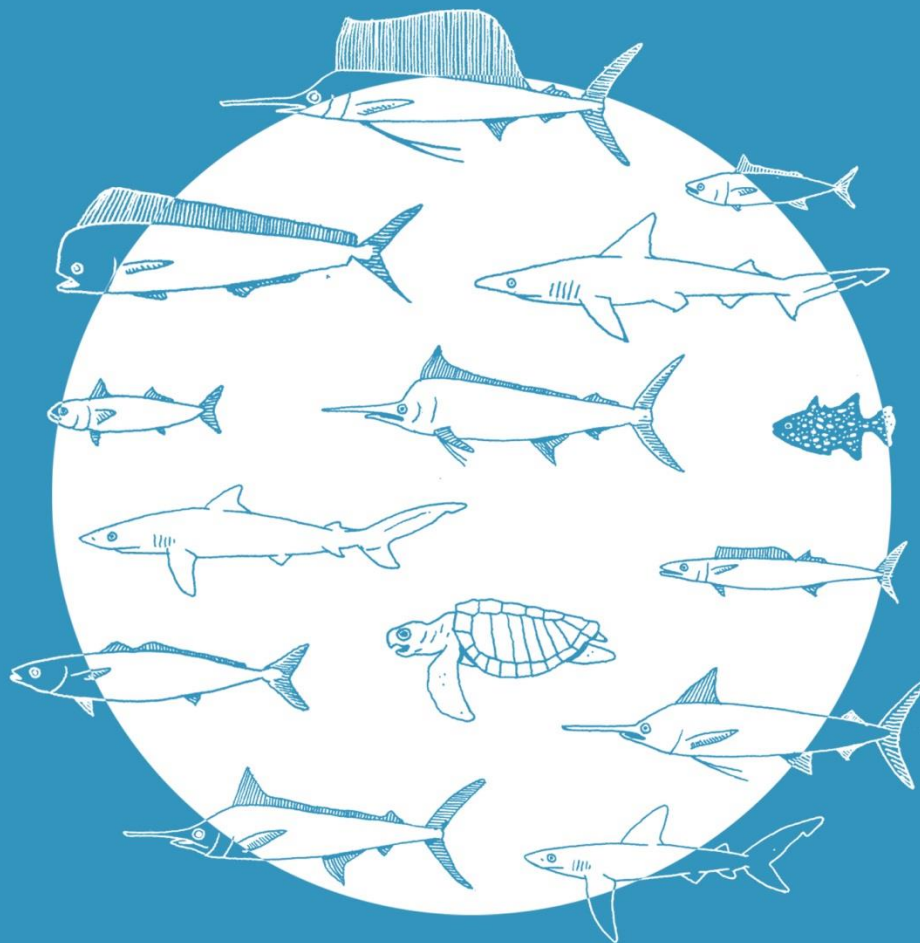


Biodiversity and habitat preferences of the by-catch communities from
the tropical tuna purse-seine fishery in the pelagic ecosystem:
The case of the Indian, Pacific and Atlantic Ocean

Nerea Lezama Ochoa



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**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 Ocean**

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Nerea Lezama-Ochoa

Thesis Director

Dr. Hilario Murua

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*A Saioa y Ainhoa:
mi fuerza sobre las olas,
mi viento del Norte,
mi esperanza envuelta en salitre*

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" The cure for anything is salt water – sweat, tears, or the sea."
– Isak Dinesen, Writer

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RESÚMEN

La pesquería de cerco de atún tropical, principalmente centrada en la pesca de rabil (*Thunnus albacares*), listado (*Katsuwonus pelamis*) y patudo (*Thunnus obesus*), es la más importante en términos de capturas de túnidos tropicales a nivel mundial en todos los océanos (60% del total de las capturas mundiales) (Murua, 2015). Además de los túnidos tropicales, al igual que en otras pesquerías, se capturan especies llamadas “by-catch” o especies de captura incidental, tales como peces espada, tortugas, manta-rayas, tiburones, etc.. (Hall, 1996), lo que puede afectar a la estructura, funcionalidad y biodiversidad del ecosistema marino pelágico. La mortalidad de las especies “by-catch”, puede llevar a la sobre-explotación de sus especies más vulnerables debido a sus características biológicas (largos ciclos de vida, tasas de crecimiento lentas y bajos potenciales reproductivos) (Lewison et al. 2004). La principal consecuencia debido a la mortalidad de estas especies es la disminución de sus poblaciones (Cook, 2003), pero también los cambios asociados que pueden ocurrir a nivel de comunidad y ecosistema, los cuales son más difíciles de detectar (Lewison, 2004). De este modo, el papel que juegan los grandes vertebrados marinos en la estructura de la cadena alimentaria en el ecosistema pelágico es muy importante y cualquier cambio puede modificar su abundancia y composición de especies lo que conlleva una pérdida de biodiversidad (Alverson, 1994; Cook, 2003).

A pesar de los esfuerzos realizados por la flota en tratar de minimizar las interacciones de las especies de captura incidental con la pesquería, así como de incrementar su supervivencia post-captura, la interacción, aunque pequeña, persiste. Además, la introducción de los Dispositivos Concentrados de Peces (DCPs) en la pesquería de cerco tropical a partir de 1990, intensifica aún más este problema. Esto ha provocado que todas las investigaciones sobre capturas incidentales hayan aumentado en los últimos años- sobre todo las que se centran en mitigación y conservación- y que la reducción de su mortalidad y estudio de su diversidad se haya convertido en una prioridad para las Organizaciones Regionales de Ordenación Pesquera (OROP) atuneras. Sin embargo, los estudios publicados sobre biodiversidad del ecosistema pelágico y el hábitat de las especies de captura incidental de la pesquería de cerco tropical son escasos. Los estudios más relevantes publicados hasta la fecha incluyen diferentes niveles de diversidad marina (especies y/o hábitats) (Gaertner et al., 2008; Gerrodette et al., 2012; Sequeira et al., 2012; Torres-Irineo et al., 2014), pero no incluyen descripciones y preferencias de hábitat (a nivel de comunidad) de una manera más integrada y global, ni comparaciones entre océanos; concretamente entre el Océano Índico, Atlántico y Pacífico.

Una de las principales causas de esta falta de información es que la investigación sobre la pesquería de cerco tropical siempre se ha centrado en estudiar y evaluar poblaciones de especies individualmente, así como estudiar la mitigación de la interacción de las especies de by-catch pero sin prestar demasiada atención a la posibilidad de estudiar el tema de la biodiversidad pelágica con los datos obtenidos por los observadores. A pesar de que las investigaciones centradas en una sola especie pueden proporcionar información muy útil sobre la dinámica poblacional, este tipo de estudios raramente proporciona señales sobre los cambios de biodiversidad de las especies a escala global o del impacto que produce la pesquería sobre el hábitat.

Esto que ha sido una pauta general en la investigación pesquera, ha llevado que en los últimos años se haya evolucionado hacia un nuevo enfoque de gestión de la pesca, llamado “Enfoque Ecosistémico en la Gestión de la Pesca” (ESGP); un concepto que surgió de la relación entre la gestión de los ecosistemas y la pesca, con el objetivo de asegurar la sostenibilidad de todo el ecosistema. Así, es considerada como una herramienta útil para evaluar y gestionar la estructura y la función de los ecosistemas marinos, incluyendo su biodiversidad (donde estarían enmarcadas las especies de captura incidental) de una manera más integrada y holística (Motos and Wilson 2006). Esto permite que todos sus componentes sean considerados e integrados en un marco común y, por ende, una gestión más correcta de la pesca.

Sin embargo, no es una tarea nada fácil describir la biodiversidad en un área tan inmensa y compleja como es el ecosistema pelágico, y por lo tanto, hay una falta general de conocimiento sobre cuál es la mejor manera de medir y analizar la composición, estructura y las características del hábitat de las comunidades de especies de captura incidental en la pesquería de cerco tropical.

Como se describe en la **introducción** de esta tesis, una de las mejores opciones es la aplicación de indicadores de biodiversidad, tales como medidas de diversidad y modelos, que ayuden a explorar los patrones de diversidad y la distribución potencial de hábitat de esta comunidad de especies. La Directiva Marco sobre la Estrategia Marina (DMEM) adoptada por la Comisión Europea en 2008, desarrolló por ejemplo un conjunto de once descriptores e indicadores para alcanzar un buen estado ambiental del océano y contribuir a una gestión de las aguas marinas basada en los ecosistemas (Bourlat et al. 2013). Entre estos descriptores, el descriptor “Diversidad Biológica” (D1), incluye indicadores tales como “patrones de distribución” o “composición del ecosistema” (hábitats y especies). Concretamente, este tipo de indicadores pueden ser utilizados para describir las diferencias que puede haber en el número de especies y/o abundancia en el espacio y tiempo, o para comparar la diversidad entre diferentes áreas de pesca (Motos and Wilson, 2006).

El estudio desarrollado en esta Tesis surge principalmente de la falta de información sobre la biodiversidad y hábitat de las especies del ecosistema pelágico que son capturadas incidentalmente por la pesquería de cerco de atún tropical y por la necesidad de avanzar hacia un enfoque ecosistémico de las pesquerías cambiando las ideas preconcebidas hasta ahora sobre el manejo de pesquerías. A fin de satisfacer esta necesidad, esta Tesis explora diferentes medidas de diversidad y modelos de distribución y/o de hábitat en relación tanto a factores abióticos (tipo de lance) como bióticos (oceanografía, cambio climático).

Los principales **objetivos** de esta tesis doctoral son:

- 1) Describir la diversidad Alpha (riqueza y uniformidad) y Beta (diferencias en la composición de especies entre áreas) de las comunidades de captura incidental en el Océano Indico Occidental, el Océano Atlántico Oriental y el Océano Pacífico Oriental en los dos principales tipos de pesca (Lances sobre Dispositivos Concentradores de Peces (DCPs) y Lances a Banco Libre) de los atuneros congeladores tropicales;
- 2) Explorar las preferencias espaciales, temporales y oceanográficas de las comunidades de especies de captura incidental que contribuyen a explicar sus patrones de diversidad en el Océano Indico Occidental, el Océano Atlántico Oriental y el Océano Pacífico Oriental en los dos principales tipos de pesca (Lances sobre Dispositivos Concentradores de Peces (DCPs) y Lances a Banco Libre) de los atuneros congeladores tropicales;
- 3) Describir el hábitat potencial de las especies de captura incidental *Carcharhinus falciformis* (tiburón sedoso) y *Canthidermis maculata* (pez ballesta) y evaluar sus posibles cambios de distribución bajo el escenario de cambio climático A2 en los tres océanos.

Dichos objetivos han sido estudiados en cuatro capítulos diferentes.

En el **capítulo 1** estudiamos la diversidad de las comunidades de especies de captura incidental, analizando tanto su estructura como composición y su relación con variables ambientales en el Océano Indico Occidental entre 2003 y 2010 utilizando diferentes medidas de diversidad y Modelos Aditivos Generalizados en los dos tipos de lances. Los análisis mostraron que los lances sobre DCPs podrían usarse como observatorios de biodiversidad en combinación con los lances a Banco Libre para estudiar las comunidades de especies de captura incidental en el ecosistema pelágico tropical. En general, obtuvimos que las comunidades de especies observadas en DCPs

son más diversas, con mayor número de especies y más uniformemente distribuidas que las comunidades de especies observadas en lances a Banco Libre. Además, la composición de especies en lances sobre DCPs parece estar correlacionada, y por lo tanto, explicada por factores ambientales. Los modelos sugirieron que la mayor diversidad está relacionada con el afloramiento costero de Somalia durante el monzón de verano (relacionada con la corriente de Somalia) y con la circulación de remolinos en el Canal de Mozambique durante el monzón de invierno. Ambas áreas concentran altas cantidades de nutrientes como consecuencia de sus procesos oceanográficos sustentando una gran diversidad en la zona.

En el **capítulo 2** estudiamos los patrones de diversidad y las preferencias ambientales de las comunidades de captura incidental en diferentes áreas del Océano Pacífico Oriental entre 1993 y 2011 usando diferentes medidas de diversidad y Modelos Aditivos Generalizados. Los principales resultados mostraron que el número total de especies observadas en lances sobre DCPs y en lances a Banco Libre fue similar (tal y como lo muestran las curvas de acumulación y en contra de lo tradicionalmente pensado) y que el tamaño de muestra y la tasa de cobertura de observación (con una cobertura del 100%) fue la causa de este descubrimiento; jugando un papel esencial para la correcta estimación de diversidad y aportando robustez a los resultados. Sin embargo, aunque en número total observado de especies es similar en los dos tipos de lances, la diversidad (basada en el índice de riqueza y el índice de diversidad de Shannon) fue mayor en lances sobre DCPs que en lances a Banco Libre. En general, encontramos que hay mayor diversidad al norte de la zona ecuatorial y alrededor del Golfo de Panamá que en los afloramientos costeros permanentes de Perú y California; los cuales sustentan una alta productividad pero baja diversidad al tratarse de sistemas altamente inestables y energéticos. Concretamente, la diversidad se relacionó directamente con el afloramiento estacional ecuatorial, el sistema Frontal y el domo de Costa Rica en los lances sobre DCPs y con el afloramiento estacional costero de Panamá en los lances a Banco Libre. Variables como la temperatura, salinidad, clorofila y profundidad de la termoclina jugaron un papel esencial para explicar la distribución de hábitat de estas comunidades en ambos tipos de lances.

En el **capítulo 3** estudiamos la biodiversidad de las comunidades de especies de captura incidental y sus preferencias ambientales en el Océano Atlántico Oriental entre 2003 y 2011 y concluimos que dichas comunidades se mostraron más diversas (con mayor número de especies y más uniformemente distribuidas) en lances realizados sobre Dispositivos Concentradores de Peces

(DCPs) que en lances a Banco Libre. Además, los patrones de diversidad observados con los modelos de distribución entre los dos tipos de lances variaron acorde con las características oceanográficas concretas del Océano Atlántico. Así, la corriente superficial ecuatorial del norte y los sistemas termales, como el domo de Guinea y el domo de Angola explicaron la distribución de la diversidad de las comunidades de especies de captura incidental en los lances sobre DCPs. Por otro lado, esta diversidad pareció estar relacionada con los sistemas de afloramiento estacional costero cerca de Senegal y basado en la estrategia de pesca en los lances realizados a Banco Libre.

