (IATTC, 2015).

Target species were not considered in the analysis because i) they are caught in much more quantities than bycatch species and could drive all the analysis and ii) the objective was to improve the information of the bycatch assemblages related to fishing mode and environmental characteristics.

Data recorded by observers include information about the trip and fishing activities (set type, position of the set, day and hour of the set), and the capture of the bycatch in biomass or number for the different species groups (Lezama-Ochoa et al., 2015). In this study, the numbers of individuals were used to perform the analysis. Bycatch species groups were divided in billfishes, bonyfishes, sharks, rays, turtles and marine mammals. Bycatch was identified to species level in general and to genus or family level in some cases (see "Selection of taxonomic categories" section) (Lezama-Ochoa et al., 2015).

The fishing set was considered as the data unit for the analysis and was categorized into FAD sets and School sets (Lezama-Ochoa et al., 2015). In this study Log sets (sets on natural drifting objects) were removed because of their low number in most recent years (IATTC, 2010), and therefore, only FAD sets were included in the analysis. A total of 45068 sets were observed Lezama-Ochoa et al

|           |       |         |          | FA       | ۵     |         |         |        |      |         |          | Scho     | o     |         |         |        |
|-----------|-------|---------|----------|----------|-------|---------|---------|--------|------|---------|----------|----------|-------|---------|---------|--------|
| Trimester | z     | Obs. SR | Richness | Rich. se | Chao2 | Chao se | Shannon | Sh. se | z    | Obs. SR | Richness | Rich. se | Chao2 | Chao se | Shannon | Sh. se |
| -         | 7171  | 58      | 2.71     | 1.53     | 62    | 3.5     | 0.59    | 0.46   | 3560 | 52      | 1.30     | 0.61     | 54    | 2.51    | 0.14    | 0.28   |
| 2         | 10723 | 52      | 3.31     | 1.89     | 20    | 23.62   | 0.69    | 0.45   | 1893 | 42      | 1.24     | 0.53     | 50    | 11.66   | 0.11    | 0.25   |
| e         | 9320  | 57      | 3.80     | 2.15     | 98    | 49.08   | 0.80    | 0.47   | 1306 | 40      | 1.38     | 0.73     | 42    | 2.64    | 0.16    | 0.30   |
| 4         | 0966  | 55      | 3.60     | 1.94     | 58    | 3.24    | 0.80    | 0.44   | 1135 | 44      | 1.31     | 0.69     | 104   | 71.01   | 0.14    | 0.29   |
| Total     | 37174 | 68      | 3.40     | 1.95     | 71    | 3.49    | 0.73    | 0.46   | 7894 | 56      | 1.30     | 0.63     | 68    | 13.15   | 0.14    | 0.28   |
|           |       |         |          |          |       |         |         |        |      |         |          |          |       |         |         |        |
|           |       |         |          |          |       |         |         |        |      |         |          |          |       |         |         |        |



**FIGURE 1** Distribution of sets with presence of bycatch in FAD and School fishing mode between 2005 and 2011.

between 2005 and 2011, from which 7894 were School sets and 37174 were FAD sets. The number of sets in both fishing modes is presented in **Table 1** and **Figure 1**.

#### Selection of Taxonomic Categories for Biodiversity Study

In the case of high level taxa records (genus, family, order and other levels), the distribution of species and their abundance was assigned based on the species composition for the same group (e.g., genus, family) in the same area (Lezama-Ochoa et al., 2015) for one particular year. As species level identification for the Families Belonidae, Diodotidae and Myliobatidae, and the Genus *Sphyraena* were not possible, they were considered as morphospecies -taxa that are distinguishable on the basis of the morphology (Oliver and Beattie, 1996)—and treated as species in species richness estimates (Lezama-Ochoa et al., 2015).

The list of species selected comprised a total of 72 species (6 billfish species, 20 sharks, 34 bony-fishes, 4 turtles and 8 species of rays).

#### **Environmental Data**

For each fishing set (date and position), which covered the period January 2005- December 2011, values of oceanographic variables were provided by CLS (Collecte Localisation Satellite, France, https://www.cls.fr) in the form of global geographic maps for each variable. Temperature at 20, 30, 50 and 75 m depth (SubT20, SubT30, SubT50, and SubT75; in  $^{\circ}$ C); depth of the thermocline (Therm. Depth; in m); gradient of the thermocline (Therm. Grad; in  $^{\circ}$ C); salinity at 20, 30, 50, and 75 m depth (Sal20, Sal30, Sal50, and Sal75; in PSU); and total surface current speed (WT; in kn) are outputs of MERCATOR general ocean circulation model (http://www.mercator-ocean.fr/en/), with

a 25 Km spatial resolution and a frequency of 2/3 days. Sea Surface Temperature (SST; in  $^{\circ}$ C) was derived from AVHRR and MODIS satellite data with 4 km resolution, acquired, respectively from NOAA CLASS (https://www.class.ncdc. noaa.gov/saa/products/welcome;jsessionid=64A6E9D799B84B4 9C1AEC15FB5A00900) and NASA OBPG (https://oceancolor.gsfc.nasa.gov). Chlorophyll concentration the same day of the fishing set and 18 days before (Chl and Chl-18 in mg m-3) with a 4 km resolution was derived from MODIS and MERIS satellite data, acquired, respectively from NASA OBPG and ESA. Sea Level Anomaly (SLA; in cm) and geostrophic current speed (WG; in kn) from altimetry were available with 25 km resolution. These altimetry maps were computed by CLS from different combinations of satellites ERS-2, Topex/Poseidon, Jason-1/2, ENVISAT, GFO, and CRYOSAT.

#### **METHODS**

#### Alpha Diversity

Alpha diversity measures the species diversity of a particular community, defined by two components: the number of species present (species richness) and how even their numerical participation in the community is (evenness) (Magurran, 2004).

Alpha diversity's first component (species richness) was calculated as the total number of observed species and represented using species accumulation curves. This technique shows the cumulative number of species recorded as a function of the sampling effort (i.e., number of samples) or the rate at which new species are found within a community. As a result, a smooth curve is produced by repeating a process of randomly adding the samples to the accumulation curve and then plotting the mean of these permutations (normally as value of 100) (Coleman et al., 1982). All the possible species can be considered found when the asymptote of the curve is reached. In this work, a simulation (5 replicates) of species accumulation curves for both types of fishing selecting randomly the same number of sets (N = 1,000) were also carried out.

Some authors have demonstrated that a raw count of the number of species in an area is far from the best estimate of true species richness (Reese et al., 2014). Despite its wide appeal and apparent simplicity, accurate estimates of species richness can be remarkably difficult to achieve using only the observed number of species. For that reason, there are some extrapolation techniques, such as non-parametric estimators, which allow the total number of species to be estimated using solely information of the observed number of species (Magurran and McGill, 2011). The Chao2 non-parametric estimator (Chao, 1984) (which represents the asymptote of the species accumulation curve), which adjusts the observed species richness by the number of rare taxa defined on occurrence data, was also used to obtain the estimated total species richness vs. observed species richness.

The mean value of the Species richness index was also calculated to compare diversity of the bycatch assemblages between both fishing types and trimesters.

The relative abundance of a species in an assemblage is the main factor that determines its importance in a diversity measure (Magurran, 2004). Thus, the second component of Alpha diversity (evenness) is better to describe the variability in species abundances of an area. A community in which all species have approximately equal numbers of individuals would be considered as an extremely even community (Magurran, 2004).

One of the best known and most informative methods to study the relative abundance of species is the rank/abundance plot or dominance/diversity curve. The vertical axis provides information about the logarithm of abundance, while the horizontal axis provides information about the number of species.

The log-abundance curves represent the relative abundance of the species (number of individuals for each species) from the most abundant to the rarest one. In this work, log-rank abundance curves were constructed for each fishing mode (FAD vs. School) to obtain the abundance of each species.

The shape of the log-rank abundance for each fishing mode can be fitted to different species abundance models: Geometric, Log-series, Log-normal and Broken stick models (Magurran, 2004); which describe the structure of the community. Therefore, the slope of the rank abundance plot describes community structure and diversity. Steep slopes signify assemblages with a high dominance of few species, such as the one that might be found in a Geometric or Log-series distribution, while smaller slopes imply higher evenness, consistent with a Log-normal or a Broken stick model (Magurran, 2004). Whittaker (1965) indicated that low diversity communities are Geometric while medium diversity communities are Log-series and high diversity communities are Log-normal.

The data was fitted to the following species distribution models (using the "vegan" package and "radlattice" function in R software): Null model (or Broken Stick model), Preemption model (or Geometric model), Log-normal model, Zipf model and Zipf-Mandelbrot model. The functional form for each model is explained in Pielou (1975) and Wilson (1991). The best model fit, according to the lowest AIC value or Akaike's Information Criterion (Akaike, 1974), represents best the community structure (Kindt and Coe, 2005).

Other indices, such as the Shannon diversity index, which includes information not only about the number of species of the assemblage but also about the relative abundance (Magurran, 2004), were used.

The Shannon diversity index (Shannon and Weaver, 1949) is defined as,

$$H' = -\Sigma pi \ln \ \cdot \ pi$$

where pi is the proportion of individuals of ith species found. Values range between 1.5 and 3.5; increasing diversity with the increase of the Shannon index. The mean value of the Shannon diversity index was calculated to compare diversity of the bycatch assemblages between both fishing types and by trimesters.

## Geographical and Habitat Characteristics of Bycatch Species

Generalized Additive Models (GAMs) (Hastie and Tibshirani, 1990; Guisan et al., 2002) were constructed to identify the spatial

and habitat characteristics of the bycatch species in relation with Species richness and Shannon diversity index between 2005 and 2011. Spatial (latitude and longitude), temporal (month), the type of association (FAD vs. School sets) and oceanographic variables were included in the analysis. The type of fishing was considered as covariate to determine if each bycatch species assemblage has different habitat characteristics. These models were chosen over generalized linear models as they are able of modeling continuous or categorical variables, replacing the linear function by a sum of smooth functions (Hastie and Tibshirani, 1990).

All environmental covariates were considered initially in the models, except those highly correlated between them (Pearson correlation r > 0.6) to avoid overfitting (Wood, 2006). Only one variable was included in the final model when high correlation was found between two variables.

To validate the model performance, a cross-validation was applied with a k-fold partitioning method (with k = 5) (Kohavi, 1995; Elith and Leathwick, 2009). Data was split into two different sets: one set used to fit the model (80% of data), called the training data, and the other set used to validate and obtain the predictions, called the testing data (20% of data).

The degrees of freedom of the smooth functions were determined for each explanatory variable as part of the model fitting process (Lopez et al., 2017). Each GAM was fitted using (i) thin plate regression splines to model nonlinear covariate effects, except for monthly variation, where a cyclic cubic regression spline was used (Wood, 2006) and (ii) a two-dimensional thin plate regression spline surface to account for spatial effects attributable to the location (latitude, longitude) of each fishing set (Lopez et al., 2017).

A GAM with a QuasiPoisson error distribution and logisticlink function was used to model the Species richness index. A GAM with a Gaussian error distribution with identity-link function was used to model the Shannon diversity index. The selection of the family and link function was determined by the distribution of the response variable for each index, respectively. In the case of Species richness index a slight over-dispersion of the response variable was observed; in contrast, for the Shannon index, the response variable showed a normal distribution.

The selection of the effective covariates to include in each GAM was performed applying backward stepwise procedure and selecting significant *p*-values for each geographical/ oceanographic variable. The variables which explain the diversity patterns were considered as the variables included in the final model. After fitting the model, residuals were plotted and Spearman's rank correlation coefficient (rs) was calculated to evaluate the model accuracy. *P*-values lower than 0.05 and correlation coefficients higher than 0.1 provide good model accuracy (Lauria et al., 2011). Model bias was also evaluated using Wilcoxon's signed-rank test to compare observed vs. predicted values. This test compares the median observed vs. predicted diversity, to test biased in the predictions.

Predictions are considered bias (underestimated/ overestimated) if test values are lower than 0.05 (Montero et al., 2016). Finally, the residuals were also plotted to obtain information about the fitting performance.

Spatial prediction maps of average, minimum, maximum and standard deviation of both diversity indices were calculated from

the trained model and using only test data. Spatial prediction maps by fishing mode and trimesters were also produced using the corresponding testing data in each case.

All the analyses were carried out using "vegan" (Oksanen et al., 2013), "BiodiversityR" (Kindt and Kindt, 2015) and "mgcv" (Wood and Wood, 2007) packages of R-3.3.2 free software (R Core Team, 2016).

## RESULTS

#### Alpha Diversity

In general, both fishing modes showed different number of species (**Table 1**), with slightly higher number of species observed in FAD sets (68) in comparison with School sets (56). The simulation of species accumulation curves for both types of fishing showed similar number of total observed species between both fishing modes (Supplementary Material Figure 2). The Kruskall-Wallis statistical test showed not significant differences in the number of species between both fishing modes (Supplementary Material Figure 2) in the simulation.

The Chao2 estimator showed that a total of 71 and 68 species could be observed in FAD and School sets, respectively, if the sample size is large enough (ant in this case, represented by the asymptote in the species accumulation curves) (**Table 1**, **Figure 2**).

The most abundant species in FAD sets was the *Coryphaena hippurus* (2044000 individuals) and *Caranx sexfasciatus* (75299 individuals) in School sets. The 10 most abundant species formed 95.8% with respect the total species in FAD sets and 90.1% in School sets (**Table 2**). In both types of fishing, and with the exception of the silky shark (*Carcharhinus falciformis*), the most bycaught species were small bony-fishes.

After fitting the different species abundance models to the rank abundance curves in both fishing modes, results showed that bycatch assemblages in FAD sets followed a Log-normal distribution, and the bycatch assemblages in School sets a Zipf-Mandelbrot distribution or Log-series distribution based on the lowest AIC values (**Figure 3** and Supplementary Material Table 1). The shape of the curves lead us to suggest that bycatch species are more evenly distributed in FAD sets than in School sets.

Finally, the mean Species richness and Shannon diversity index were calculated in both fishing modes and by trimesters and results are shown in **Table 1**. Bycatch assemblages have higher number of species (3.40) and diversity (0.73) in FAD sets than in School sets.

Mean richness and Shannon index, stratified by quarters in FAD and School sets showed high diversity in the third and fourth quarter (**Table 1**).

# Geographical and Habitat Characteristics of Bycatch Species

The final model for species richness included as explanatory variables spatial variables (latitude-longitude interaction), temporal variables (month), type of fishing mode (type as factor) and environmental variables (sea surface temperature,