En el **capítulo 4** estudiamos el hábitat potencial del tiburón sedoso, catalogado como vulnerable (www.iucn.org) (*Carcharhinus falciformis*) y el pez ballesta (*Canthidermis maculata*) normalmente descartado en el Océano Indico, Atlántico y Pacífico usando el modelo de hábitat de Máxima Entropía (MaxEnt) y utilizando las ocurrencias de las especies obtenidas de los programas de observadores. Además, también fue analizado la contribución relativa de diferentes variables ambientales y el impacto del cambio climático sobre la distribución de estas especies bajo el escenario climático A2 (escenario con concentraciones medias de dióxido de carbono de 856 ppm para el año 2100). Los resultados mostraron que estas dos especies se distribuyen potencialmente y con mayor probabilidad de ocurrencia alrededor de la banda ecuatorial, cerca de algunos afloramientos costeros en los tres océanos y en relación con las principales zonas de pesca.

La temperatura superficial del mar fue la variable que mayormente contribuyó a explicar la distribución de hábitat de las dos especies en los tres océanos. Bajo el escenario de cambio climático A2, el mayor cambio del hábitat presente se observó en el Océano Atlántico (alrededor de 16% para las dos especies), mientras que dicho cambio fue menor en los otros dos océanos. Ambas especies podrían perder hábitat alrededor de Somalia, la banda ecuatorial Atlántica y el área de afloramiento costero de Perú. Mientras, las dos especies de captura incidental podrían ganar hábitat en el sistema de Benguela, la zona al sur del ecuador en el Océano Índico y la costa de América Central como consecuencia del calentamiento global.

Finalmente, en la **discusión general**, los resultados obtenidos en los diferentes capítulos son analizados de forma integrada (describiendo diferencias y similitudes entre océanos) y en relación con los objetivos establecidos en esta tesis. En general, los resultados de esta Tesis apoyan la idea de que la diversidad (tanto en el número de especies como en abundancia relativa) de las comunidades de especies de captura incidental en este tipo de pesquería es variable en el espacio y tiempo, mostrando preferencia por diferentes variables oceanográficas dependiendo del tipo de

pesca y del océano. Concretamente, la diversidad de esta comunidad de especies (estudiada con la diversidad Alpha) es mayor en DCPs que en Lances a Banco Libre en los tres océanos. La estructura de las comunidades (estudiadas en el **capítulo 1, 2 y 3** ajustando las curvas de abundancia a modelos de distribución de especies) parece ser la misma en los tres océanos en lances sobre DCPs (explicadas con el modelo Log-normal) y en lances a Banco Libre (explicadas con el modelo Zipf-mandelbrot). La composición de especies (estudiada con la diversidad Beta) depende del tipo de lance y las características oceanográficas de cada océano. Los Modelos Generalizados Aditivos muestran que la temperatura superficial del mar y la clorofila podrían ser consideradas como los principales factores que explican la diversidad en los dos tipos de lances en términos de preferencias de hábitat; mostrando relación directa con zonas de afloramiento y regiones cálidas. Esta Tesis también muestra que el tamaño de muestreo y la tasa de cobertura de observación juegan un papel muy importante en la correcta estimación de la diversidad de especies de captura incidental; tal y como se muestra en el **capítulo 2** en el Océano Pacífico Oriental en relación a la estimación total del número de especies por tipo de lance. Así, para la correcta implementación de futuras medidas de conservación y aplicación del enfoque ecosistémico, los estudios de biodiversidad deben tener datos suficientes y de calidad. Finalmente, esta Tesis también contribuye a explicar que el hábitat de algunas especies de captura incidental puede verse afectado como consecuencia del cambio climático.

En **conclusión**, los estudios desarrollados en el marco de esta Tesis doctoral proporcionan nueva información acerca de la estructura, diversidad y las preferencias de hábitat de las comunidades de especies de captura incidental de la pesquería de cerco de atún tropical en los Océanos Índico, Atlántico y Pacífico. Dicha información puede ser de gran apoyo para la futura implementación de un “Enfoque Ecosistémico de la Gestión de la Pesca” (EFP), dejando atrás la idea de la gestión individual de las especies y considerando tanto a las especies como a su hábitat dentro de un mismo marco de gestión. Así, los problemas de pérdida de la biodiversidad marina causados por la actividad pesquera deben ser resueltos de una forma holística y con aplicación de distintas medidas de gestión (por ejemplo, cierres espacio-temporales, áreas marinas protegidas, etc..) diseñadas de acuerdo a las características específicas de cada Océano, del tipo de lance y de la estrategia de vida de las especies.

GLOSSARY OF THE MOST IMPORTANT ABBREVIATIONS

EPO	Eastern Pacific Ocean
WIO	Western Indian Ocean
EAO	Eastern Atlantic Ocean
FS	Free School
FAD	Fish Aggregating Device
EAFM	Ecosystem Approach to Fishery Management
SST	Sea Surface Temperature
SSS	Sea Surface Salinity
Chl	Chlorophyll
SLA	Sea Level Anomaly
SDM	Species Distribution Model
GAM	Generalized Additive Model
ITCZ	Inter-Tropical Convergence Zone
NEC	North Equatorial Current
SEC	South Equatorial Current
NECC	North Equatorial Counter Current
ENSO	El Niño Southern Oscillation
RFMO	Regional Fisheries Management Organization
IRD	Institut de Recherche pour le Développement
IATTC	Inter-American Tropical Tuna Commission
ICCAT	International Commission for the Conservation of Atlantic Tunas
IEO	Instituto Español de Oceanografía
IOTC	Indian Ocean Tuna Commission

DEFINITIONS

The following terms used in this Thesis are defined as follows:

Alpha diversity	Species diversity of a particular and heterogeneous community (Whittaker 1960).
Beta diversity	Gradient of change in the composition of species between different communities (Whittaker 1960).
Biodiversity-Species diversity	The variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are a part; this includes diversity within species, between species, and of ecosystems (Diversity 2003). Also, it can be defined as the variety and abundance of species in a defined unit of study (Magurran 2004).
By-catch	The part of the capture that is not a target catch and that can be discarded or retained (Amandè et al. 2012).
By-product	The part of the by-catch that is kept for a particular use, i.e. to be consumed on board or sold later on the local African market (Amandè et al. 2010).
Catch	The part of the capture retained for utilization (consumption, sale, use as bait, etc.) (Hall et al. 2000).
Community	A group of interacting species populations occurring together in space (Stroud et al. 2015).
Discards	The portion of a catch of fish which is not retained on board during commercial fishing operations and is returned, often dead or dying, to the sea. Discards form part of the by-catch of a fishing operation (Catchpole et al. 2005).

Diversity index	A single statistic that incorporates information on richness and evenness. Also called “heterogeneity” measures (Magurran 2004).
EAFM	Managing fisheries including all components of the ecosystem in a holistic, synthetic and integrated fashion (Garcia 2003).
Ecosystem	A unit comprising a community (or communities) of organisms and their physical and chemical environment, at any scale in which there are continuous fluxes of matter and energy in an interactive open system (Willis 1997).
Evenness	The relative abundance of species or the variability in species abundances (Magurran 2004).
FAD set	Fishing mode in the tropical tuna purse seine fishery characterized by using a man-made object which attracts tuna and other species. They are usually formed by a bamboo raft with panels of netting submerged underwater, carrying a GPS beacon transmitting its position (Hall and Roman 2013).
Free School sets	Fishing mode in the tropical tuna purse seine fishery in which the tuna schools are detected visually at the surface of sea during light hours through the visualization of breezes, jumpers, boilers or foams (Hall and Roman 2013).
Generalize Additive Model	Non-parametric generalization of multiple linear regression to fit nonlinear relationships between response and smoothed explanatory variables (Guisan et al. 2002).
Habitat distribution model	Models which identify relationships between known species distribution data and their environment for predicting the potential suitable habitat for species in an area (Franklin and Miller 2009).

Release alive	The part of the capture which is released and survives to the fishing operation (Hall 1996).
Species richness	The number of species in the unit of study (Magurran 2004).
Overfishing	The harvesting of a fish population at a rate greater than the population can replenish itself through growth and reproduction (Pauly et al. 2002).

OVERVIEW

Context and relevance of the work

This Thesis is focused on the tropical tuna purse seiner fishery for which the fishing grounds are located in the tropical area of the Western Indian, Eastern Atlantic and Eastern Pacific Oceans. One of the most important impacts of this fishery is the by-catch mortality of some vulnerable species (such as billfishes, turtles, sharks, etc... (Hall 1996)) which are removed from the ecosystem. Some of those species are more prone to overexploitation due to their special biological characteristics such as long life spans, slow growth rates, and low reproductive potential (Lewison et al. 2004).

These species which are normally taken in association with tuna schools in purse-seiners (PS) tend to be the same in all regions, reflecting similar environmental characteristics and structure of the pelagic communities in the three oceans (Hall and Roman 2013). For that reason, the mortality of these species may affect the structure, function and the biodiversity of the tropical marine pelagic ecosystem.

The by-catch issue became very visible in the Eastern Pacific Ocean due to the large dolphin by-catch mortality during the 1960s which was the cause of the significant decline on their population (Hall 1998). Furthermore, with the rapid growth in the use of Fish Aggregating Devices (FADs) in the early 90s oceanwide, the number of by-catch species and the number of small bigeye and yellowfin tunas caught with this fishing mode increased significantly (Hall and Roman 2013). Although efforts are done to minimize the interaction of fishing gears with and to increase the post-release survivorship of those iconic species, the by-catch problem persists (Lewison et al. 2014). For that reason, the by-catch research- specially research on mitigation measures, reduction of the mortality and the conservation of by-catch species- has become a research priority of Tuna Regional Fisheries Management Organizations (RFMOs) (Safina 2008).

To date, most of the literature on by-catch species is descriptive and sometimes it is included within the analyses made about the purse-seine fishery and its target-species (Amandè et al. 2008a; Amandè et al. 2010; Amandè et al. 2011b; Chassot et al. 2009; Chassot et al. 2010; Davies et al. 2014; Delgado de Molina et al. 1999; Floch et al. 2012; Fonteneau et al. 2000; Gaertner et al. 2002; Gaertner and Dreyfus-Leon 2004; Hall and Roman 2013; Roman-Verdesoto et al. 2005; Romanov 2002; Sarralde et al. 2006). In contrast, the studies published about the interactions of PS with the marine megafauna are more specific but less in number (Bourjea et al. 2014; Capietto et al. 2014; Escalle et al. 2015; WCPFC 2012).

The studies published about the biodiversity of by-catch species on tropical purse-seine fishery are scarce. Despite the growing literature on biodiversity (Magurran 2004) (Figure 1), little information is yet available for marine biodiversity in general and for this specific group of species in particular. The most important studies published to date include different levels of marine diversity (species and/or habitats) without including comparisons between tropical oceans (Gaertner et al. 2008; Gerrodette et al. 2012; Sequeira et al. 2012; Torres-Irineo et al. 2014).

One of the main problems to obtain a global perspective about the diversity of these species in the tropical area and their relationship with the environment is that fisheries science has commonly focused on studying and managing single species stocks.

Although the single stock assessments are widely used, rarely provide insights into a broader suite of changes on ecosystem biodiversity or the fishing impacts on habitats. Thus, a new approach called “Ecosystem Approach to Fisheries Management” (EAFM) was developed as a tool to assess and manage the structure and function of marine ecosystems, including their biodiversity (where the by-catch species are considered), in a holistic and integrated way (Motos and Wilson 2006).

Nevertheless, it is not an easy task to measure the biodiversity in a vast and complex system such as the pelagic ecosystem and therefore, there is a general knowledge lack about the ways of describing and analyzing the composition, structure and habitat characteristics of the by-catch communities on the PS fishery.

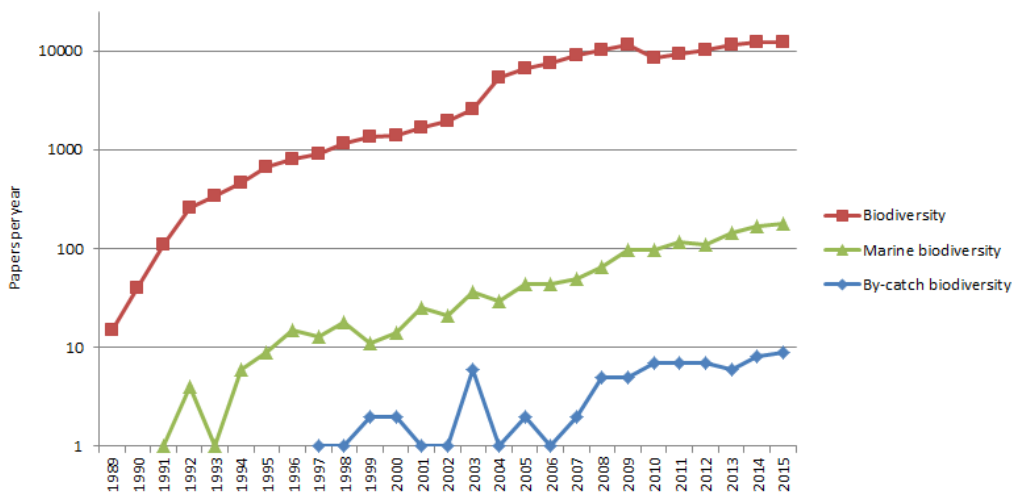


Figure 1. The number of papers per annum (between 1989 and 2015) that mention "Biodiversity", "Marine biodiversity" or "By-catch biodiversity" in their titles, abstracts or keywords. Note log scale on y axis. (Source: *Web of Science* (<http://wos.mimas.ac.uk/>)).

In that sense, an alternative could be the application of indicators of biodiversity (such as diversity measures and models) to explore the diversity patterns and the habitat distribution of the by-catch communities, and concretely, for describing differences on species number and abundance over time, or comparing diversity among fished and un-fished areas (Motos and Wilson 2006). For example, the Marine Strategy Framework Directive adopted by the European Commission in 2008, developed a set of 11 descriptors and indicators to achieve a Good Environmental Status (GES) of the ocean and to contribute to an ecosystem approach management of the marine waters (Bourlat et al. 2013). Among those descriptors, the “Biological diversity” descriptor, which includes diversity measures, can be a key facet to incorporate into the EAFM for studying the health of the ecosystem and biodiversity of the by-catch communities.

Thus, we proposed the application and combination of two indicators of species diversity: species richness (the number of species in the unit of study) and evenness (the variability in species abundance) to study the diversity of the pelagic ecosystem. These indicators as well as different components/aspects of them will be studied. Species richness is one of the most common biodiversity measure used in terrestrial ecology; however despite its important, the majority of studies does not incorporate the abundance of species (i.e. all the species are treated equally without making differences between most abundant species and those that are extremely rare) (Magurran 2004). Nevertheless, in marine ecosystem, and especially in fishery science, the relative abundance of a species is also important to consider in conjunction with species richness as abundance also plays an important role in population dynamics and in the productivity of the populations harvested. This is also the case for the tropical purse-seine fishery when investigating the effect of this fishery in the ecosystem as well as when trying to apply the EAFM.

Besides species diversity, knowing the habitat preferences and the potential distribution of these species is essential for the correct management of the most vulnerable species or habitats. Moreover, the possible habitat losses may also set the basis for the implementation of conservation plans which take into account not only the species, but also the factors of the ecosystem which influence their distribution. When environment factors such as thermocline depth, sea surface temperature or chlorophyll concentration may delimit the habitat distribution of these species, it is essential to model and evaluate each environmental factor to prevent any change in the future distribution of the species. In that sense, the habitat distribution models have the ability of integrate the occurrence of species and many environment variables in order to describe their distribution under present conditions and under the future effect of climate change.

In light of this issue, and with the aim to determine how the abiotic (fishing type) and biotic (oceanography, climate change) factors determine the diversity patterns and the habitat distribution of the by-catch communities, I have investigated the number, abundance, structure/composition of species in the tropical tuna purse seiners, the relationship of the species caught with the environment and the changes on their distribution under the A2 scenario of climate change through the application of a variety of diversity measures and distribution/habitat models.

The indicators developed in this work may provide the basis for reducing the mortality of these species through the application of future conservation plans and contribute to an Ecosystem Approach to Fishery Management of the tropical tuna fisheries in the three oceans.

Working hypothesis

The working hypothesis is a “provisional, working means advancing investigation” (Shields and Tajalli 2006), and it has as a main function to guide the lines of inquiries. It connects the problem organization, data collection and interpretation. Therefore, it is a useful tool to structure the hypothesis (Dewey 1938). It assesses merely a provisional conjecture, as a result of acquired information from the literature, the experience of the author that will guide investigation and analysis performed. The working hypothesis should be in the form of a statement of expectations; they are supported with empirical evidence.

As such, information in the literature on different techniques for measuring biodiversity and for modelling the species/habitat distribution, the experience acquired and analysis carried out by the author during the research process contribute to address the questions considered to observed data in order to test the following working hypothesis:

“The assessment and management of the tropical tuna purse-seine fishery requires information about the structure of the by-catch communities, by-catch species number and abundance, as well as the main biotic factors (i.e. environment processes, climate change) and abiotic factors (i.e. fishing type) which may influence the distribution and/or biodiversity of those species.

Describing the diversity patterns of the by-catch communities (i.e. Alpha diversity and Beta diversity) and investigate the geographical, temporal and environment preferences of those species (i.e. equatorial areas, sea surface temperature, etc) as well as the changes in their distribution of habitat as response to climate change (i.e. under A2 scenario) will contribute to the integration of

different components of the ecosystem towards the application of the EAFM, and the tropical tuna fishery management, in the Western Indian Ocean, Eastern Pacific Ocean and Eastern Atlantic Ocean”.

Objectives

The aim of this PhD study is to describe the biodiversity and the habitat preferences of the by-catch communities in the Western Indian Ocean, Eastern Pacific Ocean and Eastern Atlantic Ocean by analyzing diversity metrics and oceanographic variables affecting the diversity and potential habitat distribution of these species. Besides, it aims to assess the influence of certain abiotic factors (e.g., fishing type) on the diversity patterns of the pelagic ecosystem as well as the changes in habitat use as response to climate change.

This study emerged from the need of changing the preconceived ideas until now about how to manage the fisheries. For this, it is necessary to improve the knowledge about the by-catch communities and their habitat. Secondly, it is necessary to learn how to integrate and interpret all the factors which affect the habitat of these species.

In order to address this need, the PhD Thesis presents scientific research results about the development of various diversity metrics and species/habitat distribution models in relation with environment/oceanographic variables of the tropical tuna fishery by-catch communities.

As such, this PhD Thesis aimed to answer the following questions:

1. How the biotic (environment) and abiotic factors (fishing type of the tropical tuna PS fisheries) affect the diversity and habitat distribution of the by-catch communities?
2. How will climate change affect the present distribution of *Carcharhinus falciformis* and *Canthidermis maculata* by-catch species of the tropical tuna PS fisheries?

with the motivation to investigate different indicators of biodiversity which will contribute to the implementation of the EAFM and conservation of the pelagic ecosystem.

To answer to these questions, it has been proposed the underlying hypotheses:

- Diversity of the by-catch communities along the tropical area are highly variable in space and time depending of the oceanographic characteristics of each ocean and the fishing type. The number of by-catch species, their abundance and the species composition is different in both

fishing modes; with higher diversity found in FAD sets than in Free School sets in the three oceans.

- The potential present distribution of *Carcharhinus falciformis* and *Canthidermis maculata* could be affected with changes in the habitat distribution of these species as consequence of climate change. These changes respond to specific oceanographic characteristics of each ocean.

In order to test the previous hypothesis four main objectives were stated within this PhD Thesis (specific objectives are further detailed in each chapter).

- 1- To describe Alpha (species richness and evenness) and Beta diversity (differences in species composition between areas), as well as to explore the spatial, temporal and oceanographic preferences of the by-catch communities which contribute to explain their diversity patterns in the Western Indian Ocean in both fishing modes (FAD/Free).
- 2- To describe Alpha and Beta diversity, as well as to explore the spatial, temporal and oceanographic preferences of the by-catch communities which contribute to explain their diversity patterns in the Eastern Pacific Ocean in both fishing modes.
- 3- To describe Alpha and Beta diversity, as well as to explore the spatial, temporal and oceanographic preferences of the by-catch communities which contribute to explain their diversity patterns in the Eastern Atlantic Ocean in both fishing modes.
- 4- To describe the potential habitat and to evaluate the possible changes on the distribution of *Carcharhinus falciformis* and *Canthidermis maculata* by-catch species under the A2 scenario of climate change.

Structure of the Thesis

This PhD dissertation conforms to the following structure:

- It starts with the Introduction section. The purpose of this section is to introduce the concept of biodiversity to the reader. It describes the biodiversity in marine research and the pressures affecting it such as climate change or overfishing. Furthermore, worldwide tropical purse-seine fishery is reviewed and the main concerns related to the by-catch species of this fishery are described. It provides an up-to-date overview of the possible solutions for the conservation of these species through the application of different indicators (diversity measures and models) with the objective of integrating the management of those species within an ecosystem-based fishery management. These indicators are explained in the Material and Methods section.

- Subsequently, the Study Area is defined. This section describes the general circulation and oceanography of the Western Indian Ocean, Eastern Pacific Ocean and Eastern Atlantic Ocean. The main equatorial and coastal upwelling systems are described, as well as front systems and dome systems. Oceanography of different oceans is presented as this will help to interpret the results in the context of oceanographic differences within and among oceans. Then, the specific investigations carried out in order to answer the above mentioned overarching questions and to achieve the stated main objectives are presented and structured in four Chapters. Each chapter includes a short abstract, starts with an introduction to contextualize the study and the specific objectives of the chapter, followed by the material and methods applied and the results obtained, and finished with a discussion and conclusions of the main findings.
- Then, the major findings achieved along this PhD Thesis together with the limitations encountered are discussed in the General discussion section. All the differences and similarities found in diversity patterns among oceans are compared and discussed based on the specific oceanographic characteristics of each of them.
- The dissertation ends with the Conclusions. This section enumerates the main conclusions drawn from the General Discussion. In addition, the Thesis is given.

INTRODUCTION

1. MARINE BIODIVERSITY

Biodiversity is “the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are a part; this includes diversity within species, between species, and of ecosystems (Diversity 2003). The term biodiversity is a contraction of “biological diversity”. It appeared for the first time in 1988 (Wilson 1988) and thereafter it spread very quickly in the literature (Haila and Kouki 1994). Biodiversity is a basic property of life and essential for the survival of the ecosystems. It can be considered at all levels of organization and at any geographic scale (local, regional or global). The concept of biodiversity encompasses from genetic diversity and functional diversity to the species and ecosystem diversity, and the patterns of global distributions of life forms (Grassle et al. 1991). It is usually measured quantitatively as the number of species or the value of a diversity index for a given community or area (Grassle et al. 1991).

Estimates of the total number of species on Earth vary between 5 millions and 30 millions. In general it is very difficult to estimate the real number of species because 1) the same species may be described with different names 2) two species may be considered the same when in fact are different, or 3) not all species has been discovered. The problem of synonyms (“taxonomic name which has the same application as another”) has been especially severe in species of fishes, corals, crabs and mollusks because they have been the groups of most interest for travelers, collectors and scientists (Bouchet and Duarte 2006). The exploration of the world to discover, describe and name new species was one of the most important activities during 1850-1900s for the scientific community. However, as it was thought that majority of species were discovered by the end of the 20th century, the institutional effort slowed down being insufficient to complete the inventories of species of fauna and flora (Bouchet and Duarte 2006). As consequence, the global number of species that have been formally identified at the present is only between 1.4 and 1.7 million and therefore, they only represent a small portion of total species richness (Bouchet and Duarte 2006). Thus, many species remain to be described because of insufficient taxonomic effort and expertise (Sala and Knowlton 2006). Around 86% of the species on Earth and 91% in the ocean still await description (Mora et al. 2011).

Marine biodiversity or the variety of life at sea includes variation at all levels of complexity, from species to ecosystems. Although the marine ecosystems cover 70.8% of the Earth's surface, our knowledge about marine diversity at present is poor in comparison with terrestrial diversity (Sala and Knowlton 2006). The number of taxonomists per taxon for most marine organisms is very low compared to that for terrestrial vertebrates or plants (Sala and Knowlton 2006). Thus, the total number of marine species is not known in order of magnitude, with estimates ranging from 178000 species to more than 10 million species. It is believed that there are approximately 300000 described marine species, which represent about 15% of all described species. Around 1635 new marine species are currently described every year. The Crustaceans and Molluscs are the taxa with higher number of new species described (Bouchet and Duarte 2006). The two biggest areas of marine biodiversity are coral reefs (because of the high number of species per unit area) and the deep sea (because of its enormous area) (Sala and Knowlton 2006).

1.1. Patterns of marine biodiversity

The spatial pattern of global marine biodiversity shows well defined gradients with respect to latitude, longitude and depth (Figure 2) (Sala and Knowlton 2006; Tittensor et al. 2010). The latitudinal gradient of the diversity (i.e. the highest numbers of species in the tropics and gradual decrease poleward) is a well-recognized pattern in terrestrial ecology. It has been documented for plants, birds, mammals or reptiles. For example, the number of genera and families of trees increases from poles to tropics, where the highest diversity values are found in tropical rain forests. A similar pattern has been observed in the marine system, with an increase in species diversity from arctic to tropics (Gray 1997). However, some groups are less diverse in the tropics; for example seabirds and various groups of insects. These examples may just be an exception of a general phenomenon (Ormond et al. 1998).

The first theory of decreasing diversity with latitude was formulated in late 1950ies for hard bottoms epifauna. He suggested that the macrobenthos is more diverse in the tropical shallow seas than that in boreal locations. He explained that the differences are due to long time stable conditions which occur in the tropics in contrast to environmental stressors of boreal communities. However, the tendency from the Antarctic to the tropics is not as clear as from the Arctic to the tropics, and therefore, more research in diversity patterns of the Southern hemisphere is needed (Gray 1997).

In reference to the longitudinal patterns, diversity decreases from west to east in the tropical Pacific and Atlantic (Gray 1997). In the Pacific Ocean, the most well-known diversity pattern is

that of coral communities, which show the highest values (600 species) in the Indonesian archipelago. Coral reef diversity decreases radially from there across the Pacific and Atlantic Ocean (Veron 1995). The reason for this high level of diversity in this region is the result of a long period of evolutionary stability and the existence of a large diversity of types of islands and archipelagos of different sizes situated very far from sources of colonizing species (Gray 2001).

In contrast, the Indian Ocean diversity decreases from the high diversity epicentre and dipping and then rising in the Red Sea and Africa in some groups and with lowest diversity in the Caribbean (Gray 1997). In general, marine diversity is higher in coastal areas than in oceanic area, where the pelagic species live (Angel 1993).

Another very important difference between terrestrial and marine systems is that the latter has a third dimension: depth. Thus, diversity increases from shallow areas to deep sea, as showed by Sanders (1968), who studied the soft sediments and suggested that deep ocean provides more stable environmental conditions and therefore, hosts a more diverse benthic biota. Grassle and Maciolek (1992) also found the same depth pattern in the sea. They found that highest diversities of benthic invertebrates were found at intermediate depth of 2000-3000 m whereas the lowest diversity was found on the upper slope and the abyss. Sanders described this pattern, but he also mentioned the stability-time hypothesis; which describes that in shallow and/or polar areas with high environment variability, adaptation by individuals is mainly to the physical environment rather than to competition with other species. On the other hand, in the deep sea and tropical areas the adaptation is also due to the competition with other species. Thus, the species richness of shallow and polar areas is “physically controlled”, whereas that of the deep sea and tropical areas is “biologically accommodated” (Sanders 1968).

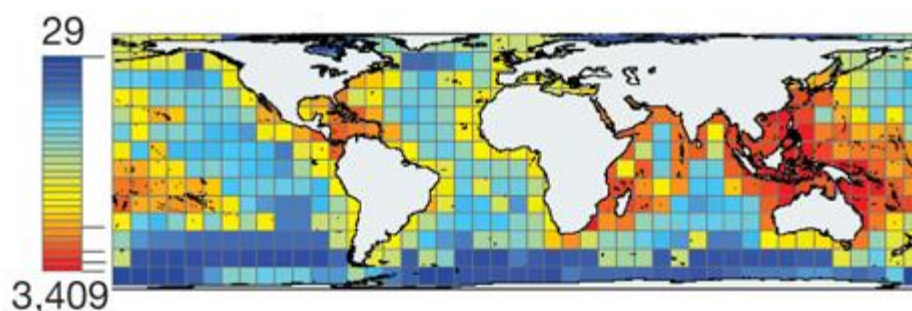


Figure 2. Global marine species richness for all taxa (Source: Titterson *et al.* 2010).

1.2. Threats to marine biodiversity

Globally it has been shown that human exploitation of living marine resources is considered among the single greatest threat to marine biodiversity (Duraiappah et al. 2005). Thus, human activities can directly or indirectly affect biodiversity of marine ecosystems (Gaston 2000). The most important direct threats to marine biodiversity and ecosystem service are habitat change (tourism, loss of coral reefs and damage to sea floors due to trawling), invasive alien species, pollution (e.g marine litter, algal toxins, etc) and overexploitation (Gray 1997); which can lead to a decline in overall biodiversity (Figure 3). Furthermore, climate change is another important threat that varies geographically. It includes temperature change, ocean acidification, sea-level rise, and consequently changes to ocean stratification, upwellings, currents, and weather patterns (Costello et al. 2010). Most of these threats to biodiversity are located in coastal zones as a result of the human population and demographic increasing trends (Gray 1997).