#### TABLE 2 | Species abundance in FAD and School sets.

| SpeciesRankAbundanceSpeciesRankAbundanceChyphenop Nipuxan1724400Conscienterability17799Acenthocybium solundri2125782Conscienterability311199Ballet Kohrinstein4417874Decateras macandus311191Elagiste Kohrinstein6127289Mala main68587Carcharturus Indeformis6127289Mala main85511Carcharturus Indeformis792031Naucrates doctar79216Aldenas conducturus1037153Aconthocybium solundri1042681Carana endanciabat1037073Malcula tarbation1042681Carana endanciabat1138741Photophen streatschiner1142971Lobates schwanoses13224101Photophen streatschiner122372Kophana analyzan1518900Marta tarbation131913Lobates schwanoses1324401Photophen streatschiner131921Lobates schwanoses1324401Photophen streatschiner142407Kophana analyzan1618469Sphyram sep.151207Kophana analyzan187771Senda nochan18271Kophana analyzan187771Senda nochan191818Lobates schwanoses191818Malabat sochan191818Kophana angenan18271 <th></th> <th>FAD sets</th> <th></th> <th colspan="5">School sets</th>  |                            | FAD sets |           | School sets                |      |           |  |  |
|--|----------------------------|----------|-----------|----------------------------|------|-----------|--|--|
| Corphaters hipsours         1         2044000         Caratro socialization         1         75239           Acandros functions         2         1225752         Corphaters inpunus         2         63837           Eligistis biprinutis         4         447574         Dicaptons indicadius         3         17499           Eligistis biprinutis         5         828341         Cardrohmits indications         5         11183           Cardrohmits finitations         6         122789         Moh moh         6         9577           Adverse scriptions         7         95391         Ancintociphan saturation         7         9510           Adverse scriptions         10         37173         Mohatro function         10         2802           Corphateria equisations         12         29219         Mohatro function         11         2427           Dicaptoris macrohitis         13         2707         Mohatro function         13         1613           Scription macrohitis         12         29219         Mohatro function         13         1613           Scription macrohitis         13         29400         Eligistis phyroutin         13         1613           Scription macrohitis         13         29400   | Species                    | Rank     | Abundance | Species                    | Rank | Abundance |  |  |
| Acardhophur asanchi212572Cycyhaara hegyyaa213537Candhodemin maculata31092801Seriata karva414447Sechtor ogyuna5127259Mole mole655101Sechtor ogyuna6127259Mole mole655101Alterns scoptura716331Mule ratio factorinki655110Alterns scoptura867237Candholythir maculata754061Corphetens acyuta1037073Molu thrustorin102407Corphetens acyuta1139241Honogenes Stockholythir Scienchi112427Decastaria macarabus1229219Molu farustorin131611Serida kandi1395400Engents bipronuta131613Serida kandi142008Istephroze plaipterus141507Serida kandi1395400Engents bipronuta131613Serida kandi142008Istephroze plaipterus141507Serida kandi18207171532207/141320653Serida kandi193690Mulcu targacara199630160101010Nauceta kata193690Mulcu targacara1996301601010101010Nauceta kata193690Mulcu targacara19100101010101010101010<  | Coryphaena hippurus        | 1        | 2044000   | Caranx sexfasciatus        | 1    | 75299     |  |  |
| Cardinbermin mancababa31002811Selection contractions311081Eligistis bipinnulatis44147574Decatories micraroble5111853Cardnahning shortomic6127289Mole mole65857Altorias scriptication70501933511Cardnahning shortomic867237Cardinblemis maculatios93436Altorias scriptication993436321132021Cardnahning standardia1037073Machaba truttorin93436Carana sudacababa1037073Molocul granication122014Carana sudacababa1232219Molocul granication131613Carana sudacababa1324060Eligistis bismututi131713Stokia talana1424058Molocul granication141507Kyholasse anabagas1518306Matababa truttorin141507Kyholasse anabagas1618499Shyhoranation151217Kyholasse anabagas187771Sarota molentia19981Makara ingrana212262Sphyma lewni203758Sarota provintia232202Makara ingrana21683Sarota provintia242020Makara ingrana23578Sarota provintia232402Makara ingrana24382Sarota provintia2423022302378S   | Acanthocybium solandri     | 2        | 1225782   | Coryphaena hippurus        | 2    | 63837     |  |  |
| Engatic pipmulate41987Decaptions maxemata41987Sacitator copuna5288041Carchaminus facilormis511163Carchaminus facilormis6127250Mol molu665737Altorss sociotos7925911Naucrates ductor765101Corportana aquisate957189Actaribiophum sociotanci99498Corportana aquisate1037073Molcul mutarini1024207Corportana aquisate1136241Principiera stendachmeri112427Decaptieras maxemalus122014102101421014Loboies surfamentis1325400Eligitis bipinutata131517Seriota helend1618459Saryasen seques162217Kipchous analogitanu1618459Saryasen seques16221Naucrates ductor171512Solio helend182721Naucrates ductor187771Solio helenda19968Naucrates ductor182721Solio helenda21663Soliyara suppers28287Markar agricana21663Soliyara suppers292620Salyymu lewini26232Soliyara suppers212620Salyymu lewini26232Soliyara suppers2126202630263263263Soliyara suppers28974Salyara supers26332<  | Canthidermis maculatus     | 3        | 1092891   | Seriola lalandi            | 3    | 17199     |  |  |
| Sectal or opunal511183Carcharhinus falolomis511183Carcharhinus falolomis625957Aldens sorphus792091Aldens sorphus997159Acartholomis incaledus8Carons sontascitus997159Acartholomis incaledus8Carons sontascitus1037073Mobula fluetorin1028001Sarola lalandi1136241Phinoplara standachandi112427Carons sontascitus1222010Mobula guaria131613Sarola lalandi1325400Eligalis bpinnutala131613Lobotes simanomasis1518860Maria tersaria161207Kiphosus aralegnas1618860Maria tersaria161207Kiphosus aralegnas1711352Corphaena equisalis17121Kiphosus aralegnas187771Sarola incalina18777Kishara indica193590Mobula fragman20676Sphynan zygaena21262Sphyman zygaena23578Sphynan zygaena222284Precolaritypon volscad24683Sorial parama232020Makina indica24578Sphyman zygaena24183Applas zygaena23278Sphyman zygaena24183Applas zygenolasca24298Carcharhinus indianus251914Applas zygenolasca23<   | Elagatis bipinnulata       | 4        | 417874    | Decapterus macarellus      | 4    | 14847     |  |  |
| Cardiantian failational61927Malar and southar61957Alutarus acceptus712281Naucrates ductor75510Corphone aquiseis957163Cardindatermi maculatus854211Corphone aquiseis1037073Mobule hurstori112427Carans cardiscastita1138241Phinoptra standachneri112427Decaptures macmalia122014Mobule japanica122014Labdes surfamentamis1325000Englast biphnutla131513Seniola nolaria1424003Elisphoras plotypens141597Kiphosa atalogos1518000March texts171217Kiphosa atalogus1618453Sphyraem spp.182921Naucrates ductor171152Corphrame aquiseis172911Makara nigricast171525Kalkara adactar196961Urapis helota212852Kalkara adactar216961Seniola prunan232920Makara infrions236961Seniola prunan241939Adoptas sparafolocus24694Seniola prunan241939Adoptas sparafolocus24694Seniola prunan26924Sphyram mokara263920Seniola prunan282020Makara infrions293620Carcharhinus inhatura306316314Sphyram mokara <td>Sectator ocyurus</td> <td>5</td> <td>283641</td> <td>Carcharhinus falciformis</td> <td>5</td> <td>11163</td>  | Sectator ocyurus           | 5        | 283641    | Carcharhinus falciformis   | 5    | 11163     |  |  |
| Alterius corplands76281Naucrates ductor76510Altarus monocensos867237Canthiderma macutatus86211Canars sostascitutis9671150Anantholerma macutatus962431Canars sostascitutis103703Mobula fluxistori102829Decatorius macanitus1222014Mucuta generic122014Lobotes sumannensis1325400Blagatis bipinulata131613Lobotes sumannensis1444908bipinulata151297Kyboous anatogua161490Shyrana soon161297Kyboous anatogua1711352Corphana soutasits17121Makara indica193939Mobula tangacans18727Makara indica193939Mobula tangacans13171Makara indica193939Mobula tangacans20650Sinda nangacans21252Kijka oudox21650Sinda paranan222244Perceptinytrygon voltacau21650Sinda paranan236714Mohair ingitas26429Caracharius timptamus26924Syntra mokara26429Solyman app.27912Makair indica27382Sinda paranan28924Syntra mokara28429Caracharius timptamus29924Syntra mokara29429Solyma   | Carcharhinus falciformis   | 6        | 127259    | Mola mola                  | 6    | 5857      |  |  |
| Adversary acquisableB67237Cantheckernia macaluthatB5211Coryphanan equisable057763Acanthocyburn solandri03438Carvas aedisacturas1037073Mobal furston102487Sariola ilaradi1135241Principlera steindachineri112427Carvas aedisacturas1229210Mobal gancia131613Deceptors macroscola1325400Elagatis bipinulata131613Sariola involanta142400Istochorus platypterus141997Kyphosus analogus1518060Mota birostris169241Naucrates ductor1618459Sphyraena gyne acquisele17281Naucrates ductor187771Sariola involanta19088Naucrates ductor203526Sphyraena equisele19088Naucrates ductor212822Kajka audax21683Sariola pranana222020Makaira ingicuras23678Sariona purana241914Appas paleque24604Sariona purana241914Appas paleque24604Sariona purana241914Appas paleque24604Sariona purana241914Appas paleque24604Sariona purana261914Appas paleque24604Sariona purana281914Appas paleque24604 </td <td>Aluterus scriptus</td> <td>7</td> <td>92391</td> <td>Naucrates ductor</td> <td>7</td> <td>5510</td>  | Aluterus scriptus          | 7        | 92391     | Naucrates ductor           | 7    | 5510      |  |  |
| Carphrane equivalies957:59Acardracyatoris93438Carlar saukassitus1037073Mobula thurstori102880Carlar saukassitus1138241Pinopera steindachneri122014Decapterus macarellus1229219Mobula japania122014Lobotes surinamensis132800Bizgotis bipinulata131613Schola indamin1424098Mobula japania161771Kyphosus elagistas araikagus1518805Merta bizcatris151297Kyphosus elagistas araikagus1618459Stypravar app.162424Naucrates ductor1711362Coryphaena equivaleits17921Makafa indira187771Sorida involana18727Makafa inginicars187771Sorida involana13727Makafa inginicars193590Mobula trapacana13727Sphyma syganna222824Piropalytrypan viducea23656Sphyma syganna232020Makafa indica23650Sohna hovini241930Appas superalicous24936Sohna hovini251914Appas paragis26924Sphyma hovini26924Sphyma makara26924Sphyma hovini28897Burace anymchus28937Sphyma hovini29897Burace anymchus29924 <td>Aluterus monoceros</td> <td>8</td> <td>67237</td> <td>Canthidermis maculatus</td> <td>8</td> <td>5211</td>   | Aluterus monoceros         | 8        | 67237     | Canthidermis maculatus     | 8    | 5211      |  |  |
| Caranx selasistab.1037073Mobula thurstori102800Saniola kilandi1135241Principlara staindachneri1224271Carbo kilandi1229710Mobula tipranica131613Lobotes surhamenses1424080Blagatis bipinnibulata131613Sorica nolama1424080Blagatis bipinnibulata131613Kiphosus aratiogus1518066Manta birostris1512971Kiphosus selgars1618490Sphyreena spine182721Makata ingicars187771Seriola rolama182721Makata ingicars187771Seriola rolama206856Sphyrma sypeena205856Sphyrma levini206850Sphyrma sygeena212852Kajika audax216850Sphyrma sygeena232202Makara ingicars23678Sphyrma sygeena251914Alpae speldicus24640Sphyrma sygeena26924Sphyrma synehara28924926Sphyrma sygeena26924Sphyrma zynehara29626924Sphyraena spo.211914Alpae speldicus29926926Carcharinus Indiatus30631Sphyrma zynehara313131Sphyraena spo.211914Alpae speldicus313131Sphyraena spo.21926Makar  | Coryphaena equiselis       | 9        | 57159     | Acanthocybium solandri     | 9    | 3436      |  |  |
| Seriala lalandi         11         35241         Phinophera sehandachneri         11         2427           Decapterus macarelus         12         28219         Mobula japanica         12         2014           Lobotes surinamentos         13         25400         Bialgais bipinvulata         13         1913           Seriala rivolana         14         24008         Istlophorus platypterus         14         1927           Kyphosus elegans         16         1456         Schyrane space         18         221           Naucratas cluctor         17         11352         Corpheare equiselis         17         180           Naucratas cluctor         18         771         Schola krolana         18         727           Makara indica         19         3599         Mobula tarapacare         19         688           Urasys fehola         20         2854         Schola trapacare         21         685           Seriala peruana         21         285         Schyran typino triviana seque         22         650           Safar crumenchthatmus         23         2202         Makara indica superians         23         526           Safar crumenchthatmus         25         1914         Alopias superiansus<  | Caranx sexfasciatus        | 10       | 37073     | Mobula thurstoni           | 10   | 2680      |  |  |
| Decaptenus macarelus         12         28219         Mobula japanica         12         2014           Lobotes suriamensis         13         25400         Elegats binimulata         13         1513           Schlan Avallana         14         24090         Islighorbus faitylipturus         14         1597           Kyphosus analogus         15         18806         Marta binostris         15         1297           Kyphosus degars         16         18459         Sphyrame sp.         16         924           Makaira indica         17         11352         Copyheare aquisolis         17         921           Makaira indica         20         3559         Mobula tarapacana         19         6663           Sphyrana zygaena         21         2852         Kalkia valkar         21         663           Sphyrana zygaena         23         2020         Mekaira infricaras         21         663           Sphyrana kinik         23         2020         Mekaira infricaras         23         264           Sphyrana kinik         24         1939         Alopas superaliosus         24         294           Sphyrana kinik         27         1914         Alopas superaliosus         28   | Seriola lalandi            | 11       | 35241     | Rhinoptera steindachneri   | 11   | 2427      |  |  |
| Lobotes summennesis         13         25400         Elagatis bipinulata         13         1613           Seniote involaria         14         24903         Isticphonus plitypterus         14         1997           Kyphosus indegus         15         18800         Marka binstris         15         1297           Kyphosus indeguas         16         1440         Syhyaana sp.         16         242           Naucrates ductor         17         11352         Corphaena equiselis         17         261           Makaria nigricans         18         7771         Seriota involaria         18         727           Makaria nigricans         19         3599         Makaria nigricans         21         668           Seriota peruana         22         2284         Pteropletrynygon violacea         23         676           Seriota peruana         23         202         Makaria nigricans         23         576           Malar main         24         1309         Malaria indica         24         504           Selar commenchrhaitmus         26         924         Prenpletrynygon violacea         29         682           Carcharhinus induca         20         681         Malaria indica         21   | Decapterus macarellus      | 12       | 29219     | Mobula japanica            | 12   | 2014      |  |  |