Since the first published news of worldwide loss of biological diversity, the attention of scientists, the media or the general public has focused on study the diversity, mainly in the terrestrial ecosystem (Norse 1993). Despite the loss of biodiversity in marine systems, it was largely ignored until the end of 1980s. It was not until 1989 when (Vermeij) examined some aspects of marine biodiversity in a group of papers from a symposium organized by the Society for Conservation Biology and the Ecological Society of America (Norse 1993). Carlton et al. (1999) reported the first extinction of a marine invertebrate in an ocean basin; which was discovered to be extinct 60 years later. Finally, the same year, Thorne-Miller (1999) provided the first book about marine biological diversity loss. After that, a book titled “Global Marine Biological Diversity: A strategy for Building Conservation into Decision Making” (Norse 1993) was published as an effort to focus on maintaining the sea’s biodiversity. Since then, the numbers of works which study the loss of marine biodiversity and extinctions have increased (Carlton et al. 1999; Dulvy et al. 2003; Duraiappah et al. 2005; Myers and Ottensmeyer 2005).

1.3. Why is biodiversity loss a concern?

Goods and services are defined as “direct and indirect benefits people obtain from ecosystems”. The marine biodiversity contributes directly and indirectly in providing essential goods and services for human life, including food security, protection against coastal erosion, recycling of pollutants, climate regulation and recreation. Thus, biodiversity loss may affect ecosystems services from local to global scales (Sala and Knowlton 2006). Many people have benefited over the last century from the conversion of natural ecosystems to human-dominated ecosystems and

the exploitation of biodiversity (Duraiappah et al. 2005). Unlike natural changes, human impacts are usually not random. Society targets selected species and habitats, which difficult their recovery. In the coastal zone the human activities (including fishing, industrial operations, mineral extraction and coastal development) need to be evaluated (Grassle et al. 1991). In the ocean, the changes are similar to those on land but they are more difficult to detect and evaluate beneath the sea surface.

Changes in biodiversity due to human activities have been more rapid in the past 50 years than at any time in human history. These threats and changes are caused by increasing human population and increasing resource consumption which is accompanied by a general lack of knowledge about the consequences of biodiversity loss (Norse 1993). However, the real problem is that the drivers of these changes are currently stable or even increasing in intensity and therefore, the resilience or the ability of an ecosystem to recover from a perturbation becomes more difficult than 50 years ago (Duraiappah et al. 2005).

Some marine areas are especially important for conservation because of their high species diversity, endemism or productivity. Other areas which are considered spawning areas, nursery grounds or migration corridors for some species (Norse 1993) could be vulnerable to pollution or habitat degradation. For example, chemical pollutants may be found in marine populations thousands of kilometers from significant human population habitats.

Given these problems, conservation tools in marine ecosystems have to be applied on larger spatial scales than those on land. A better understanding of species biology and oceanography, as well as of the causes of biodiversity loss, is essential to conserve marine biodiversity.

2. MAIN CAUSES OF BIODIVERSITY LOSS

A combination of human threats has caused a rapid decline in global marine biodiversity, with changes on ecosystem functions and a reduction in the provision of ecosystem services (Sala and Knowlton 2006).

The causes of biodiversity loss related, among others, to the destruction of coral reefs and mangroves, the development of the tourist industry as well as the changes in sediments loads from the rivers have led to changes in coastal and in general, in marine ecosystems (Gray 1997).

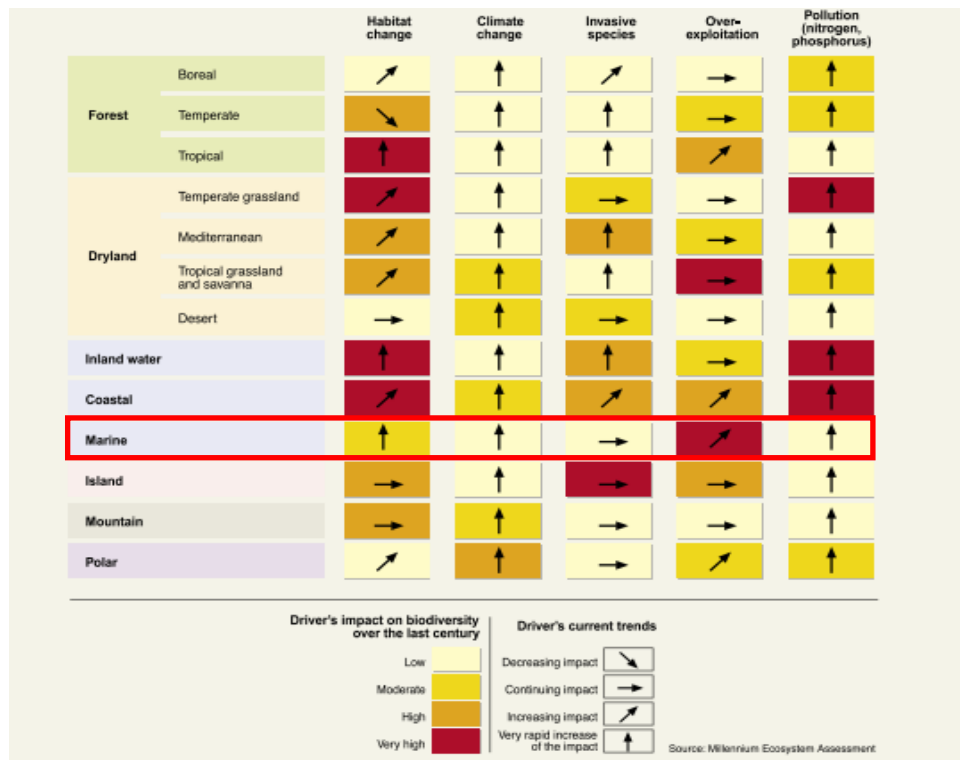


Figure 3. Driver's impact on biodiversity over the last century. The cell color indicates the impact to date of each driver on biodiversity in each biome over the past 50-100 years. The arrows indicate the trend in the impact of the driver on biodiversity. Horizontal arrows indicate a continuation of the current level of impact; diagonal and vertical arrows indicate progressively increasing trends in impact (Source: Duraiappah et al. 2005).

2.1. Habitat change

Habitat loss and degradation has been generally associated to significant declines in overall abundance and diversity of marine organisms, being considered as the most critical threat to marine biodiversity (Airoldi et al. 2008).

Southeast Asia contains 30% of the world's coral reefs. Based on the work published by Wilkinson (1993), 60% of the coral reefs are already destroyed or close to be destroyed and most of the reefs could be eradicated during the next 40 years as consequence of habitat loss (Gray 1997). Mangrove forest destruction is also occurring on the same alarming rate. Indonesia has the largest areas of mangroves (21011 km²) but 45% have been lost and the rate continues to increase (Airoldi et al. 2008). The destruction of habitat of coral reefs and mangrove are probably very significant in terms of losses of biodiversity but other critical coastal habitats are also disappearing. Some anthropogenic activities which destroy the coastal habitat include the urbanization, aggregation and extraction of sand or gravel, and/or recreation and developments of harbors and industries. The tourism is other significant threat to many coastal habitats over the

world. However, in marine coastal areas few studies have been done that quantify species loss in relation to the habitat loss (Gray 1997).

On the other hand, in offshore waters, the extraction of oil and gas threaten marine habitats, mainly by the discharges of oil and other pollutants. Fishing activities such as bottom trawling can also damage the marine diversity. Deep-water trawling may also cause long-term habitat losses in seabed such as cold-water coral reefs in Norwegian, Scottish and Irish waters (Airoldi et al. 2008).

2.2. Invasive alien species

A non-native species is a species introduced intentionally or accidentally into an environment outside its geographical range or habitat. Once invasive species become established in marine habitats, it can be very difficult to eliminate them (Molnar et al. 2008). Such species are described as 'invasive' if they are ecologically and/or economically harmful. Invasive species are found primarily in disturbed areas, such as harbours, bays, estuaries and semi-enclosed seas where the communities are weakened by various types of pollution (Cohen 2004). These species can dramatically change the structure and function of marine ecosystems by changing biodiversity and eliminating vital components of the food chain.

Species in general tend to adjust to each other and adapt to available resources by occupying different ecological niches within communities. If all resources are utilized optimally and all available niches are filled, biodiversity is maxima. However, various factors influence the functional integrity of a community. If changes occur gradually over a long timescale, species have enough time to adapt and to occupy available niches. In contrast, if changes happened very fast, new niches could be developed and invaded (Cohen 2004).

2.3. Pollution/marine litter

The heavy metals seldom are considered a threat to marine biodiversity despite there are local areas where high concentrations are cause of concern, such as industrialized estuaries or fjords (Gray 1997). Instead, there are remarkable concerns about the long-term effects on marine populations of organic chemicals. Polychlorinated biphenyles (PCBs) and dioxins seem to imitate the female oestrogenic hormones with the consequence of having severe reproductive changes in terrestrial species. However, more research is needed before quantifying this threat to marine biodiversity. Furthermore, toxins produced by algal blooms may affect coastal aquaculture and

human health in both developed and developing countries (Gray 1997). Finally, marine litter is an increasing problem for marine life and tourism. Litter can be drainage on land, left on beaches or discarded from commercial and fishing vessels, such as the plastic and old nets. Almost 75% of this litter is plastic with Styrofoam, metal, glass and wood as their major components and turtles are particularly vulnerable to them (Gray 1997).

2.4. Anthropogenic climate change

Before humans began to intensively exploit the oceans, the only changes that caused biodiversity losses were environmental perturbations (Sala and Knowlton 2006). At present, the same environmental perturbations such as the increase of temperature are being accelerated as consequence of global warming by human action (Figure 4).

So, by the end of the 21st century, climate change and its impacts could be the main direct cause of biodiversity loss and extinction for many species, especially those with low population numbers which live in restricted or patchy habitats, and/or with limited temperature ranges (Duraiappah et al. 2005).

The Intergovernmental Panel on Climate Change under projections of different scenarios predicts an increase of 2.0-6.4°C in global mean surface temperature by 2100 (Norse 1993). These higher temperatures could affect the productivity of phytoplankton. A number of models predict an increase of between 1% and 8% in global primary production by 2050, when compared to pre-industrial times (Sarmiento et al. 2004). This is alarming because phytoplankton is an important basis of the marine food web and, therefore, any change in the abundance or in the species composition of the phytoplankton could affect the whole food web.

Concretely, the most noticeable change in marine biodiversity caused by climate change affects the abundance and distribution of individual species (Perry et al. 2005). Recent changes in climate have already had significant impacts on biodiversity and ecosystems. Thus, the most common changes are changes in species distributions, changes in migrations pattern, and global extinctions caused by global warming and increased of human activities (Duraiappah et al. 2005).

The species movements in an area impacted by climate change are towards the poles in general. These patterns have been recorded in zooplankton, fish and benthic species since the late 1980s,

when the global warming was accelerated as consequence of the industry revolution and the increase of greenhouse gases (Brander et al. 2003).

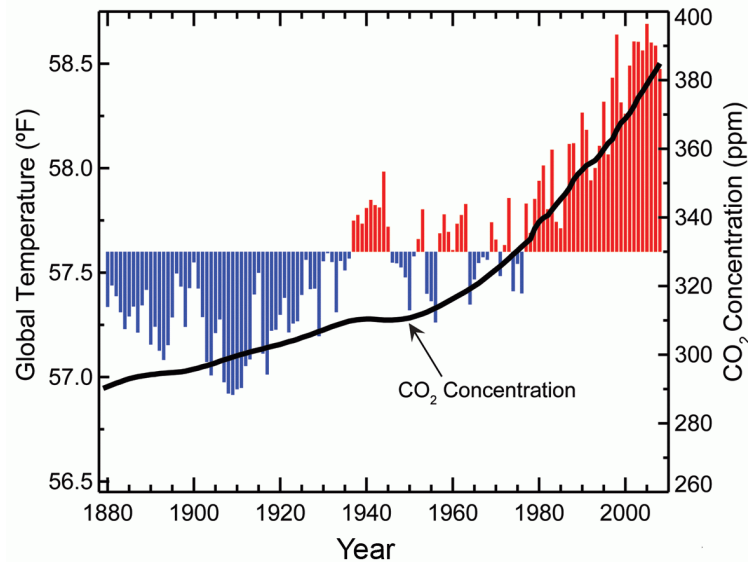


Figure 4. Global average temperature (as measured both land and oceans) for the period 1880-2010 (Source: NOAA/NCDC).

2.5. Fishing

Humans have always exploited marine resources to support their needs for food and other items. However, during the 20th Century their activity has increased significantly (Grainger and Garcia 1996). Thus, at the present, fishing is one of the major direct anthropogenic force affecting the structure, function, and biodiversity of the oceans.

Overfishing, defined as the harvesting of a fish population at a rate greater than the population can replenish itself through growth and reproduction, is the principle cause of the decline of many fish and marine resources over the world (Pauly et al. 2002). However, despite the fact that science has clearly identified overexploitation as a problem, overfishing persists in many of the world's fisheries.

The risk of collapses of regional marine fisheries has increased in the last decades as consequence of the constant demand for fish as food for people and as feed for aquaculture production. Thus, the current size and geographic extent of fishing has raised serious questions about the sustainability of present exploitation rates (Caddy and Cochrane 2001; FAO 1997).

The overall catch and the immense majority of the world's fish stock biomasses have plateaued or declined. The United Nations Food and Agriculture Organization (FAO), which monitors the state of world fisheries, has estimated that about 61.3% of fish stocks are fully exploited or overexploited (FAO 2014). This results in the predominance of smaller-sized species dominating the fish communities of the world's oceans and with lower number of highly migratory species (e.g. tunas, billfishes) than there were 50 years ago (Link 2010).

The main effects of overfishing on the ecosystem comprise the reduction in diversity and the increase of by-catch, greater variability in abundance of species, decline in mean trophic level, greater anthropogenic habitat modification (Hall 1999); and in extreme cases, a change to alternative stable species regimes (Steele 1998).

There is increasing belief that biodiversity can be affected by fishing, not only to species levels, but also in a spatial and temporal scale. Fishing activities lead to changes in the structure of marine habitats and the relative abundance of species, and can determine the diversity, biomass and productivity of the associated biota (Jennings and Kaiser 1998). Fishing can also disturb the community structure by increasing mortality of vulnerable species such as turtles or marine mammals (Dayton et al. 1995), which affect the whole marine ecosystem (Hall et al. 2000). Furthermore, changes in species composition or population demographics may reduce the resilience of the ecosystem to recover from perturbations of non-biological origin, and therefore, the capacity of marine systems to support sustainable fisheries.

Because there are no new fishing areas to discover, other trophic levels were captured to maintain world catches at current levels; which results in a major shift in the structure of the world's marine ecosystem (Pauly et al. 1998). The average trophic level of global landings has been declining since the onset of industrialized fishing (Pauly et al. 1998). There are two ways in which this phenomenon could occur. The first is through the sequential replacement in catch of high-value upper-trophic-level species by less valuable lower trophic-level species ("fishing down the food web"). The second mechanism is through the sequential addition of lower-trophic-level fisheries within an ecosystem ("fishing through the food web") (Essington et al. 2006).

Regarding to the tropical ocean, although it includes almost 50% of the total area of all open water, it produces only about 16% of global fish production. However, in some species/fisheries most of the production comes from tropical oceans (e.g. tunas). Concretely, the global tropical tuna fishery has been harvested by humans for more than 6000 years (Joseph 2003) and has become one of the most important fishing activities worldwide. Tuna fisheries have always been

widely fished; however, in recent years, the increase in fishing pressure has been very large (Joseph 2003).

3. TROPICAL TUNAS

Globally, the total catch of tuna and tuna-like species is about 6 million tons. The most commercially important tropical tuna species are bigeye (*Thunnus obesus*, BET), skipjack (*Katsuwonus pelamis*, SKJ), and yellowfin (*Thunnus albacares*, YFT). The total catch of marketed tuna species has increased continuously from 1950 to 2007, with the highest values obtained in 2005 and 2013 around 4.5 million tons (Murua 2015) (Figure 5).

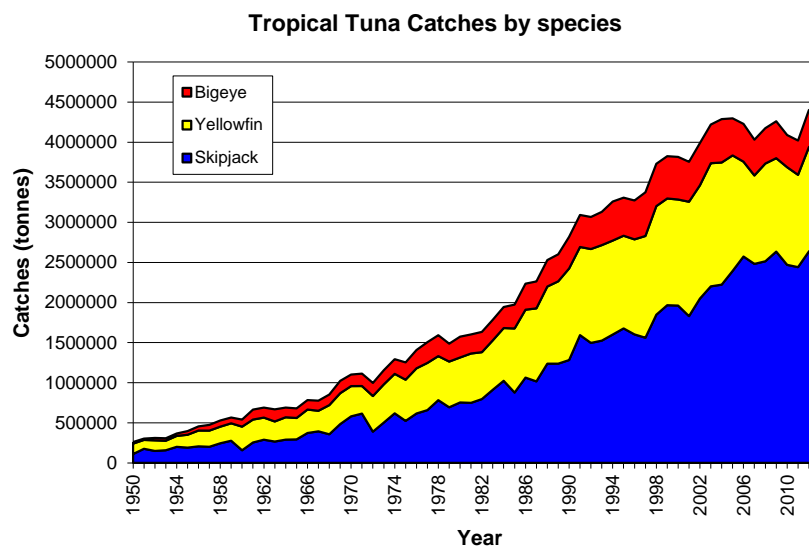


Figure 5. Worldwide catches of the major commercial tropical tunas from the 50st to 2013 (Source: Murua, 2015).

As a result of the increasing demand for canned tuna, the industrialized fishery started in the 50s with a progressive and continuous increase of catches until the present, mainly due to the expansion of the tropical tuna fisheries: yellowfin tuna, skipjack tuna and bigeye tuna. They account for most of the catches (93%), being the total catch in 2013 around 4.5 million tons. The individual contribution to total catch of principal tropical tuna species was around 24% for yellowfin, 59% for skipjack and 10% for bigeye. In contrast, the worldwide catches of temperate tunas were only around 0.3 million tons (Arrizabalaga et al. 2012).

3.1. Evolution by fishing gear

Different fishing gears capture tropical tuna, but some differences are observed between these tuna fisheries: the longline fishery targets mainly large bigeye and yellowfin tuna, the pole-and-line (termed also bait boat) fishery targets mainly skipjack, followed by yellowfin and bigeye (Dakar, Canary, Azores), and the purse seine fishery targets yellowfin and skipjack.

Historically, most of the catches were taken with troll line (20%) and pole-and-line (40%) gears. The catches on these fishing gears rapidly decreased with the expansion of longline fleets which accounted for around 50% of the catches by 1960 and with the development of the purse seine fishery in the early 1980s. The global purse seine catch continuously increase since 60s reaching its highest level observed of around 3 million tons in 2005. Since then, catches has been maintained at around that level (Figure 6).

At present, purse seine tuna is the predominant type of fishing in terms of tropical tuna catches in all the world's oceans (60% of world tuna catches), followed by tuna longline and pole and line, which represent approximately 15% and 11%, respectively (Miyake and Nakano 2004).

Since the 1990s, purse seine fishing effort has also grown globally at an average rate of about 2% per year. In parallel, the effort in floating object purse seine sets has increased by 70%, compared to about 20% for free-school purse seine fishing effort. Joseph (2003) estimates there are 600 high seas purse-seine vessels with a total fishing capacity of 600000 tons. Most of the growth in tropical purse seine catch is due to increasing skipjack catch, which was at -2.8 million tons in 2012 (Scott and Lopez 2014).

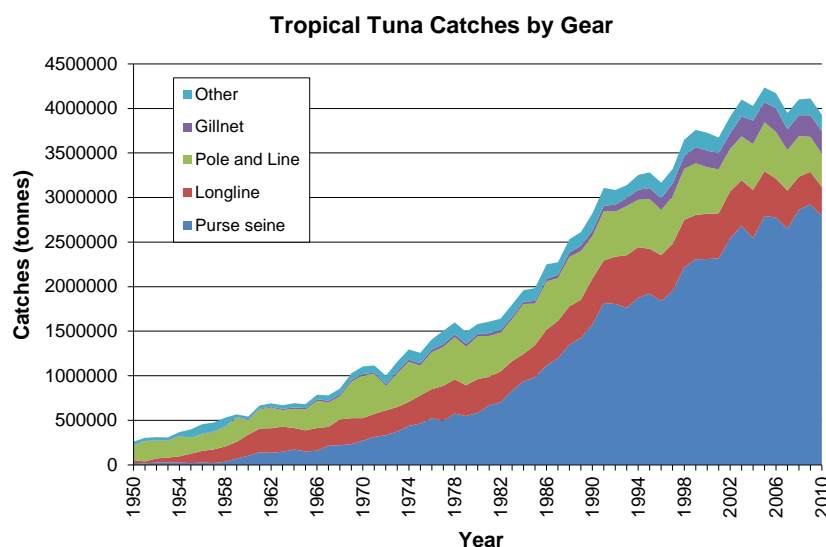


Figure 6. Tuna catch (thousand tons) by gear from 1950 to 2010 (Source: Murua, 2015).

3.2. Evolution by Ocean

The Pacific Ocean provides 68% of the global catch of tropical tunas and 77% of global purse seine catches; with the skipjack tuna and yellowfin as the main catches. In contrast, the Indian and Atlantic Oceans account for 23% and 10%, respectively (Murua 2015).

Since 1950s the total catch of tropical tunas in the Pacific Ocean has been increasing, reaching more than 3 million tons in 2014 (Murua 2015).

In the Atlantic Ocean, the total catch of tropical tuna has increased steadily since 1950, reaching the maximum of 491000 tons in 1994. After that, tropical tuna catches declined until 2006 (around 310000 t) but an increase of catches has been observed during last years with more than 400000 tons (Murua 2015).

In the Indian Ocean, the total annual catch of tropical tunas has increased significantly since the early 1980s with the introduction of the purse-seine fishery in this area and the development of fishing aggregating devices (FADs) (Figure 7). Average annual catch reached more than 1.1 million tons between 2003 and 2006. Then, catches continuously decreased up to 800000 tons in 2011. Since then catches has increased reaching 960000 tons in 2014 (Murua 2015).

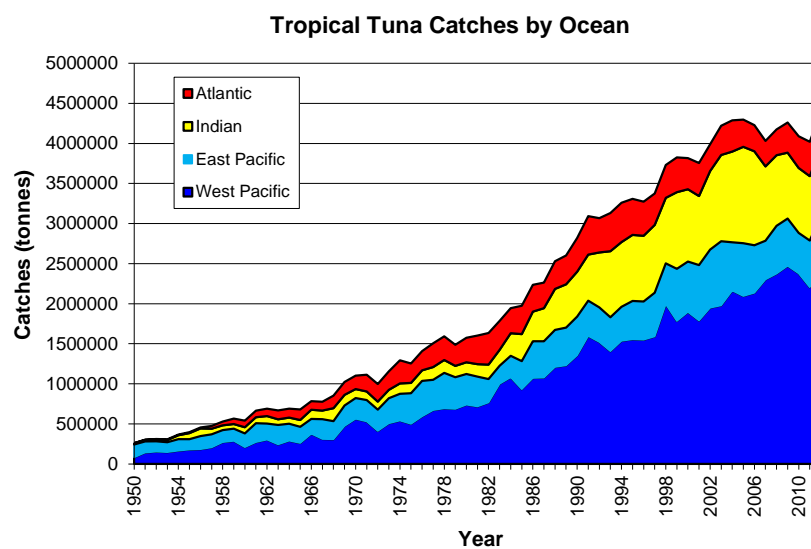


Figure 7. Tuna catch (tonnes) by ocean from 1950 to 2012 (Source: Murua, 2015).

4. PURSE SEINE GEAR

The tropical purse seine vessels range between 20 and 120 meters in length and are characterized by a net which are set vertically in the water. The top of the net consists of buoys and floats of plastic forming a surface barrier. When a school is detected, the vessel is placed next to the school and encircles the school very quickly. Once the encirclement is finished, the extremity of the net that stayed attached to the skiff is relocated aboard the purse seiner and the net is closed through the bottom along a seine or steel cable (Figure 8). Once closed, the closed net prevents that fish escape. Then, the fish are harvested from the purse seine using a large scoop net called the “brailer”. Finally, when the purse seine net has been recovered, the tunas are stored in fish-wells where it will be frozen at -20°C in brine (Hall and Roman 2013; Torres-Irineo 2012). Setting takes 7–8 minutes, and pursing 20–25 minutes (Kim and Park 2009). Besides the technology employed to handle the net, most seiners display a series of instruments to improve navigation, and detection of tuna schools. They include: bird radar, sonar, echo sounders and GPS (Scott and Lopez 2014).

The purse seine nets may be different in design and depending on the fleet. The most important characteristic is the depth of nets, as this has implications for the species composition of the catch. Some species live deeper than others and depending on the net depth the catchability of those species can vary (Hall and Roman 2013). The construction of the nets must take into account the oceanographic characteristics of the areas where they will be used (e.g. thermocline depths, surface currents), and the behavior of the target species.

The net length may reach more than 2200 m and its depths are usually from 150 m to 350 m. The shallow nets are commonly used in the Atlantic Ocean (around 220 m depth) (Gaertner and Sacchi 2000; Santana et al. 2002). In the Indian Ocean the nets reach the 275 m depth (Santana et al. 2002) and more than 300 m depth in the Pacific Ocean (Itano 1998).

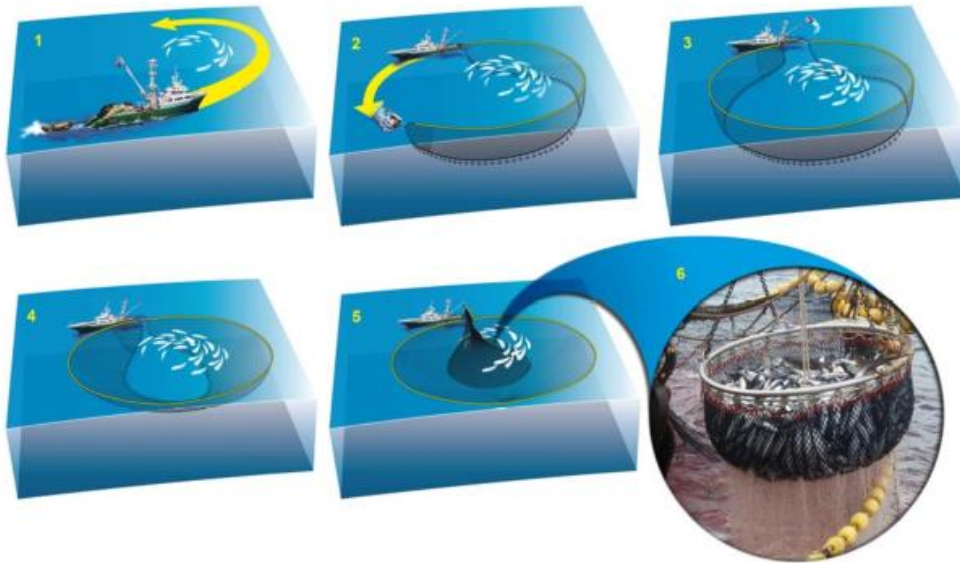


Figure 8. Different phases in the deployment of a purse seine (Source: IRD, EME).

4.1. Development of the purse seine tuna fishery

Fishers have captured tunas for millennia, with a multiple gear types. The search for tunas started to increase with the use of “baitboats”, vessels prepared to catch tuna with pole and line, using live bait prior to 1950. The purse seine fishery is a relatively old technique which began to develop in the early 50’s. This technique was focused on capture yellowfin and skipjack tuna using the free school mode. After the World War II, this fishery grew rapidly and extended to all worlds’ oceans (Fonteneau 1991).

In the Eastern Pacific Ocean (EPO), before to 1959 pole-and-line fleet dominated the tuna catches (Calkins 1963). However, after the World War II, many purse seine fishermen from Alaska and the Pacific Northwest entered the California fisheries (Shimada and Schaefer 1956). The vessels at that time were smaller than now, averaging approximately 120 t of capacity (Calkins 1963). During the period 1959-1961 most of the large bait boats were converted into purse seiner, the purse seiner fleet was modernized and the fishing effort began to expand offshore, reaching the 150°W longitude during the 1970s. In the 1980s the most exploited areas were around 10°N latitude, the Mexican coast and the Gulf of Panama. Finally, in 1990 many vessels from USA left the EPO to expand their fishery to other areas, with a consequent reduction in the fleet. Furthermore, during this period, the introduce of fish aggregation devices in the fishery caused the expansion of the purse seine fishery along the equator, from the coast of Central America to

the 150°W longitude (Lennert-Cody and Hall 2000). At present, Ecuador, Mexico and Venezuela have the main purse seine fleets operating in the EPO.