| Seriola rivolana         14         24908         Isticphorus platypterus         14         1577           Kyphosus elgens         15         19806         Marta birestris         15         1297           Naucrates ductor         17         11352         Coryphaena equiselis         17         921           Makaira indican         18         7771         Seriola rivolana         18         727           Makaira indican         19         5909         Mobula targacana         19         688           Uraspis helvola         20         3526         Sphyrma isewini         20         675           Sphyrma isgup         21         2852         Kajka auduk         21         680           Sphyrma isgup         23         2020         Makaira ingricans         23         578           Selar curmenophthimus         25         1914         Alopias superciliosus         25         928           Carchatrinus longimanus         26         924         Sphyrma isgup         28         928         928         928         928         928         928         928         928         928         928         928         928         928         928         928         928         928   | Lobotes surinamensis       | 13       | 25400     | Elagatis bipinnulata       | 13   | 1613      |  |  |
| kiphoaus analogus         15         18806         Manta birostris         15         1297           Kiphosus elegaris         16         14499         Sphyraen spp.         16         024           Makaira nigricans         18         7771         Sariola rivoliana         18         727           Makaira nigricans         19         3599         Mobula trapacana         19         698           Unagais hukola         20         3563         Sphyrna lowain         20         675           Sphyrna zygeana         21         2852         Kajikia audax         21         683           Sariola peruana         22         2284         Pteroplatytrygon violacea         22         650           Sphyrna zygeana         23         2020         Makara nigricans         26         429           Salor currenorphthalmus         25         1914         Alopias speciliosus         26         429           Garcharhinus longimanus         26         924         Sphyrae zygeana         26         429           Garcharhinus longimanus         28         927         Balaise inricana         28         32           Sphyraen zygeana         29         689         Eucooclus volitans         29 <td< td=""><td>Seriola rivoliana</td><td>14</td><td>24908</td><td>Istiophorus platypterus</td><td>14</td><td>1597</td></td<>   | Seriola rivoliana          | 14       | 24908     | Istiophorus platypterus    | 14   | 1597      |  |  |
| Kyphoaus elegans         16         14459         Sphyraena spp.         16         924           Naucrates ductor         17         11382         Corphaena equiselis         17         921           Makaira inficans         18         771         Sariola inviciana         19         698           Urasois helvola         20         3526         Sphyra lawini         20         675           Sphyra organa         21         2822         Kalika audrak         20         676           Sphyra organa         22         284         Pteroplatytrygon violacea         22         680           Sohra organa         23         202         Makaira infricans         23         678           Mola mola         24         1914         Alopias pelogicus         25         429           Carcharhinus longimanus         26         924         Sphyran mokaran         26         922           Sphyrane spp.         27         912         Makaira infricans         29         322           Kajika audax         28         977         Isuras organinchara         30         322           Kajika audax         28         977         Isuras organinchara         30         322           <  | Kyphosus analogus          | 15       | 18806     | Manta birostris            | 15   | 1297      |  |  |
| Naucrates ductor         17         1352         Coryphaena equiselis         17         921           Makaira indipcars         18         7771         Sorloa holena         18         7271           Makaira indipcars         18         7771         Sorloa holena         18         7271           Makaira indipcars         20         3528         Sphyma lewini         20         6751           Sphyma zygaena         21         2852         Kajika audax         21         683           Seriola peruana         22         2284         Pteroplatytrygon violacea         22         650           Sphyma lewini         23         1914         Alopias superollosus         24         504           Selar crumenophtalmus         25         1914         Alopias pelogicus         25         429           Sphyma engana         27         912         Makaira indica         27         382           Carcharhius longimanus         28         897         kustas aindica         28         378           Peroplatytrygon violocea         29         640         Autarus monoceras         31         301           Stardarhius linbatus         30         631         Sphyma angaera         32         2777 <td>Kyphosus elegans</td> <td>16</td> <td>18459</td> <td>Sphyraena spp.</td> <td>16</td> <td>924</td>   | Kyphosus elegans           | 16       | 18459     | Sphyraena spp.             | 16   | 924       |  |  |
| Makaira nigricans         18         7771         Seriola rivoliana         18         727           Makaira indica         19         3599         Mobula trapacana         19         683           Uraspis helvola         20         3526         Sphyrna Jewini         20         675           Sphyrna Jegena         21         2852         Kajiki audax         21         660           Seriola peruana         22         284         Pteropletytrygon violacea         22         650           Solar crumenophthalmus         23         2702         Makaira ingricans         23         578           Mole mole         40         1939         Alopias superolitosus         25         429           Carcharthinus longimanus         25         1914         Alopias superolitosus         26         382           Sphyraen aspp.         27         912         Makaira indica         29         382           Sphyraen aspp.         27         912         Makaira indica         30         328           Isturs onyrinchus         30         631         Superonichus woniccurs         31         301           Isturs onyrinchus         32         294         Prionace glauca         32         297   | Naucrates ductor           | 17       | 11352     | Coryphaena equiselis       | 17   | 921       |  |  |
| Makara indica         19         3599         Mobula tarapacana         19         698           Uraspis helvola         20         3526         Sphyma kwini         20         675           Sphyma pagena         21         2552         Kajika audax         21         680           Sphyma lewini         23         2202         Makaina ingicans         23         578           Mola mola         24         1939         Alopias superollosus         24         504           Selar cumenophthalmus         25         1914         Alopias superollosus         26         392           Garcharbinus longimanus         26         924         Sphyma mokaran         26         392           Sphyma espis         27         912         Makaina indica         27         392           Sphyma mokaran         28         897         Lsurus oryinchus         29         362           Staphonus platypterus         31         406         Alutarus monocaros         31         301           Surus oryinchus         32         224         Prionace glauca         33         240           Mobula thurstori         34         208         Mobula murkina         34         203   | Makaira nigricans          | 18       | 7771      | Seriola rivoliana          | 18   | 727       |  |  |
| Uraspis halvola         20         3526         Sphyma lewini         20         675           Sphyma zogeana         21         2852         Kaljkla audax         21         663           Seriola peruana         22         2202         Malar injorcans         23         578           Mola mola         23         2202         Malar injorcans         23         578           Mola mola         24         1939         Alopias superciliosus         24         504           Selar crumenophthalmus         25         1914         Alopias pelogicus         26         392           Sphyran alewini us longinanus         26         924         Sphyran alewini notas         28         378           Carcharhinus longinanus         27         912         Malaria indica         28         378           Pteroplatyrgon violacea         28         897         Isurus onyrinchus         28         378           Carcharhinus limbatus         30         631         Sphyran alewina rus onyrinchus         30         282           Sphyran lewiny rus olacea         31         406         Aluterus monoceros         31         301           Istrus onyrinchus         32         294         Prionace glauca         32   | Makaira indica             | 19       | 3599      | Mobula tarapacana          | 19   | 698       |  |  |
| Sphyma zygaena         21         2852         Kajika audax         21         663           Seriola peruana         22         2284         Pteroplatyrygon violacea         22         650           Sphyma lewini         23         2202         Makara ingicans         23         578           Mola mola         24         1939         Alopias pelagicus         24         504           Selar curmenophthalmus         25         1914         Alopias pelagicus         25         429           Carcharhinus longimanus         26         924         Sphyma mokaran         26         392           Sphyna spp.         27         912         Makara indica         27         382           Kajika audax         28         897         Isurus oxyrinchus         28         378           Pteroplatytrygon violacea         29         689         Exocetus volitans         29         362           Staurs oxyrinchus         31         406         Aluterus monoceros         31         301           Isurus oxyrinchus         32         224         Prionae glauca         32         247           Sphyma mokaran         33         222         Carcharhinus limbatus         33         240  | Uraspis helvola            | 20       | 3526      | Sphyrna lewini             | 20   | 675       |  |  |
| Nombod         Percoplatytrygon violacea         Percoplatytrygon viol | Sphyrna zygaena            | 21       | 2852      | Kajikia audax              | 21   | 663       |  |  |
| Sphyma lewini         23         2202         Makara nigrcans         23         578           Mola mola         24         1939         Alopias superciliosus         24         504           Selar curnenophthalmus         25         1914         Alopias superciliosus         25         429           Carcharhinus longimanus         26         924         Sphyma mokaran         26         392           Sphyrana spp.         27         1912         Makaira indica         27         382           Kajika audax         28         897         Isurus oxyrinchus         28         378           Pieroplatytrygon violacea         29         689         Exocoetus volitars         29         362           Carcharhinus limbatus         30         631         Sphyma zygaana         30         281           Isiorus oxyrinchus         32         294         Prionace glauca         32         277           Sphyma mokaran         33         222         Carcharhinus limbatus         33         240           Mobula turustoni         34         203         Balistes polylepis         36         149         Xiphias gladius         36         141           Alopias suporitiosus         36         149 <td>Seriola peruana</td> <td>22</td> <td>2284</td> <td>Pteroplatytrygon violacea</td> <td>22</td> <td>650</td>  | Seriola peruana            | 22       | 2284      | Pteroplatytrygon violacea  | 22   | 650       |  |  |
| Mola mola         24         1939         Alopias superciliosus         24         504           Selar crumenophthalmus         25         1914         Alopias pelagicus         25         429           Carchathinus fongimanus         26         924         Sphryma nokaran         26         392           Sphryaena spp.         27         912         Makaira indica         27         382           Sphryaena spp.         28         897         Isurus oxyrinchus         28         378           Pteroplatytrygon violacea         29         689         Exocoetus volitans         29         362           Carcharhinus limbatus         30         631         Sphryma oncoeros         31         301           Isurus oxyrinchus         32         294         Prionace glauca         32         240           Mobula trustori         34         208         Mobula munkiana         34         203           Balistes polylepis         35         183         Aluterus scriptus         35         184           Tetraturus angustrostris         36         149         Xphias gladius         36         178           Alopias superciliosus         40         96         Kyphosus analogus         40 <td< td=""><td>Sphyrna lewini</td><td>23</td><td>2202</td><td>Makaira nigricans</td><td>23</td><td>578</td></td<>  | Sphyrna lewini             | 23       | 2202      | Makaira nigricans          | 23   | 578       |  |  |
| Selar orumenophthalmus251914Alopias pelagicus25429Carcharhinus longimanus26924Sphyma mokaran26932Sphynean spp.27912Makaia indica27382Kajika audax28397Isurus oxyrinchus28378Pleroplathytyon violacea29689Exocoetus voltans29362Carcharhinus limbatus30631Sphyma zygaena30328Istiophorus platypterus31406Aluterus monoceros31301Isurus oxyrinchus32222Carcharhinus limbatus33203Sphyma mokaran34203Aluterus scriptus35184Mobula trustoni34203Aluterus scriptus35184Tetrapturus angustrostris36149Xiphias gladius36178Mobula spancia37137Alopias volginus36178Alopias superciliosus39125Lobotes surinamensis39104Alopias superciliosus4096Kyphosus analogus4054Rarzania laevis4189Carcharhinus porosus4134Alopias vulpinus45361783136Iepidocheys olivacea4270Remora remora4231Alopias superciliosus4096Kyphosus analogus4054Alopias superciliosus4189Carcharhinus porosus4134 <td>Mola mola</td> <td>24</td> <td>1939</td> <td>Alopias superciliosus</td> <td>24</td> <td>504</td>   | Mola mola                  | 24       | 1939      | Alopias superciliosus      | 24   | 504       |  |  |
| Carcharhinus longimanus         26         924         Sphyrna mokarran         26         992           Sphyraena spp.         27         912         Makaira indica         27         382           Kajika audax         28         897         Isurus oxyrinchus         28         378           Pteroplatytnygon violacea         29         689         Exocoetus volitans         29         362           Carcharhinus limbatus         30         631         Sphyrma zygaena         30         328           Istorborus platytpterus         31         406         Aluterus monocearos         31         301           Isturs oxyrinchus         32         294         Prionace glauca         32         277           Sphyrma mokarran         33         222         Carcharhinus limbatus         33         240           Mobula thurstori         34         208         Mobula surptinus         33         240           Mobula pancia         35         183         Aluterus monocearos         33         240           Mobula pancia         36         183         Aluterus monocearos         33         240           Mobula fayancia         36         183         Aluterus soriptus         36         184 </td <td>Selar crumenophthalmus</td> <td>25</td> <td>1914</td> <td>Alopias pelagicus</td> <td>25</td> <td>429</td>   | Selar crumenophthalmus     | 25       | 1914      | Alopias pelagicus          | 25   | 429       |  |  |