In the eastern tropical Atlantic, the purse seiner fishery was introduced in the Gulf of Guinea in the early 1960s (Fonteneau and Marcille 1993), with obtaining the first catch statistical data in 1962 in the western Atlantic and 1963 in the East, both from Spanish and French purse seiners. In mid-1970, the fishery extended to coastal water off Western Africa, from 25°N latitude to 25°S latitude (Fonteneau and Marcille 1993). In 1980, the fishery expanded beyond the Gulf of Guinea, increasing the catch of larger yellowfin tuna. In this period, France and Spain were the main purse seine fleets. However, some events like the high CPUEs observed by exploratory baitboats in the Indian Ocean and the low catches obtained in 1984 in the Atlantic as consequence of the deepening of the thermocline, resulted to a partial movement of PSs from the Atlantic to the Indian Ocean.

From the 1980s to the present, European purse seiners (France, Spain and associated flags) comprise the most important fleet in the tuna fishery in the Atlantic and Indian Ocean, whereas other fleets are the major component in the Pacific Ocean (both in the East and Western/Central areas).

In 1990, the fishery expanded mainly due to the introduction of the Fish Aggregating Devices (FADs) fishing mode in all oceans. The incorporation of GPS technology into the drifting radio buoys and echo-sounder buoys provided facilities for fishermen to find and capture the fish and reduced the probability of realizing null sets (Delgado de Molina et al. 1999).

Concerning the tuna catches, purse seine catches were dominated by yellowfin until 1980. Since then, the skipjack catches increased as consequence of the introduction of FADs in the Atlantic Ocean. At the present time, skipjack represent over 50 percent of world tuna catches (Miyake et al. 2010).

5. TYPES OF FISHING SETS

Despite the tropical tuna purse seining operation is always the same, there are different ways in which tunas are detected and encircled, classifying the purse seine sets in different types. The fishing is mainly made on free school sets and floating objects drifting sets. However, in the EPO, tunas, mainly yellowfin tuna, are frequently associated with groups of dolphins. Fishermen take advantage of this association to find tuna schools and this fishing mode is very important in the

Eastern Pacific. Although each of these fishing modes are described here, only the free school and floating objects drifting sets were studied in this work.

5.1. Free School sets

Tuna schools are detected visually at the surface of the sea during light hours through the observation of breezes, jumpers, boilers or foamers (Figure 9a). This type of set is the most difficult to detect because the fish behavior may change rapidly in response to environmental or biological factors. The main problem associated with this type of set is that the target tuna school is not “fixed” in space, and therefore, fishing on free-school requires more time in the searching process than the other types of set.

Thus, another problem related with the movement of the fish is that the encirclement with the net is much more difficult, and may result in a “skunk” or failed set (no or little capture). Sets made on the vicinity of whales (tunas are associated to whale during foraging) are considered as free school sets due to their same species composition and size of the fish (Pallarés and Petit 1998).

5.2. Dolphin sets

In 1959, an increase in catches of large yellowfin tuna were observed in the Eastern Pacific Ocean in association with groups of spotted (*Stenella attenuate*) and spinner (*Stenella longirostris*) dolphins, with the common dolphin (*Delphinus delphis*) and occasionally with the striped dolphin (*Stenella coeruleoalba*) (Hall 1998). The tuna purse seine catches on dolphins are made mainly from the coast to around 140°W longitude along and north and south of the 10°N latitude. This association is very rare with other tuna species and in other ocean areas (Figure 9b).

Because of natural factors (e.g., currents), equipment malfunctions, or lack of expertise or motivation of skippers and crews, many dolphins died incidentally during 60's in relation with this fishing operations (Hall 1998). This issue caused a considerable controversy around ethical, legal, economic and ecological problems, and many purse seiners switched the fishery from dolphin to the FAD-fishing (Hall 1998). However, the mortality of dolphins was reduced by 98% with the modification of the net and nowadays the dolphins set are still done in the Eastern Pacific.

5.3. Log sets and Drifting Fish Aggregating Devices (DFADs) sets

Fishers discovered that many species of tropical marine species, especially tunas, are attracted and aggregated in association with floating objects. As consequence, fishermen began to use Fish Aggregating Devices to take advantage of tuna aggregative behavior, which increased tuna catchability. The floating objects can be natural (e.g. logs) (Figure 9c) or man-made and displayed by fishermen (Fish Aggregating Devices, FADs) (Figure 9d) (Castro et al. 2002; Dagorn et al. 2013)

Tuna fishing on natural floating objects were used by most purse seine fisheries since the early 1960s in coastal areas where they were abundant (Fonteneau et al. 2000). The purse seine made on natural floating objects were (called log sets by the fishers) formed by tree trunks, branches and other material, which come from the river runoffs. They are found mainly in coastal waters in regions of abundant forests and tropical rivers, carrying a lot of organic material during the rainy season. Therefore, these areas of logs are very productive because they come from areas with high concentration of nutrients.

In contrast, the man-made floating objects are called Fish Aggregating Devices (FADs). They are usually formed by a bamboo raft with panels of netting submerged underwater, carrying a buoy beacon which provides information about its position, allowing the fisherman to locate the object (Delgado de Molina et al. 1999). Moreover, some new buoys are equipped with an echosounder which estimates the biomass associated underneath (Dagorn et al. 2013). Normally, tunas are associated with FADs during night and then leave the object in the morning, so the most number of sets are carried out during the sunrise (Hall 1998).

The aggregation behavior of tunas has the advantage of make the detection and the capture of tunas easier than for free school sets, because the school is kept relatively fixed in space. Therefore, sets on FADs have a high level of success (95%) compared with Free School sets (55%) (Floch et al. 2012).

Since the introduction of fishing aggregation devices in the fishery, this fishing mode has shown a substantial development worldwide. The catches of tropical tunas have increased and the costs related to searching process have decreased. Along this manuscript the acronym FAD will include both natural (e.g. logs) and anthropogenic floating objects such as man-made bamboo rafts equipped with radio-range beacons or echo sounders.

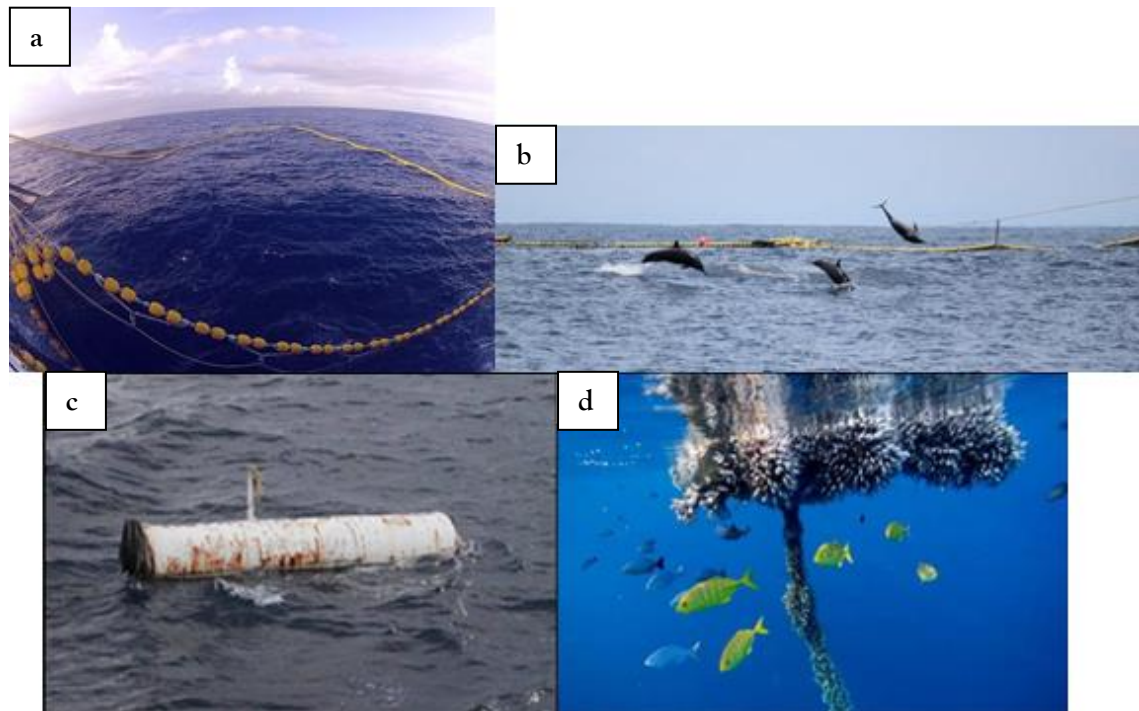


Figure 9. a) Free school set (Source: ISSF), b) Dolphin sets (Source: www.fecop.org), c) Natural-log sets (Source: www.nunas.com) and d) artificial Fish Aggregating Devices (FADs) (Source: www.alexhoffordphotography.com).

The tuna species usually caught in FAD sets are the skipjack and juvenile yellowfin and bigeye. Furthermore, floating objects also attract a very diverse range of pelagic animal species, such as other tunas, fin-fishes, but also including other non-fish species such as turtles, sharks, or rays. The reasons of the aggregation of these species are not well known (Castro et al. 2002); however, there are several hypotheses to explain the aggregative behavior around floating objects. 16 different hypotheses were reviewed by Fréon and Dagorn (2000) and two of these hypotheses are considered the most credible: the meeting point hypotheses (Dagorn and Fréon 1999) and the indicator-log (Hall et al. 1992) hypotheses.

The meeting point hypothesis suggests that tuna and other tuna non-species tend to meet around floating objects with the aim to facilitate or improve schooling behavior, which is considered to provide several advantages to members of the school.

On the other hand, the indicator-log hypothesis proposes that tunas would relate floating objects with rich areas. Natural floating objects are often located in productive areas because they come from river runoffs providing an important source of nutrients to the oceans. Despite being two of the most supported hypothesis, none have been demonstrated yet.

5.3.1. The ecology trap theory

The introduction of FADs in the purse seine fishery has caused changes in the environment of tropical oceans and fishing patterns. In that sense, the possible effects and changes associated with the use of FADs at sea are (Dagorn et al. 2013; Fonteneau et al. 2000): increase of skipjack's catches, alteration of normal movements of tunas, reduction in yield per recruit of yellowfin and bigeye and increase of by-catch. These changes, which can modify the habitat and the behavior and biology of tuna, have been defined under the “ecological trap” hypothesis (Marsac et al. 2000). This hypothesis suggested that the use of FADs may alter the natural movements of tuna from biological productive areas, where natural logs tend to drift, towards less productive areas where FADs can be drifted. Thus, FADs may act as an ecological trap “drifting” tunas to poor areas and, hence, affecting tuna growth, movements and condition.

6. BY-CATCH

The capture and mortality of non-target species, often called “by-catch” (Hall 1999), can be considered one of the major effect of fishing. In the last 20 years, the by-catch has become a major issue in global fisheries management and conservation (Kelleher 2005) (Figure 10).

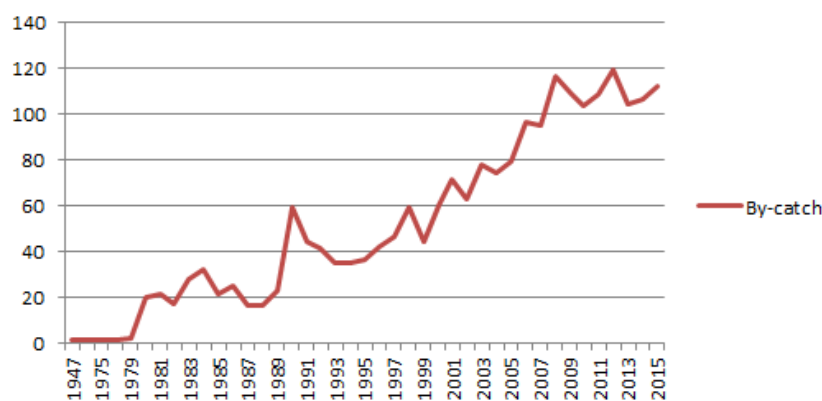


Figure 10. Number of peer-reviewed publications per year containing any word associated with “by-catch” in the title, abstract, or keywords between 1947 and 2015 based on a Web-of-Science (Source: <http://wok.mimas.ac.uk>).

There are many definitions of the term “by-catch” in the scientific literature. The concept has been related, among other, to the “trash” fish caught in the shrimp trawl fisheries, the discards of undersized individuals of target species, or the mortality of species with long life spans, slow growth rates, and low reproductive potential such as sharks, sea turtles, seabirds, and marine mammals (Lewison et al. 2004).

It is difficult to develop a standard international definition of by-catch due to the diverse nature of the world's fisheries, their historical definitions and their different interpretations of by-catch (FAO 2011).

In the tropical tuna purse seine fishery, the definition of by-catch is different depending of the ocean and the country where the fleet is established. Some of these definitions are depicted in Table 1. Thus, for some authors, the term by-catch refers to the catch of non-target species regardless their fate (release at sea alive, discarded dead or retained on board) (Amandè et al. 2010). This definition introduces the concept of "by-product" which is the part of the by-catch that is kept for a particular use, i.e. to be consumed on board or sold later on the local African market. Thus, "faux poisson" (false fish) is a peculiar term used for the by-product of the purse seine fishery which is sold in West Africa and concretely, in the port of Abidjan (Ivory Coast). It is comprised of a mix of damaged or undersized target tunas, minor tuna species and other fish species, that are sold on the local market (Romagny et al. 2000).

Table 1. Some of by-catch definitions.

Source	Definition
(Saila 1983)	"That part of the gross catch which is captured incidentally to the species toward which there is directed effort. Some, all or none of the by-catch may become the discard catch".
(McCaughan 1992)	"That portion of the catch returned to the sea as a result of economic, legal or personal considerations, plus the retained catch of non-targeted species".
(Alverson 1994)	"Discarded catch plus incidental catch", where discarded catch is "that portion of the catch returned to the sea as a result of economic, legal or personal considerations" and incidental catch is "retained catch of non-targeted species".
(Hall 1996)	"The part of the capture that is discarded dead or assumed to die as a result of the fishing operation".
(Hall et al. 2000)	"That portion of the capture that is discarded at sea dead (or injured to an extent that death is the most likely outcome) because it has little or no economic value or because its retention is prohibited".
(Amandè et al. 2010)	"All non-target species plus small or damaged target tuna species that are not marketed through canneries. The bycatch may be divided in by-products and discards".
Lezama-Ochoa et al. 2016	"The catch of non-target species, whether retained and sold or discarded".

In contrast, for others, by-catch is the part of the capture that is discarded dead or assumed to die as a result of the fishing operation (Hall 1996).

The dissimilarities between definitions, confirm the different perceptions among different stakeholders about the by-catch issue, which includes different economic, ecological, political, conservation views about the problem. Different definitions of by-catch difficult the comparison of by-catch levels between different fisheries and the accuracy on the global estimates of by-catch by ocean (Kelleher 2005).

Sometimes, the term “discard” has been confused with the term “by-catch” in the literature, which has caused a significant difficulty to develop works about their management. In any case, by-catch/discards have negative connotation because it is a resource wasted unnecessarily (if they are not retained or sold) that should be reduced due to conservation, economic and ethical concerns (Harrington et al. 2005; Kelleher 2005).

In this Thesis, the “by-catch” is defined as the catch of non-target species, whether retained and sold or discarded (Figure 11).

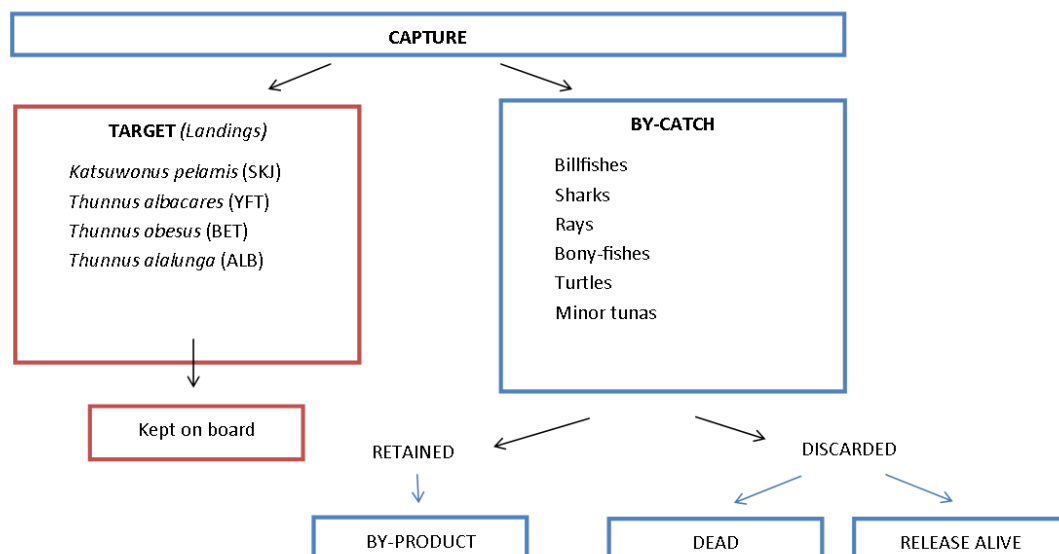


Figure 11. Conceptual scheme of the fate of by-catch, the definition of by-catch and the terms used in this study using as an example the purse seiners fishery targeting tropical tunas (Source: modified from Amandé et al. 2012).

The by-catch groups included in this definition are: billfishes (marlins, sailfish, etc), sharks (silky, oceanic whitetip, hammerheads, etc), rays (mantas, devil rays, pelagic stingrays, etc), pelagic bony fishes (rainbow runner, mahi-mahi, wahoo, rough triggerfish, etc), sea turtles (leatherback, loggerhead, etc) and marine mammals (fin whale, common dolphins, etc) (Figure 12).



Figure 12. Some examples of by-catch species (Source: Nerea Lezama-Ochoa)

By-catch in the purse seiners may happen because a species does not have value in the market, because an individual of a marketable species doesn't have the adequate size for the market or is damaged during the fishing operations (Hall and Roman 2013). The population-level consequences of by-catch vary across species and geographic regions (Safina 2008). The most recognizable consequences of fisheries by-catch are population declines (Cook 2003). Some populations are under heavier pressure from fisheries or are less resistant to a given level of mortality than others (Safina 2008). Concretely, some species with 'slow' life histories such as sharks or turtles are particularly vulnerable to mortality caused by human activities (Heppell et al. 2000). The negative consequences of by-catch are the mortality of these species, but also the changes which may occur at community and ecosystem level, often called "high-order" effects, which are more difficult to detect (Lewison et al. 2004). Thus, large marine vertebrates play an important role in food-web structure and any change may modify their abundance and species composition with an associated loss of biodiversity (Alverson 1994; Cook 2003). Furthermore, mortality of by-catch species may disturb the ecosystem by transferring biomass between water layers (Hill and Wassenberg 2000), causing anoxia as consequence of the accumulation of this biomass and therefore, affecting the normal flow of nutrients and matter (Dayton et al. 1995). Other indirect but negative consequences of the by-catch are the gear damage, the lost fishing time, the loss of income and the problems associated with the safety of fishermen (Hall 1996).

6.1. The by-catch problem in the purse-seine fishery

By-catch emerged as a problem for marine conservation in the 1960s when hundreds of thousands of dolphins died annually in the Eastern Pacific Ocean by the tuna purse-seine fishery (Hall et al. 2000). As consequence of the pressure from environmental organizations, the Marine Mammal Protection Act (MMPA) was implemented in 1992 (Hall et al. 2000). Furthermore, at that time fisheries observer programs were created to monitor fishing operations and by-catch. Since then, several Regional Fishery Management Organizations (RFMOs) operate with the objective of managing these problems and reduce by-catch values within a regional/ocean context: in 1949 the Inter American Tropical Tuna Commission (IATTC) in the Eastern Pacific Ocean (EPO), in 1969 the International Commission for the Conservation of Atlantic Tunas (ICCAT) in the Atlantic Ocean and adjacent seas and in 1996 the Indian Ocean Tuna Commission (IOTC) in the Indian Ocean.

Although purse seine fishery has proven to be more selective than other fisheries (Alverson 1994), since two decades by-catch in the tropical tuna purse-seine fishery is subject to special attention with the introduction of FADs.

The main problem associated with the expansion of the FAD fisheries is the increase of captures of juvenile bigeye and yellowfin tunas (Hall and Roman 2013). Furthermore, a high number of by-catch species are normally caught in FAD sets in comparison with Free School sets. Despite to FAO has steered these problems through the different international plans and Technical Consultations, the problem is unresolved (Alverson 1994; FAO 2009; Kelleher 2005).

6.2. By-catch estimations in the purse-seine fishery

Globally, by-catch rates are different depending on the fishery and vary greatly in space and time in function of several other factors such as the technical, economic or environmental factors (Kelleher 2005).

The tropical shrimp trawl fisheries, for example, have the highest by-catch rates with 62.3%, whereas the long-line account about 28.5% (Hall and Roman 2013).

In geographical terms the highest by-catch rates are in the Northeast Atlantic and Northwest Pacific. In contrast, small-scale fisheries such as purse-seine (5.1%), handline (2%), or pole and line (0.4%) fisheries generally have lower by-catch rates than industrial fisheries (Hall and Roman 2013).

In tuna fisheries, the long-line fishery has the highest by-catch rates (22%). In the case of purse seiners, the by-catch rates vary from 1.5% in small Mexican seiners to 6.9% in the IATTC area. Furthermore, the by-catch rates for industrial PS are 7.5% in the Atlantic Ocean and 3.54% in the Indian Ocean (Amandè et al. 2008a; Amandè et al. 2010; Hall and Roman 2013). In the case of industrial purse seiners, by-catch includes undersized target species, non-commercial tunas, shark, rainbow runner, dolphinfish, triggerfish, billfish and mantas (Amande et al., 2010). Non-commercial tunas are the vast majority of the by-catch in all oceans, followed in importance by the large pelagic bony fishes (Hall and Roman 2013). Tuna discards represent 54% of total by-catch in the Indian Ocean (Amandè et al. 2008a). The remaining 46% of the by-catch consisted mainly of bony-fishes (33.7%), billfishes (1.5%), sharks (10.1%) and rays (0.7%). In the case of the Atlantic Ocean, tunas represented 83% of the total by-catch. The remaining 17% of the by-catch consisted of bony-fishes (10%), billfishes (5%) and sharks and rays (2%) (Amandè et al. 2010). In the Eastern Pacific Ocean, the tuna discards rate of the bycatch (of the three main species: yellowfin, skipjack and bigeye) is around 5%. From the rest of 95 % of the bycatch, about 89% of this by-catch comes from sets on floating objects, 10% from school sets and 4% from dolphin sets (Hall and Roman 2013). The remaining by-catch consisted of bony-fishes (94%), billfishes (0.4%), sharks (4.6%) and rays (0.4%) (Hall and Roman 2013).

The total amount of by-catch and discards for purse seine fishery in FAD sets is large and has been estimated at 100000 t annually (Fonteneau et al. 2013), for which most is comprised by tunas and bony-fishes. It represents about 4-5% of total catch by weight, which are lower rates than those than estimated for some other tuna fisheries such as longline (Gerrodette et al. 2012). However, these relatively low levels of by-catch can have a large effect on some population's viability due to the special life history characteristics of the megafauna (Heppell et al. 2000). In the case of the Free School sets, it is only 1-2% of total catch by weight.

7. ECOSYSTEM APPROACH TO FISHERY MANAGEMENT (EAFM)

Maintaining of ecological systems and their biodiversity allows social and economic welfare of human beings (Rosenberg 2003). However, the overexploitation of many fish stocks (FAO 1997) and the impact on communities as well as the mortality of vulnerable species (Dayton et al. 1995; Hall 1999) have contributed to change the philosophy about the fisheries management. Thus, marine ecosystems require urgent implementation and development of measures for the management and conservation of their marine resources (Halpern et al. 2008).

7.1. The origin of EAFM

The 1995 Code of Conduct for Responsible Fisheries (the Code) of the Food and Agriculture Organization of the United Nations (FAO) (Garcia 2000) demands that fishing be conducted with due respect for the environment. Moreover, the Code also recommends the preservation, protection and conservation of biodiversity of ecosystems by reducing fisheries impacts on non-target species and the ecosystem in general.

Thus, the Ecosystem Approach to Fishery Management (EAFM) is a concept which emerged from the link between ecosystem and fisheries management, based on the recognition of the interdependence between ecosystem health and human well-being (FAO 2009) and with the objective of reducing by-catch levels.

Moreover, the concepts and principles of an Ecosystem Approach to Fishery Management (EAFM) are not new. Some other conferences (Stockholm Conference (1972), United Nations Conference on Environment and Development (1992)), agreements (United Nations Agreement on Straddling Fish Stocks and Highly Migratory Fish Stocks (1995)), and conventions ((Law of the Sea (1982), Biological Diversity (1992))), served also as origins, stimulated the development of the sustainable initiative and were the precursors to EAFM. The UN Conference on the Environment and Development (1992) defined sustainable, whereas the Convention on Biological Diversity (1992) called for conservation of biodiversity at the genetic, species and ecosystem levels (Motos and Wilson 2006). Furthermore, the protection and conservation of biodiversity was agreed in the declaration from the World Summit on Sustainable Development in Johannesburg (2002) (Motos and Wilson 2006). Finally, the most important step was taken with the adoption of the FAO Reykjavik Declaration on Responsible Fisheries in the Marine Ecosystem in 2001, which introduces ecosystem considerations into fisheries management (Link 2010) and recognizes the complex interrelationships between fisheries and marine ecosystems.

7.2. From single-species approach towards Ecosystem Approach to Fishery Management

Responsible fisheries management has become important and of great interest to the scientific community, resource managers, policy makers, stakeholders, and the general public. However, most fisheries management systems have been generally designed to focus only on managing one species. Single-species (SS) approaches may provide very useful insights into population dynamics of a stock, but it has limitations and has become less viable for many reasons (Link 2010). In general, single species management approaches will never be able to provide information about

changes in ecosystem structure and functioning, fishing gear impacts, biodiversity or impacts on habitat (Link 2010). As they are currently used, they may not provide information about how a particular stock might be impacted by other factors such as thermal restrictions, species interactions, predation mortality or other environmental factors which influence their distribution.

The correct design of the management plan for a given fishery may include the identification of the stakeholders, a description of the fishery and the area in which it takes place, the identification of the objectives, identification of the main management measures, decision rules and plans for monitoring, and finally, assessment and review of the actions taken (Motos and Wilson 2006).

For that reason, it appeared the new approach called Ecosystem Approach to Fishery Management (EAFM), or Ecosystem-based Fisheries Management (EBFM), defined by Link (2010) as “managing fisheries to coordinate, account for, and include all factors in a holistic, synthetic and integrated fashion”. Although fisheries are emphasized, the marine mammals, protected species or non-target species and their interaction with the environment are also included in these terms.

The main objective of EAFM is “maintaining the structure and function of marine ecosystems including their biodiversity” (Motos and Wilson 2006). Thus, the EAFM approach is better than the Single-Species approach because this broader approach introduces the effects of fishing on non-target species, protected species, habitat, etc. and recognize that marine ecosystems provide “goods and services”, which are essential for the human well-being.

7.3. Characteristics and benefits of EAFM

For implementing EAFM there are a list of issues that need to be considered, such as: the geography (key features of the ecosystem: lake, open sea, etc), the key species (size of species, taxonomy of species), the abiotic factors (thermocline, frontal systems, upwelling systems), the economic factors (value of the species) and the fishery context (type of gear, fishing effort, effort distribution) (Link 2010). Obviously, there are some challenges to overcome before to routinely implement EAFM (Link 2010). For example, there are costs associated to adopting EAFM, particularly relating to data availability, which increases complexity, and increases uncertainty.

However, there are also benefits of EAFM, some of which are: 1) provide more conservative management recommendations; 2) provide specific managements about by-catch species, habitats

or vulnerable species; 3) provide more accurate assessment and evaluations of the dynamics of Living Marine Resource (LMR) populations and communities; 4) provide long-term sustainability for intergenerational equity; 5) improve short-and long-term economics for participating fishers; and 6) directly address trade-offs among and within sectors and also trade-offs across biomass allocation (Link 2010).

8. INDICATORS

Marine ecosystems are complex and sometimes it is difficult to distinguish the origin of the impacts on species and areas. Therefore, it is necessary to develop indicators for ecosystem assessment to separate the effects of fishing from natural fluctuations and from the global environmental changes (Motos and Wilson 2006).

8.1. Selection of indicators

An indicator is a “quantifiable variable (measure), model, pointer or index that relate to a criterion” (Jackson et al. 2001; Motos and Wilson 2006). Indicators are needed to reflect the economic, physical and biological state of the ecosystem. Moreover, indicators are used to inform managers, stakeholders and the public about the decisions and the conservation measures to be implemented for the correct management of the fishery (Motos and Wilson 2006). However, it is difficult to select appropriate indicators related to management objectives which reflect the impact of fishing.

Guidelines to select the correct indicator and develop frameworks for their application are essential. Some of the conditions to select an effective ecological indicator are (Duraiappah et al. 2005): the indicator should provide information about changes; be sensitive enough to detect important changes at the appropriate temporal and spatial scale; be based on reliable data that are available to assess trends; and be easily understood by policy-makers.