| Sphyraena spp.         27         912         Makaira indica         27         382           Kajikia audax         28         897         Isurus oxyrinchus         28         378           Pteroplatytrygon vidacea         29         689         Exocoetus volitans         29         682           Carcharhinus limbatus         30         631         Sphyrae zgeena         30         328           Istiophorus platypterus         31         406         Aluterus monoceros         31         301           Isurus oxyrinchus         32         294         Prionace glavca         32         277           Sphyrae mokarran         33         222         Carcharhinus limbatus         33         240           Mobula thurstoni         34         208         Mobula munkiana         34         203           Bailses polylepis         35         183         Aluterus scriptus         36         178           Mobula japanica         37         137         Alopias ygladius         37         162           Alopias superciliosus         39         125         Lobotes surinamensis         39         104           Alopias superciliosus         41         89         Carcharhinus porosus         41         <  | Carcharhinus longimanus    | 26       | 924       | Sphyrna mokarran           | 26   | 392       |  |  |
| Arrow         28         897         Isurus oxyrinchus         28         378           Pteroplatytrygon violacea         29         689         Exocoetus volitans         29         362           Carcharhinus limbatus         30         631         Sphyrna zygaena         30         328           Istophorus platybterus         31         406         Aluterus monoceros         31         301           Isurus oxyrinchus         32         294         Prionace glauca         32         277           Sphyrma mokarran         33         222         Carcharhinus limbatus         33         240           Mobula thrustoni         34         208         Mobula murkiana         34         203           Balistes polylepis         35         183         Aluterus scriptus         36         178           Mobula typanica         37         137         Alopias vulpinus         37         162           Xiphias gladius         38         129         Sectator ocyurus         38         161           Alopias supercilicusus         39         125         Lobotes surinamensis         39         104           Alopias supercilicusus         41         89         Carcharhinus porosus         41 <t< td=""><td>Sphyraena spp.</td><td>27</td><td>912</td><td>Makaira indica</td><td>27</td><td>382</td></t<>   | Sphyraena spp.             | 27       | 912       | Makaira indica             | 27   | 382       |  |  |
| Percoplatytrygon violacea29689Exocoetus volitans29362Carcharhinus limbatus30631Sphyrna zygaena30328Istiophorus platypterus31406Aluterus monoceros31301Isurus oxyrinchus32294Prionace glauca32277Sphyrma mokarran33222Carcharhinus limbatus33240Mobula thurstoni34208Mobula munkiana34203Balistes polylepis35183Aluterus scriptus35184Tetrapturus angustrostris36149Xiphias gladius36178Mobula japanica37137Alopias vulpinus37162Xiphias gladius39125Lobotes surinamensis39104Alopias superciliosus4096Kyphosus analogus4054Ranzania laevis4189Carcharhinus porosus4134Ubulu tarapacana4270Remora remora4231Lepidochelys olivacea4354Tetrapturus angustirostris4330Prionace glauca4536Lepidochelys olivacea4517Alopias vulpinus4536Lepidochelys olivacea4517Alopias vulpinus4536Lepidochelys olivacea4517Alopias vulpinus4536Lepidochelys olivacea4516Remora remora4720Ablennes hians47<  | Kajikia audax              | 28       | 897       | Isurus oxyrinchus          | 28   | 378       |  |  |
| Carcharhinus limbatus30631Sphyrna zygaena30328Istiophorus platypterus31406Aluterus monoceros31301Isurus oxyrinchus32294Prionace glauca32277Sphyrna mokarran33222Carcharhinus limbatus33240Mobula thurstoni34208Mobula munkiana34203Baltse polylepis35183Aluterus scriptus36184Tetrapturus angustirostris36149Xiphias gladius36178Mobula japanica37137Alopias vulpinus37162Xiphias gladius86129Sectator coyurus38161Alopias superciliosus4096Kyphosu analogus4054Ranzania laevis4189Carcharhinus porosus4134Mobula tarapacana4270Remora remora4231Lepidochelys olivacea4354Ertapturus angustirostris4330Prionace glauca4536Lepidochelys olivacea4424Motula tarapacana4536Lepidochelys olivacea4517Alopias vulpinus4536Lepidochelys olivacea4517Alopias vulpinus4628Kyphosus elegans4616Remora remora4720Ablennes hians4714Evocoetus volttans4813Taractes rubescens4811 <td>Pteroplatytrygon violacea</td> <td>29</td> <td>689</td> <td>Exocoetus volitans</td> <td>29</td> <td>362</td>   | Pteroplatytrygon violacea  | 29       | 689       | Exocoetus volitans         | 29   | 362       |  |  |
| Istophorus platypterus31406Aluterus monoceros31301Isurus oxyrinchus32294Prionace glauca32277Sphyrna mokarran33222Carcharhinus limbatus33240Mobula thurstoni34208Mobula munkiana34203Balistes polylepis35183Aluterus scriptus35184Tetrapturus angustirostris36149Xiphias gladius36178Mobula japanica37137Alopias vulpinus37162Xiphias gladius38129Sectator ocyurus38161Alopias superciliosus39125Lobotes surinamensis39104Alopias superciliosus4096Kyrphosus analogus4054Ranzania laevis4189Carcharhinus porosus4134Mobula tarapacana4270Remora remora4231Lepidochelys olivacea43541612424Manta birostris4354Tetraptruus angustirostris4330Prionace glauca4556Myliobatidae4424Manta birostris4628Kyrphosus elegans4616Remora remora4720Ablennes hians4714Exocoetus volitans4813Taractes rubescens4811Chelonia mydas498Carcharhinus longimanus497  | Carcharhinus limbatus      | 30       | 631       | Sphyrna zygaena            | 30   | 328       |  |  |
| Isurus oxyinchus         32         294         Prionace glauca         32         277           Sphyrna mokarran         33         222         Carcharhinus limbatus         33         240           Mobula thurstoni         34         208         Mobula munkiana         34         203           Balistes polylepis         35         183         Aluterus scriptus         36         184           Tetrapturus angustirostris         36         149         Xiphias gladius         36         178           Mobula japanica         37         137         Alopias vulpinus         37         162           Xiphias gladius         38         129         Sectator ocyurus         38         161           Alopias superciliosus         39         125         Lobotes surinamensis         39         104           Alopias superciliosus         40         96         Kyphosus analogus         40         54           Razania kevis         41         89         Carcharhinus porosus         41         34           Mobula tarapacana         42         70         Remora remora         42         31           Lepidochelys olivacea         43         54         16         17         14 <t< td=""><td>Istiophorus platypterus</td><td>31</td><td>406</td><td>Aluterus monoceros</td><td>31</td><td>301</td></t<>   | Istiophorus platypterus    | 31       | 406       | Aluterus monoceros         | 31   | 301       |  |  |
| Sphyma mokarran         33         222         Carcharhinus limbatus         33         240           Mobula thurstori         34         203         Mobula munkiana         34         203           Balistes polylepis         35         183         Aluterus scriptus         35         184           Tetrapturus angustirostris         36         149         Xiphias gladius         36         178           Mobula japanica         37         137         Alopias vulpinus         37         162           Xiphias gladius         38         129         Sectator ocyurus         38         161           Alopias superciliosus         39         125         Lobotes surinamensis         39         104           Alopias superciliosus         40         96         Kyphosus analogus         40         54           Ranzania laevis         41         89         Carcharhinus porosus         41         34           Mobula tarapacana         42         70         Remora remora         42         31           Lepidochelys olivacea         43         54         Tetrapturus angustirostris         43         30           Prionace glauca         44         54         54         Remora remora         45 </td <td>Isurus oxyrinchus</td> <td>32</td> <td>294</td> <td>Prionace glauca</td> <td>32</td> <td>277</td>   | Isurus oxyrinchus          | 32       | 294       | Prionace glauca            | 32   | 277       |  |  |
| Nobula thurstoni34208Mobula munkiana34203Balistes polylepis35183Aluterus scriptus35184Tetrapturus angustirostris36149Xiphias gladius36178Mobula japanica37137Alopias vulpinus37162Xiphias gladius38129Sectator ocyurus38161Alopias pelagicus39125Lobotes surinamensis39104Alopias superciliosus4096Kyphosus analogus4054Ranzania laevis4189Carcharhinus porosus4134Mobula tarapacana4270Remora remora4231Lepidochelys olivacea4354Tetrapturus angustirostris4330Prionace glauca4628Kyphosus elegans4616Remora remora4720Ablennes hians4714Exocoetus volitans4813Taractes rubescens4811Chelonia mydas498Carcharhinus longimanus497  | Sphyrna mokarran           | 33       | 222       | Carcharhinus limbatus      | 33   | 240       |  |  |
| Balistes polylepis35183Aluterus scriptus35184Tetrapturus angustirostris36149Xiphias gladius36178Mobula japanica37137Alopias vulpinus37162Xiphias gladius38129Sectator ocyurus38161Alopias pelagicus39125Lobotes surinamensis39104Alopias superciliosus4096Kyphosus analogus4054Ranzania laevis4189Carcharhinus porosus4134Mobula tarapacana4270Remora remora4231Lepidochelys olivacea4354Tetrapturus angustirostris4330Prionace glauca4450Myliobatidae4424Alopias vulpinus4628Kyphosus elegans4616Remora remora4720Ablennes hians4714Exocoetus volitans498Carcharhinus longimanus497   | Mobula thurstoni           | 34       | 208       | Mobula munkiana            | 34   | 203       |  |  |
| Tetrapturus angustirostris36149Xiphias gladius36178Mobula japanica37137Alopias vulpinus37162Xiphias gladius38129Sectator ocyurus38161Alopias pelagicus39125Lobotes surinamensis39104Alopias superciliosus4096Kyphosus analogus4054Ranzania laevis4189Carcharhinus porosus4134Mobula tarapacana4270Remora remora4231Lepidochelys olivacea4354Tetrapturus angustirostris4330Prionace glauca4450Myliobatidae4424Alopias vulpinus4628Kyphosus elegans4616Remora remora4720Ablennes hians4714Exocoetus volitans4813Taractes rubescens4811Chelonia mydas498Carcharhinus longimanus497  | Balistes polylepis         | 35       | 183       | Aluterus scriptus          | 35   | 184       |  |  |
| Mobula japanica37137Alopias vulpinus37162Xiphias gladius38129Sectator ocyurus38161Alopias pelagicus39125Lobotes surinamensis39104Alopias superciliosus4096Kyphosus analogus4054Ranzania laevis4189Carcharhinus porosus4134Mobula tarapacana4270Remora remora4231Lepidochelys olivacea4354Tetrapturus angustirostris4330Prionace glauca4536Lepidochelys olivacea4517Alopias vulpinus4628Kyphosus elegans4616Remora remora4720Ablennes hians4714Exocoetus volitans4813Taractes rubescens4811Chelonia mydas498Carcharhinus longimanus497  | Tetrapturus angustirostris | 36       | 149       | Xiphias gladius            | 36   | 178       |  |  |
| Xiphias gladius38129Sectator ocyurus38161Alopias pelagicus39125Lobotes surinamensis39104Alopias superciliosus4096Kyphosus analogus4054Ranzania laevis4189Carcharhinus porosus4134Mobula tarapacana4270Remora remora4231Lepidochelys olivacea4354Tetrapturus angustirostris4330Prionace glauca4450Myliobatidae4424Alopias vulpinus4628Kyphosus elegans4616Remora remora4720Ablennes hians4714Exocoetus volitans4813Taractes rubescens4811Chelonia mydas498Carcharhinus longimanus497  | Mobula japanica            | 37       | 137       | Alopias vulpinus           | 37   | 162       |  |  |
| Alopias pelagicus39125Lobotes surinamensis39104Alopias superciliosus4096Kyphosus analogus4054Ranzania laevis4189Carcharhinus porosus4134Mobula tarapacana4270Remora remora4231Lepidochelys olivacea4354Tetrapturus angustirostris4330Prionace glauca4450Myliobatidae4424Manta birostris4536Lepidochelys olivacea4517Alopias vulpinus4628Kyphosus elegans4616Remora remora4720Ablennes hians4714Exocoetus volitans4813Taractes rubescens4811Chelonia mydas498Carcharhinus longimanus497   | Xiphias gladius            | 38       | 129       | Sectator ocyurus           | 38   | 161       |  |  |
| Alopias superciliosus4096Kyphosus analogus4054Ranzania laevis4189Carcharhinus porosus4134Mobula tarapacana4270Remora remora4231Lepidochelys olivacea4354Tetrapturus angustirostris4330Prionace glauca4450Myliobatidae4424Manta birostris4536Lepidochelys olivacea4517Alopias vulpinus4628Kyphosus elegans4616Remora remora4720Ablennes hians4714Exocoetus volitans4813Taractes rubescens4811Chelonia mydas498Carcharhinus longimanus497  | Alopias pelagicus          | 39       | 125       | Lobotes surinamensis       | 39   | 104       |  |  |
| Ranzania laevis4189Carcharhinus porosus4134Mobula tarapacana4270Remora remora4231Lepidochelys olivacea4354Tetrapturus angustirostris4330Prionace glauca4450Myliobatidae4424Manta birostris4536Lepidochelys olivacea4517Alopias vulpinus4628Kyphosus elegans4616Remora remora4720Ablennes hians4714Exocoetus volitans4813Taractes rubescens4811Chelonia mydas498Carcharhinus longimanus497  | Alopias superciliosus      | 40       | 96        | Kyphosus analogus          | 40   | 54        |  |  |
| Mobula tarapacana4270Remora remora4231Lepidochelys olivacea4354Tetrapturus angustirostris4330Prionace glauca4450Myliobatidae4424Manta birostris4536Lepidochelys olivacea4517Alopias vulpinus4628Kyphosus elegans4616Remora remora4720Ablennes hians4714Exocoetus volitans4813Taractes rubescens4811Chelonia mydas498Carcharhinus longimanus497   | Ranzania laevis            | 41       | 89        | Carcharhinus porosus       | 41   | 34        |  |  |
| Lepidochelys olivacea4354Tetrapturus angustirostris4330Prionace glauca4450Myliobatidae4424Manta birostris4536Lepidochelys olivacea4517Alopias vulpinus4628Kyphosus elegans4616Remora remora4720Ablennes hians4714Exocoetus volitans4813Taractes rubescens4811Chelonia mydas498Carcharhinus longimanus497   | Mobula tarapacana          | 42       | 70        | Remora remora              | 42   | 31        |  |  |
| Prionace glauca4450Myliobatidae4424Manta birostris4536Lepidochelys olivacea4517Alopias vulpinus4628Kyphosus elegans4616Remora remora4720Ablennes hians4714Exocoetus volitans4813Taractes rubescens4811Chelonia mydas498Carcharhinus longimanus497  | Lepidochelys olivacea      | 43       | 54        | Tetrapturus angustirostris | 43   | 30        |  |  |
| Manta birostris4536Lepidochelys olivacea4517Alopias vulpinus4628Kyphosus elegans4616Remora remora4720Ablennes hians4714Exocoetus volitans4813Taractes rubescens4811Chelonia mydas498Carcharhinus longimanus497   | Prionace glauca            | 44       | 50        | Myliobatidae               | 44   | 24        |  |  |
| Alopias vulpinus4628Kyphosus elegans4616Remora remora4720Ablennes hians4714Exocoetus volitans4813Taractes rubescens4811Chelonia mydas498Carcharhinus longimanus497   | Manta birostris            | 45       | 36        | Lepidochelys olivacea      | 45   | 17        |  |  |
| Remora remora4720Ablennes hians4714Exocoetus volitans4813Taractes rubescens4811Chelonia mydas498Carcharhinus longimanus497   | Alopias vulpinus           | 46       | 28        | Kyphosus elegans           | 46   | 16        |  |  |
| Exocoetus volitans4813Taractes rubescens4811Chelonia mydas498Carcharhinus longimanus497  | Remora remora              | 47       | 20        | Ablennes hians             | 47   | 14        |  |  |
| Chelonia mydas 49 8 Carcharhinus longimanus 49 7   | Exocoetus volitans         | 48       | 13        | Taractes rubescens         | 48   | 11        |  |  |
|  | Chelonia mydas             | 49       | 8         | Carcharhinus longimanus    | 49   | 7         |  |  |

(Continued)

#### TABLE 2 | Continued

| F                         | AD sets |           | School sets            |      |  |  |
|---------------------------|---------|-----------|------------------------|------|--|--|
| Species                   | Rank    | Abundance | Species                | Rank |  |  |
| Rhincodon typus           | 50      | 8         | Chelonia mydas         | 50   |  |  |
| Belonidae                 | 51      | 7         | Diodontidae            | 51   |  |  |
| Carcharhinus obscurus     | 52      | 6         | Carcharhinus leucas    | 52   |  |  |
| Carcharhinus leucas       | 53      | 5         | Carcharhinus plumbeus  | 53   |  |  |
| Caretta caretta           | 54      | 5         | Caretta caretta        | 54   |  |  |
| Carcharhinus porosus      | 55      | 4         | Eretmochelys imbricata | 55   |  |  |
| Caranx caballus           | 56      | 3         | Ranzania laevis        | 56   |  |  |
| Carcharhinus brachyurus   | 57      | 3         |                        |      |  |  |
| Mobula munkiana           | 58      | 3         |                        |      |  |  |
| Sphyrna media             | 59      | 3         |                        |      |  |  |
| Ablennes hians            | 60      | 2         |                        |      |  |  |
| Carcharhinus altimus      | 61      | 2         |                        |      |  |  |
| Carcharhinus galapagensis | 62      | 2         |                        |      |  |  |
| Eretmochelys imbricata    | 63      | 2         |                        |      |  |  |
| Carangoides orthogrammus  | 64      | 1         |                        |      |  |  |
| Cubiceps capensis         | 65      | 1         |                        |      |  |  |
| Diodontidae               | 66      | 1         |                        |      |  |  |
| Masturus lanceolatus      | 67      | 1         |                        |      |  |  |
| Remora osteochir          | 68      | 1         |                        |      |  |  |



chlorophyll and current speed).

$$S = f1(Lon, Lat) + f2(SST) + f3(Chl) + f4(WT)$$
$$+ f5(month) + type$$

The estimated parameters for species richness and *p*-values are listed in **Table 3** and **Figure 4**. The model explained 44% of the variance with a R2 of 0.38 with 39179 samples. The individual contribution of the variables is showed in **Table 3**; where the most significant explanatory variables for the species richness was the area (35%, lat\*long) followed by set type (29%), chlorophyll

(21%) and SST (17.5%). The correlations between the variables are showed in Supplementary Material Figure 3. The distribution of residuals is showed in Supplementary Material Figure 4. The Normal Q-Q plot showed a normal distribution; as well as the relationship between fitted and response values. The good distribution of residuals suggests a correct identification of areas of high diversity.

Predictions from GAMs (mean, minimum, maximum and standard deviation) using testing data (20% of data) are shown in **Figure 5**. Predictions from GAMs by trimesters are shown in **Figure 6**.

The results showed higher diversity observed in FAD sets than in School sets. Diversity was higher at north of the Equator (0– 10°N) and at around 85–95°W and 120–140°W during May-November. Furthermore, highest richness values were found in areas with high sea surface temperatures (>25°C), high concentrations of chlorophyll (> 2 mg/m3), and velocities of the total current lower than 3 knots.

In order to relate Shannon diversity index with environmental variables in space and time, the final model includes Shannon diversity index as response variable, latitude and longitude as geographical variables (interaction), month as temporal variable, type of association as a factor and sea surface temperature, chlorophyll, gradient of the thermocline, sea level anomaly and velocity of the current as environmental variables.

$$SH = f1(Lon, Lat) + f2(SST) + f3(Chl) + f4(WT)$$
$$+ f5(Therm.Grad) + f6(SLA) + f7(month) + type$$

Gaussian model for Shannon diversity index explained 37.4% of the variance with a R2 of 0.37 with 30081 samples (**Table 3**). Results showed similar diversity patterns as with species richness (Supplementary Material Figure 5) and therefore, only models with species richness were represented. Similar to species richness, the most significant explanatory variables (based on the individual contribution of each variable) for the Shannon diversity index was the area (31%, lat\*long) followed by set type (27%), chlorophyll (19%), and SST (15%).

In general, predicted maps for both indices showed highest diversity around the Equatorial area and lowest diversity values were found along the Peru and California coast (**Figure 5** and Supplementary Material Figure 5). Based on the predicted maps from GAMs, large diversity in FAD sets seems to be around the Equatorial area and in School sets around the Costa Rica Dome (**Figure 7** and Supplementary Material Figure 5).

The evaluation of the models using Spearman's correlation showed a good model accuracy; with significant positive correlation between observed and predicted diversity for both indices (r = 0.62, p < 0.05 for Species richness index and r = 0.63, p < 0.05 for Shannon index). In contrast, Wilcoxon's signed-rank test showed significant *p*-values lower than 0.05 using the Species richness index, suggesting some bias in the model (Supplementary Material Table 2). The latter indicates that although the model is capable of describing the species richness of the bycatch species, the model overestimated and underestimated the observed values.

#### DISCUSSION

This study examined the diversity of the bycatch assemblages with a variety of measures using data collected by observer programs from tropical tuna purse seine fishery in FAD and School sets. Results showed a variety of diversity patterns (based on the number of species and abundances) as a function of the time of year and fishing mode. Furthermore, they provided new information about the habitat characteristics of these species in the eastern Pacific Ocean. We suggest that both fishing modes represent different assemblages and therefore, the structure, diversity and environment characteristics of these bycatch assemblages and the areas where these species are found are also different.

## **Alpha Diversity**

Species diversity of the bycatch assemblages could be a useful indicator, in conjunction with other ecosystem indicators, to monitor the ecosystem status and effect of the fishery in the ecosystem provided that a good sample size is available for a correct estimation of species diversity. Our results showed that the sample size used in this study with nearly 100% coverage rate was sufficient to find almost all species in FAD and School sets, as shown by the shape of the accumulation curves where the asymptote is reached. Although it is known that the number of species of the bycatch in FAD sets is higher than in School sets (Amandè et al., 2010; Torres-Irineo et al., 2014), our work suggests that the total number of bycatch species (and not the number of species per set) caught in the tropical tuna purse seiners is the same for both set types provided that sufficient sample size and the coverage rate is reached irrespective of the fishing mode.

As such, observer programs can provide the necessary information for diversity studies; but with limitations depending on the observer coverages. For example, lower sample size and coverage rate (around 10%) is available in other oceans and, therefore the results should be discussed taking into account the observer coverages. However, accumulation curves also showed that the asymptote was reached in some cases and, hence, species richness can be used as biodiversity measures in the Indian (Lezama-Ochoa et al., 2015) and Atlantic Ocean (Lezama-Ochoa et al., submitted). Differences in the number of the total observed species between fishing modes were more notable in the Indian and Atlantic Oceans, which could be explained by the lower coverage rate, especially for School sets, in these Oceans. Thus, sufficient observer coverage is needed to detect all the possible bycatch species in both types of fishing for biodiversity studies.

Our results suggest that Chao2 estimator, as used in the work of Torres-Irineo et al. (2014) and Lezama-Ochoa et al. (2015) is a good option for estimating the total species richness in both fishing modes. The Chao2 estimator showed that FAD and School sets could reach the asymptote with 71 and 68 species, respectively, which means that almost all species caught in the purse-seine fishery in the studied area were observed and the sample size was enough for obtaining bycatch diversity estimates. Chao2 non-parametric estimator is considered to be more accurate than parametric estimators or curve extrapolations (Gotelli and Colwell, 2011) to estimate total species richness (Chao, 1984). This is because it does not need any predetermined requirement as other models (Colwell and Coddington, 1994; Chao et al., 2005).

A evenly distributed species community is more diverse than a community with the same number of species but dominated by few species (Stirling and Wilsey, 2001). The shape of the log-abundance curves showed the same results than in Lezama-Ochoa et al. (2015) for both fishing modes in the Indian Ocean in



TABLE 3 | Summary results for the optimal GAMs selected for Species richness index and Shannon diversity index.

|                      | Species  | richness |            | Shannon index |         |            |  |  |
|----------------------|----------|----------|------------|---------------|---------|------------|--|--|
| Family               | Quasip   | oisson   |            | Gaussian      |         |            |  |  |
| Link function        | Lc       | og       |            | Ider          | ntity   |            |  |  |
| Adjusted R2          | 0.0      | 38       |            | 0.0           | 37      |            |  |  |
| Deviance explained   | 44       | %        |            | 37            | 4%      |            |  |  |
|                      | Estimate | p-value  | % Deviance | Estimate      | p-value | % Deviance |  |  |
| Latitude * Longitude | 28.673   | < 2e-16  | 35         | 28.368        | < 2e-16 | 30.60      |  |  |
| Month                | 7.494    | < 2e-16  | 9.39       | 7.859         | < 2e-16 | 7.19       |  |  |
| SST                  | 6.123    | < 2e-16  | 17.50      | 7.237         | < 2e-16 | 14.80      |  |  |
| Туре                 | 1.136    | < 2e-16  | 29.6       | 0.675         | < 2e-16 | 27.10      |  |  |
| Chlorophyll          | 8.753    | < 2e-16  | 20.60      | 8.128         | < 2e-16 | 18.70      |  |  |
| WT                   | 7.972    | < 2e-16  | 3.95       | 8.234         | 1.9e-14 | 3.50       |  |  |
| SLA                  | -        | -        | -          | 1             | 0.0217  | 3.74       |  |  |
| Therm.Grad           | -        | -        | -          | 3.969         | 0.0131  | 0.48       |  |  |

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

relation with the species abundance models. In general, the Logseries distribution (Zipf model) model describes communities with higher number of rare species than the Log-normal model does. Bycatch assemblages in FAD sets are formed by permanent species (species which are aggregated under FADs for hours or days) in the same habitat and evenly distributed (Magurran, 2004), in large and natural areas (Log-normal model). On the contrary, bycatch species in School sets are formed by different and rare species that migrate in oceans for reproductive or feeding activities with migratory species, such as tunas (Zipf-Mandelbrot model) (Lezama-Ochoa et al., 2015). The structure of these bycatch assemblages let us to infer that both fishing modes represent different assemblages and therefore, with different characteristics. Richness is commonly used as the sole measure of diversity, ignoring community evenness and species' relative abundances (Connolly et al., 2013). Log-abundance curves provide good information about the most common and rarest species; in our case, about bycatch species from the tropical tuna purse-seine fishery on the pelagic ecosystem. In this work, *Coryphaena hippurus*, was the bycatch species mostly caught in FAD sets and *Caranx sexfasciatus* in Free School sets. Species having life history strategies similar to the target species, such as teleost fishes ("r" strategist species), may not be affected to the same degree as those species with significantly different life history features, such as sharks ("k" strategist species) (Alverson, 1994). The most abundant species in this work are characterized by "r" strategies; with the exception of *Carcharhinus falciformis*,



which is normally caught in FAD sets and is considered a more vulnerable species. Technological developments to mitigate incidental catch of vulnerable species, such as *Carcharhinus falciformis* are necessary to achieve effective fishery management and reduce their mortalities (Gilman, 2011). For example, in recent years, their survival rate has been increased by using new methods developed for mitigating the capture of sharks and other vulnerable species (Gilman, 2011; Poisson et al., 2014) in purse seiners.

# Geographical and Habitat Characteristics of Bycatch Assemblages

Habitat distribution of pelagic communities normally match the distribution of water masses (Angel, 1993), but determination of the dominant factors influencing the distributions of these communities is difficult. In this work, GAMs contributed to relate diversity of the bycatch assemblages with the geographical and environmental conditions in the eastern Pacific Ocean.

Our results suggest that the geographical location and the type of set are the most important predictor variables to describe diversity for these species. Specifically, the highest predicted diversity of the bycatch species is on FAD sets compared to School sets. Differences found on diversity patterns between areas and fishing modes lead us to suggest that each bycatch species assemblage has different habitat characteristics. We observed a general diversity patterns on bycatch assemblages in both fishing modes. We found that bycatch assemblages are more diverse in equatorial areas in FAD sets and in warm coastal areas (Panama, Costa Rica and Nicaragua) in School sets (Figure 7). In contrast, the permanent coastal upwelling areas of California and Peru showed high productivity rates but low species diversity. These results, as described in Irigoien et al. (2004) and Sala and Knowlton (2006), showed that diversity in general in the open oceans, and particularly in the tropics, is lower at high disturbance levels and high productivity rates. More diverse communities are located in ecosystems with stable oceanographic conditions and less undisturbed (Cusson et al., 2014) (such



as equatorial and seasonal coastal upwelling systems of this work), whereas permanent coastal upwelling areas support high disturbance levels with short trophic chains and, therefore, less diversity.

Diversity patterns of bycatch assemblages in both fishing modes in the eastern tropical Pacific match reasonably well with the principal characteristics of its oceanography, hydrography and circulation (Fiedler and Talley, 2006; Kessler, 2006; Lavín et al., 2006; Pennington et al., 2006). In the case of the environmental variables, the sea surface temperature and chlorophyll were the environment predictors that better explained diversity patterns (Table 3). Concretely, the higher values of diversity could be related to water masses associated with seasonal coastal and equatorial upwelling processes. Thus, diversity patterns from the models indicated that bycatch assemblages in FAD sets could be associated with the equatorial tongue  $(10^{\circ}N-5^{\circ}S/120^{\circ}-140^{\circ}W)$  (from August to October) which is developed when the southeast trade winds are strongest during southern Winter (Wyrtki, 1981), with the North Equatorial Countercurrent, and with two physical features particularly significant in the Tropical Surface Water (TSW): the Equatorial Front (Fiedler and Talley, 2006) and the countercurrent thermocline ridge (along 10°N) (Ballance et al., 2006; Hoegh-Guldberg and Bruno, 2010).

All these sites are characterized by warm waters  $(>25^{\circ}C)$  with low-salinity and intermediate productivity concentrations, strong currents and with great biological significance, where marine predators and prey may aggregate during September-October.

In the case of the bycatch assemblages in School sets, results from the model (low thermocline gradients and high chlorophyll concentrations) lead us to suggest that highest species diversity could be associated with coastal upwelling regions around Costa Rica and Panama in the equatorial area (Costa Rica Dome and Gulf of Panama) ( $10-20^{\circ}$ S/80- $100^{\circ}$ W). Located within the warm pool and with low thermocline depth, these warm, productive and low-salinity waters are affected by the wind jets in winter (Pennington et al., 2006). Thus, winter northwesterly strong winds, most intense from November to March (Pennington et al., 2006; Change, 2007), induce upwelling of colder and



nutrient-rich waters to the surface, giving place to cool and very productive, but stable surface waters.

#### Importance of Ecosystem Indicators for Fisheries Management

Biodiversity indices provide information on trends in species diversity regarded as important by society and have potential to inform on progress toward established management objectives (Hutchings and Baum, 2005). In that sense, biodiversity is a concept with multiple meanings which can be measured in different ways (Buckland et al., 2005). In this work, we considered the number of species and the relative abundance of them as good measures to describe the biodiversity of the bycatch assemblages. Both types of fishing should be considered to estimate species diversity indices and patterns, as the integration of data from both fishing modes provides more complete information (spatially and temporally) than separately. Nonetheless, as more species are attracted to FADs due to species aggregative behavior, more specific works are necessary to understand the complete effect of the FAD fishery on the biodiversity of the bycatch at local (specific areas) and global (Oceans) scale.

Despite the fact that trends in biodiversity can vary enormously between areas or habitats, observer programs should be designed to monitor this spatial variation (Buckland et al., 2005). These differences in biodiversity between areas could be explained by the fact that some species are restricted to some areas but, in some cases, also as a consequence of the different fishing effort, time of year or many other possible factors, such as environmental events (e.g., ENSO cycle). The major limitation of this study is the use of fisheries-dependent data, which is focused on catching tuna, not bycatch species. Thus, diversity patters could be partially biased by the nature of the data and fishery behavior (Montero et al., 2016). Although in the Atlantic and Indian Oceans the observer coverage is low (around 10% of coverage rate) (Lewison et al., 2004), which can compromise the analysis and results (Lennert-Cody, 2001), the high coverage of the eastern Pacific Ocean increase the representativeness of the estimates. IATTC observer programs





in the eastern Pacific Ocean provide important information for evaluating spatial-temporal variability of fish assemblages and impacts of commercial fisheries on the most vulnerable species (Montero et al., 2016). In that sense, the IATTC purse-seine database covers a large area and period of years compared with the other Oceans, so the information about the species involved is of high quality and quantity; even considering the limitations mentioned above (Montero et al., 2016). Anyway, the inclusion of fisheries independent data would considerable contributes to improve the conclusions of this study.

## CONCLUSION

This work has improved our understanding of diversity and habitat characteristics of the bycatch assemblages in the eastern Pacific Ocean. Indicators based on the number of species in a community and the relative abundance of them (richness and evenness) were calculated. Moreover, diversity and the environmental characteristics of the bycatch species in the eastern Pacific Ocean were explained based on both fishing modes (i.e., FAD and School sets). The prediction of diversity was good, with 40% of the variation explained by the models. Modeling the biodiversity of bycatch using data from observer programs provide new and useful information for future management plans. This study contributed to the understanding and integration of different components of the ecosystem in order to progress in the implementation an Ecosystem Approach Fishery Management.

#### REFERENCES

- Akaike, H. (1974). A new look at the statistical model identification. *Autom. Contr. IEEE Trans.* 19, 716–723. doi: 10.1109/TAC.1974.1100705
- Alverson, D. L. (1994). A Global Assessment of Fisheries Bycatch and Discards. FAO Fisheries Technical Paper. Rome: Food & Agriculture Org.
- Amandè, M. J., Ariz, J., Chassot, E., De Molina, A. D., Gaertner, D., Murua, H., et al. (2010). Bycatch of the European purse seine tuna fishery in the Atlantic Ocean for the 2003–2007 period. *Aquat. Living Resour.* 23, 353–362. doi: 10.1051/alr/2011003
- Angel, M. V. (1993). Biodiversity of the pelagic ocean. Conserv. Biol. 7, 760–772. doi: 10.1046/j.1523-1739.1993.740760.x
- Arrizabalaga, H., Murua, H., and Majkowski, J. (2012). Global status of tuna stocks: summary sheets. *Rev. Invest. Mar.* 19, 645–676.
- Ballance, L. T., Pitman, R. L., and Fiedler, P. C. (2006). Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: a review. *Prog. Oceanogr.* 69, 360–390. doi: 10.1016/j.pocean.2006.03.013
- Buckland, S., Magurran, A., Green, R., and Fewster, R. (2005). Monitoring change in biodiversity through composite indices. *Philos. Trans. R. Soc. B Biol. Sci.* 360, 243–254. doi: 10.1098/rstb.2004.1589
- Change, I. P. O. C. (2007). Climate Change 2007: The Physical Science Basis. Paris: Agenda 6, 333.
- Chao, A. (1984). Nonparametric estimation of the number of classes in a population. *Scand. J. Stat.* 11, 265–270.
- Chao, A., Chazdon, R. L., Colwell, R. K., and Shen, T. J. (2005). A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecol. Lett.* 8, 148–159. doi: 10.1111/j.1461-0248.2004. 00707.x
- Coleman, B. D., Mares, M. A., Willig, M. R., and Hsieh, Y.-H. (1982). Randomness, area, and species richness. *Ecology* 63, 1121–1133. doi: 10.2307/19 37249

## **AUTHOR CONTRIBUTIONS**

NL, HM, MH, MR, JR, NV, AC, and IS designed research; NL, HM, and MH performed research; NL analyzed data; and NL, HM, MH, and AC wrote the paper.

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#### SUPPLEMENTARY MATERIAL

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- Colwell, R. K., and Coddington, J. A. (1994). Estimating terrestrial biodiversity through extrapolation. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 345, 101–118. doi: 10.1098/rstb.1994.0091
- Connolly, J., Bell, T., Bolger, T., Brophy, C., Carnus, T., Finn, J. A., et al. (2013). An improved model to predict the effects of changing biodiversity levels on ecosystem function. J. Ecol. 101, 344–355. doi: 10.1111/1365-2745.12052
- Cullis-Suzuki, S., and Pauly, D. (2010). Failing the high seas: a global evaluation of regional fisheries management organizations. *Mar. Policy* 34, 1036–1042. doi: 10.1016/j.marpol.2010.03.002
- Cusson, M., Crowe, T. P., Araújo, R., Arenas, F., Aspden, R., Bulleri, F., et al. (2014). Relationships between biodiversity and the stability of marine ecosystems: comparisons at a European scale using meta-analysis. J. Sea Res. 98, 5–14. doi: 10.1016/j.seares.2014.08.004
- Dayton, P. K., Thrush, S. F., Agardy, M. T., and Hofman, R. J. (1995). Environmental effects of marine fishing. Aqua. Conserv. 5, 205–232. doi: 10.1002/aqc.3270050305
- Duffy, L. M., Olson, R. J., Lennert-Cody, C. E., Galván-Magaña, F., Bocanegra-Castillo, N., and Kuhnert, P. M. (2015). Foraging ecology of silky sharks, *Carcharhinus falciformis*, captured by the tuna purse-seine fishery in the eastern Pacific Ocean. *Mar. Biol.* 162, 571–593. doi: 10.1007/s00227-014-2606-4
- Elith, J., and Leathwick, J. R. (2009). Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol. Evol. Syst. 40, 677–697. doi: 10.1146/annurev.ecolsys.110308.120159
- Fiedler, P. C. (1992). Seasonal Climatologies and Variability of Eastern Tropical Pacific Surface Waters. NOAA/National Marine Fisheries Service, NOAA Technical Report NMFS, 109.
- Fiedler, P. C., and Talley, L. D. (2006). Hydrography of the eastern tropical Pacific: a review. *Prog. Oceanogr.* 69, 143–180. doi: 10.1016/j.pocean.2006.03.008
- Garcia, S. M. (2003). The Ecosystem Approach to Fisheries: Issues, Terminology, Principles, Institutional Foundations, Implementation and Outlook. FAO Fisheries Technical Paper. Rome: Food & Agriculture Org.

- Gilman, E. L. (2011). Bycatch governance and best practice mitigation technology in global tuna fisheries. *Mar. Policy* 35, 590–609. doi: 10.1016/j.marpol.2011.01.021
- Gotelli, N. J., and Colwell, R. K. (2011). Estimating species richness. *Biol. Divers.* 12, 39–54.
- Greenstreet, S. P., and Rogers, S. I. (2006). Indicators of the health of the North Sea fish community: identifying reference levels for an ecosystem approach to management. *ICES J. Mar. Sci.* 63, 573–593. doi: 10.1016/j.icesjms.2005.12.009
- Guisan, A., Edwards, T. C. Jr., and Hastie, T. (2002). Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecol. Modell.* 157, 89–100. doi: 10.1016/S0304-3800(02)00204-1
- Hall, M. A., Alverson, D. L., and Metuzals, K. I. (2000). By-catch: problems and solutions. *Mar. Pollut. Bull.* 41, 204–219. doi: 10.1016/S0025-326X(00)00111-9
- Hall, M., and Roman, M. (2013). Bycatch and Non-Tuna Catch in the Tropical Tuna Purse Seine Fisheries of the World. FAO Fisheries and Aquaculture Technical Paper 568.

Hastie, T. J., and Tibshirani, R. J. (1990). Generalized Additive Models. CRC Press.

- Hoegh-Guldberg, O., and Bruno, J. F. (2010). The impact of climate change on the world's marine ecosystems. *Science* 328, 1523–1528. doi: 10.1126/science.1189930
- Hutchings, J. A., and Baum, J. K. (2005). Measuring marine fish biodiversity: temporal changes in abundance, life history and demography. *Philos. Trans. R. Soc. B Biol. Sci.* 360, 315–338. doi: 10.1098/rstb.2004.1586
- IATTC (2010). Inter-American Tropical Tuna Commission (IATTC). 2010. Fishery Status Report n 7. La Jolla, CA: IATTC.
- IATTC (2015). Inter-American Tropical Tuna Commission (IATTC). 2015. Annual Report. La Jolla, CA: IATTC.
- Irigoien, X., Huisman, J., and Harris, R. P. (2004). Global biodiversity patterns of marine phytoplankton and zooplankton. *Nature* 429, 863–867. doi: 10.1038/nature02593
- Kessler, W. S. (2006). The circulation of the eastern tropical Pacific: a review. Prog. Oceanogr. 69, 181–217. doi: 10.1016/j.pocean.2006.03.009
- Kindt, R., and Coe, R. (2005). Tree Diversity Analysis: A Manual and Software for Common Statistical Methods for Ecological and Biodiversity Studies. Nairobi: World Agroforestry Centre.

Kindt, R., and Kindt, M. R. (2015). Package BiodiversityR.

- Kohavi, R. (1995). "A study of cross-validation and bootstrap for accuracy estimation and model selection," in *Proceedings of the 14th International Joint Conference of Artificial Intelligence (IJCAI)*, Vol. 2, (Montreal, QC: Morgan Kaufmann), 1137–1145.
- Lauria, V., Vaz, S., Martin, C. S., Mackinson, S., and Carpentier, A. (2011). What influences European plaice (*Pleuronectes platessa*) distribution in the eastern English Channel? Using habitat modelling and GIS to predict habitat utilization. *ICES J. Mar. Sci.* 68, 1500–1510. doi: 10.1093/icesjms/fsr081
- Lavín, M. F., Fiedler, P. C., Amador, J. A., Ballance, L. T., Färber-Lorda, J., and Mestas-Nuñez, A. M. (2006). A review of eastern tropical Pacific oceanography: summary. *Prog. Oceanogr.* 69, 391–398. doi: 10.1016/j.pocean.2006.03.005
- Lennert-Cody, C. (2001). Effects of sample size on bycatch estimation using systematic sampling and spatial post-stratification: summary of preliminary results. *IOTC Proc.* 4, 48–53.
- Lewison, R. L., Crowder, L. B., Read, A. J., and Freeman, S. A. (2004). Understanding impacts of fisheries bycatch on marine megafauna. *Trends Ecol. Evol.* 19, 598–604. doi: 10.1016/j.tree.2004.09.004
- Lezama-Ochoa, N. (2016). Biodiversity and Habitat Preferences of the By-Catch Communities from the Tropical Tuna Purse-Seine Fishery in the Pelagic Ecosystem: The Case of the Indian, Pacific and Atlantic Oceans. PhD Thesis. Department of Zoology and Animal Cell Biology, University of the Basque Country, 282.
- Lezama-Ochoa, N., Murua, H., Chust, G., Ruiz, J., Chavance, P., de Molina, A. D., et al. (2015). Biodiversity in the by-catch communities of the pelagic ecosystem in the Western Indian Ocean. *Biodivers. Conserv.* 24, 2647–2671. doi: 10.1007/s10531-015-0951-3
- Link, J. (2010). Ecosystem-Based Fisheries Management: Confronting Tradeoffs. New York, NY: Cambridge University Press.
- Lopez, J., Moreno, G., Lennert-Cody, C., Maunder, M., Sancristobal, I., Caballero, A., et al. (2017). Environmental preferences of tuna and non-tuna species associated with drifting fish aggregating devices (DFADs) in the Atlantic Ocean,

ascertained through fishers' echo-sounder buoys. Deep Sea Res. II Top. Stud. Oceanogr. 140, 127–138. doi: 10.1016/j.dsr2.2017.02.007

- Magurran, A. E. (2004). Measuring Biological Diversity. Cornwall: Blackwell.
- Magurran, A. E., and McGill, B. J. (2011). Biological Diversity: Frontiers In Measurement And Assessment. New York, NY: Oxford University Press.
- Montero, J. T., Martinez-Rincon, R. O., Heppell, S. S., Hall, M., and Ewal, M. (2016). Characterizing environmental and spatial variables associated with the incidental catch of olive ridley (*Lepidochelys olivacea*) in the Eastern Tropical Pacific purse-seine fishery. *Fish. Oceanogr.* 25, 1–14. doi: 10.1111/fog.12130
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R., et al. (2013). *Package 'vegan*.' R Packag Version.
- Oliver, I., and Beattie, A. J. (1996). Designing a cost-effective invertebrate survey: a test of methods for rapid assessment of biodiversity. *Ecol. Appl.* 6, 594–607. doi: 10.2307/2269394
- Olson, R. J., Duffy, L. M., Kuhnert, P. M., Galván-Magaña, F., Bocanegra-Castillo, N., and Alatorre-Ramírez, V. (2014). Decadal diet shift in yellowfin tuna Thunnus albacares suggests broad-scale food web changes in the eastern tropical Pacific Ocean. *Mar. Ecol. Prog. Ser.* 497, 157–178. doi: 10.3354/meps10609
- Olson, R. J., Popp, B. N., Graham, B. S., López-Ibarra, G. A., Galván-Magaña, F., Lennert-Cody, C. E., et al. (2010). Food-web inferences of stable isotope spatial patterns in copepods and yellowfin tuna in the pelagic eastern Pacific Ocean. *Prog. Oceanogr.* 86, 124–138. doi: 10.1016/j.pocean.2010.04.026
- Pennington, J. T., Mahoney, K. L., Kuwahara, V. S., Kolber, D. D., Calienes, R., and Chavez, F. P. (2006). Primary production in the eastern tropical Pacific: a review. *Prog. Oceanogr.* 69, 285–317. doi: 10.1016/j.pocean.2006.03.012
- Pielou, E. (1975). Ecology Diversity. New York, NY: Wiley, J. and Sons.
- Pikitch, E. K., Santora, C., Babcock, A., Bakun, E. A., Bonfil, R., Conover, D. O., et al. (2004). Ecosystem-based fishery management. *Science* 305, 346–347. doi: 10.1126/science.1098222
- Poisson, F., Séret, B., Vernet, A.-L., Goujon, M., and Dagorn, L. (2014). Collaborative research: Development of a manual on elasmobranch handling and release best practices in tropical tuna purse-seine fisheries. *Mar. Policy* 44, 312–320. doi: 10.1016/j.marpol.2013.09.025
- R Core Team (2016). R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing.
- Reese, G. C., Wilson, K. R., and Flather, C. H. (2014). Performance of species richness estimators across assemblage types and survey parameters. *Global Ecol. Biogeogr.* 23, 585–594. doi: 10.1111/geb.12144
- Sala, E., and Knowlton, N. (2006). Global marine biodiversity trends. Annu. Rev. Environ. Resour. 31, 93–122. doi: 10.1146/annurev.energy.31.020105. 100235
- Scott, M. D., Chivers, S. J., Olson, R. J., Fiedler, P. C., and Holland, K. (2012). Pelagic predator associations: tuna and dolphins in the eastern tropical Pacific Ocean. *Mar. Ecol. Prog. Ser.* 458, 283–302. doi: 10.3354/meps09740
- Shannon, C. E., and Weaver, W. (1949). Themathematical Theory of Communication. Urbana: University of Illinois Press.
- Smeets, E., Weterings, R., and voor Toegepast-Natuurwetenschappelijk, N. C. O. (1999). Environmental *Indicators: Typology and Overview*. Copenhagen: European Environment Agency Copenhagen.
- Stirling, G., and Wilsey, B. (2001). Empirical relationships between species richness, evenness, and proportional diversity. Am. Nat. 158, 286–299. doi: 10.1086/321317
- Torres-Irineo, E., Amandè, M. J., Gaertner, D., de Molina, A. D., Murua, H., Chavance, P., et al. (2014). Bycatch species composition over time by tuna purse-seine fishery in the eastern tropical Atlantic Ocean. *Biodivers. Conserv.* 23, 1157–1173. doi: 10.1007/s10531-014-0655-0
- Whittaker, R. H. (1965). Dominance and Diversity in Land Plant Communities Numerical relations of species express the importance of competition in community function and evolution. *Science* 147, 250–260. doi: 10.1126/science.147.3655.250
- Wilson, J. B. (1991). Methods for fitting dominance/diversity curves. J. Vegetation Sci. 2, 35–46. doi: 10.2307/3235896
- Wood, S. (2006). Generalized Additive Models: An Introduction with R. Boca Ratón, FL: CRC Press.
- Wood, S., and Wood, M. S. (2007). *The Mgcv Package*. Available online at: www. r-project. org.

- Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., et al. (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science* 314, 787–790. doi: 10.1126/science.1132294
- Worm, B., Sandow, M., Oschlies, A., Lotze, H. K., and Myers, R. A. (2005). Global patterns of predator diversity in the open oceans. *Science* 309, 1365–1369. doi: 10.1126/science.1113399
- Wyrtki, K. (1981). An estimate of equatorial upwelling in the Pacific. J. Phys. Oceanogr. 11, 1205–1214.
- Zhu, J., Dai, X., and Chen, Y. (2011). Species composition and diversity of pelagic fishes based on a longline fishery catch in the North Pacific Ocean. *Chin. J. Oceanol. Limnol.* 29, 261–269. doi: 10.1007/s00343-011-0122-7

**Conflict of Interest Statement:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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