Thus, a large number of indicators have already been proposed; some of them are well-described in literature, such as fishing mortality whereas others are still under development, such as aggregate system properties (Motos and Wilson 2006). In addition to this, Buckland et al. (2005) listed for example six criteria which are related to three components of biodiversity (species richness, species evenness and abundance) which any measure should satisfy. The most important criteria are also that the measure should have a good precision and not vary with the size of the

sample. With respect to the last one, some diversity indices which reflect the species richness and describe their abundances among communities are becoming the most important in the last years. For example, the Marine Strategy Framework Directive adopted by the European Commission in 2008, developed a set of 11 descriptors and indicators to achieve a Good Environmental Status (GES) of the ocean and to contribute to an ecosystem-based management of marine waters (Bourlat et al. 2013). Among those descriptors, the “Biological diversity” descriptor, for example, includes indicators such as (i) “distributional patterns”, (ii) “population abundance”, or (iii) “composition of ecosystem components” (habitats and species).

8.2. Indicators for a correct EAFM

The aim of the EAFM is not to find the best indicator, because it is impossible that all aspects of the ecosystem dynamics may be described by a single indicator (Motos and Wilson 2006). Therefore, a combination of different indicators (covering different species, environmental variables, and geographical areas) and models to describe different characteristics of the ecosystem (abundance, richness, dominance, etc) is recommended.

Many different types of indicators have been developed by EAFM to reflect a variety of aspects of ecosystems in simple terms, including biological, chemical and physical. However, one of the most basic but important ecological indicators to implement EAFM is species diversity, which is closely related to the concept of biodiversity (Motos and Wilson 2006). Thus, if the objective of EAFM is to reduce the levels of by-catch and maintain the biodiversity in the marine ecosystem, it will be necessary to consider a number of techniques which describe, analyze and model the biodiversity of the by-catch species assemblages under the impact of the fishing exploitation. To achieve this goal, ecosystem measures and model outputs can contribute to the correct management of the fishery (Link 2010). Furthermore, it is possible to provide forecast for future species distributions in short to medium term under different scenarios of climate change via habitat distribution models.

The choice and origin of these measures of biodiversity will depend on the use to be made (Safina 2008) and, as consequence, different biodiversity measures and models have appeared on the literature. There are measures which describe the structure, species composition and diversity of species in a determined area. Other measures, in contrast, such as models, are useful for describing the habitat distribution of these species. However, although significant progress has been made in modelling the properties of marine ecosystems, there are still important problems to take into account. Firstly, it is difficult to select the appropriate level of complexity of the

models and the effect of high correlation between the independent variables. Moreover, the parameter estimation sometimes is difficult because the models require large amounts of data (occurrences, environmental data) and are not always easy to obtain (Motos and Wilson 2006).

In this Thesis we used different techniques and models for measuring biodiversity of the by-catch species assemblages; which will be described below and be detailed in each Chapter.

MATERIAL AND METHODS

9. MATERIAL-DATA COLLECTION

9.1. Observer programs

The purse-seine fleets operating in the Atlantic, Indian and Pacific Oceans are required to carry observers onboard in accordance with measures adopted by the RFMOs. These requirements are planned through national, regional or RFMO-coordinated programs, or a combination of such programs (Koehler 2013). The aim of the observer programs is to collect data directly from the fishery which cannot be obtained on port or landing site (Ariz et al. 2010).

The observers collect information of fishing activities, catch of target species and by-catch species and size frequencies of by-catches.

For the European fleet, observation protocols were developed focusing on the same objective (i.e. estimation of by-catch) for Spanish and French Purse seiners. Pianet et al. (2000) showed that both countries use similar technology, have similar fishing strategy and share the same observer training technics since their implementation and therefore, the bias associated to the methodology is considered minimal (Bourjea et al. 2014). This observer program protocols are also very similar to those used by other RFMOs in East Pacific (IATTC) and Western and Central Pacific (WCPFC). In fact, those observer program protocols has been standardized (ISSF 2012).

The target coverage for observers program is around 10% of trips (per year) in the EU PS fishing in the Atlantic and Indian Ocean based on ICCAT/IOTC Resolutions and DCF requirements and around 100% in the IATTC observer programs (Amandè et al. 2008a; Hall and Roman 2013).

Despite the observer programs may vary in terms of program management or entrance requirements (Koehler 2013), the European and IATTC observer programs follow in general the same structure. Thus, the information collected by observers is basically divided into four large sections (Ariz et al. 2010):

- Information about the vessel's route and activity, and environmental parameters.
- Information about fishing operations, estimated catches of target species, tuna discards and by-catch species.
- Size distribution of tuna discards and by-catch.
- Information about FADs.

In the case of the Spain and France, their observer programs started in 2003 and in 2005 respectively under the European Data Collection Regulations (Council Regulation no. 1543/2000, Commission Regulation no. 1581/2004, Council Regulation no. 199/2008, and Commission Decision 2008/949/EC). The European Union established a mandatory sampling program to estimate the amount of by-catch and discards in the European Union fisheries. Thus, the French (Institut de Recherche pour le Développement - IRD) and Spanish (AZTI Tecnalia and Instituto Español de Oceanografía - IEO) research institutes were responsible for implementing a common framework for collecting and analyzing the by-catch data from Purse Seiner observer programs. These programs were conducted on the tropical tuna purse-seine fisheries which operate in the Atlantic and Indian oceans (Bourjea et al. 2014).

In the case of the American purse seine fishery, and in accordance with the 1999 Agreement on the International Dolphin Conservation Program (AIDCP), purse seine vessels with a carrying capacity greater than 363 metric tons (400 short tons) and that operate in the Agreement Area (which corresponds to the Inter-American Tropical Tuna Convention (IATTC) Area in the Eastern Pacific Ocean), carry an observer during each fishing trip (100% observer coverage and with weekly data submission to the Secretariat). 70% of observers are employed by IATTC and the remainder by national Observer Programs. This observer program was implemented to document exhaustively the fishing operations by all large purse seiners in the region. As a result, a very valuable dataset has been stored over decades, which includes detailed information on catches and discards for all species caught (ISSF 2014).

The information collected by observers was introduced in a common database (ObServe, Figure 13) in the case of the European fleet (Spain and France) and in the IATTC database for the case of the fleet operating in the Eastern Pacific.

The periods of the French and Spanish PS and IATTC observer programs and the database from which the data were extracted for this study are showed in Table 2.

The data collection for each program as well as the main characteristics of these observer programs in relation to their objectives and methodology applied are explained in Material and Methods section of Chapter 1, 2, 3 and 4.

Table 2. Observer programs of the European PS fishing in the Atlantic and Indian Ocean and of the PS operating in the Eastern Pacific Ocean (IATTC).

Observer programs	France		Spain		IATTC	
	Period	Institute	Period	Institute	Period	Institute
EU DCR a	2003-2010	IRD b	2003-2010	AZTI c and IEO d		
IATTC e					1993-2011	IATTC e

a European Union Data Collection Framework

b Institut de Recherche pour le Développement

c AZTI-Tecnalia Unidad de Investigación Marina

d Instituto Español de Oceanografía

e Inter-American Tropical Tuna Commission

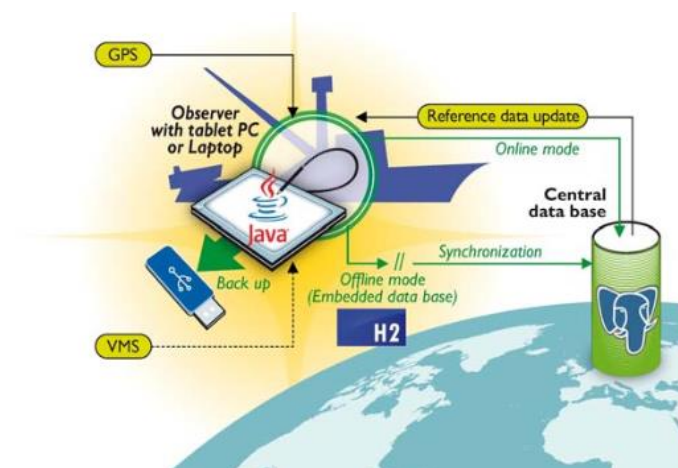


Figure 13. Diagram of the integrated information system ObServe (from Chavance et al. 2012).

9.2. Field work and correction of the Azti's database

During the first year of the thesis, a trip from 22/10/10 to 24/11/10 was carried out in the Atlantic Ocean aboard the tuna vessel “Albacora 15” to get familiarized about the work of observers, data and species composition of the tropical tuna purse seine fishery. A total of 23 sets were observed: 4 Free School (FSC) sets, 18 FAD sets and 1 Unidentified (IND) set.

In addition, and before to extract the EU PS by-catch data from the Atlantic and Indian Oceans through the “ObServe” database (shared by the three European marine institutes), the database from AZTI was entirely revised and corrected using a R script.

Through a series of ranges and parameters which were specified in the script, the following errors related to: errors with respect to the activity of the vessel; the type, the duration and the position of the set; the trip; the catch (in number or tons) of the tuna and by-catch species, the size and the species composition of the species were corrected.

After detecting the outliers/errors, observer books were reviewed and the mistakes corrected in the database. In total, all the information since 1998 to 2011 was revised and corrected in the AZTI’s database with respect to the Atlantic and Indian Ocean.

10. METHODS: INDICATORS FOR MEASURING BIODIVERSITY OF THE BY-CATCH COMMUNITIES

The objective of biodiversity studies is often to compare the biodiversity metrics and models through time or between areas. However, problems associated with the imperfect detection of the species have as consequence the underestimation of populations (when species are common) or the creation of false absences (when species are rare) (Iknayan et al. 2014). Furthermore, determination of diversity and abundance in animal communities is heavily influenced by the season in which a sample is taken, and the reproductive stage of a given taxon. Often, entire assemblages are most measurable at a given time of day. It is at these times when samples should be taken to maximize species richness/biomass (Magurran and McGill 2011). For example, it is known that tuna and by-catch species tend to appear at surface early in the morning to eat, which makes easier to capture them (Fréon and Dagorn 2000). The ability to describe and analyze biological diversity in different ways taking into account factors affecting their estimation helps to better understand how ecosystems work (Magurran and McGill 2011).

Species diversity is one of the most components used to represent biodiversity (Hamilton 2005). Species diversity in any habitat can be measured in three different ways: as Alpha diversity, Beta diversity and Gamma diversity (Table 3). Alpha diversity measures the species diversity of a particular and heterogeneous community; Beta diversity, the gradient of change in the composition of species between different communities and Gamma diversity the total species diversity in a landscape (Whittaker 1960). In this work, only Alpha and Beta diversity were considered.

Table 3. Definitions of Alpha and Beta diversity.

Diversity level	Definition by Whittaker (1960)
Alpha diversity	Measures the species diversity of a particular and heterogeneous community
Beta diversity	Measures the gradient of change in the composition of species between different communities
Gamma diversity	Measures the total species diversity in a landscape

The main characteristic of a community is that some species are abundant, other moderately common and the remainder rare. Based on that, Alpha diversity is divided into two components: species richness, which is the number of species in the unit of study; and species evenness, which is the relative abundance of each species in this unit of studio. The ability of an assemblage to resist change or recover from a perturbation is related to both measures (Magurran 2004).

10.1. Species richness estimation

In many ways species richness is the fundamental measure of biological diversity (Magurran and McGill 2011). It not only provides a measure of the variety of life as represented by the number of species, it is commonly used to identify biodiversity hotspots and plays an important role in conservation planning (Magurran and McGill 2011). Thus, species diversity is obviously linked to species richness (Magurran and McGill 2011).

However, despite its wide appeal and apparent simplicity, accurate estimates of species richness can be remarkably difficult to achieve because an increase in sampling effort always lead to an increase in richness. Thus, Gotelli and Colwell (2011) proposed different solutions for this problem with the application of species accumulation curves. This technique shows the cumulative number of species recorded as a function of sampling effort (i.e. number of samples) or the rate at which new species are found within a community. As 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). Furthermore, this cumulative number of species can be extrapolated by non-parametric estimators (i.e. Jackknife, Bootstrap, Chao, etc...) to provide a total estimate of species richness (which is represented by the value of the asymptote in the accumulation curve) (Magurran and McGill 2011). These techniques, which use information about rare species in an assemblage to adjust for the number of species present but not detected, are the most consistent way for estimating the total number of species using information about the observed number of species (Magurran and McGill 2011). In

this Thesis, the Chao2 non-parametric estimator was selected for calculating the total number of species and the species richness was calculated to compare diversity between areas and fishing modes (mean per set), as well as to model the habitat preferences of the by-catch communities.

10.2. Evenness-rank abundance curves

The relative abundance of a species in an assemblage is the main factor that determines its importance in a diversity measure (Magurran 2004). In that sense, richness measures treat the species that are exceptionally abundant in the same manner as those that are extremely rare (Magurran 2004). Thus, evenness is better to describe the variability in species abundances. A community in which all species have approximately equal numbers of individuals (or similar biomasses) would be considered as extremely even community (Magurran 2004).

One of the best known and most informative method to study the relative abundance of species is the rank/abundance plot or dominance/diversity curve. In this curve, species are plotted from most to least abundant along the horizontal (or x) axis. Their abundances are typically presented in a log₁₀ format (on the y axis) (Magurran 2004). One advantage of a rank/abundance plot is that, when there are relatively few species, all the information concerning their relative abundances is clearly visible, whereas it would be incompetently showed in a histogram format (Wilson 1991).

In this Thesis, the rank abundance curves were only constructed to obtain the most abundant by-catch species in each fishing mode. In addition, the Pielou's J-evenness index (mean evenness per set) was calculated in the three oceans as the rank abundance curves did not show clear patterns in the Atlantic/Indian Ocean due to the lower sample size. The Pielou's J-evenness index, which is calculated as $H/\ln(S)$ where H is the Shannon diversity index and S the Species richness, was applied for comparing the evenness between areas and fishing modes.

10.2.1. *Species distribution models*

Alternatively, the shape of the rank abundance plot is often used to infer which species abundance model best describes the data. Therefore, the slope of the rank abundance plot describes the structure and the community diversity. Steep plots signify assemblages with high dominance, such as the one that might be found in a Geometric or Log series distribution, while shallower slopes imply the higher evenness consistent with a Log normal or even a Broken stick

model (Figure 12) (Magurran 2004). Whittaker (1965) indicated that low diversity communities are Geometric, medium diversity communities are Log-series and high diversity communities are Log-normal.

Species distribution models are used to examine how communities are assembled. Concretely, a Geometric series distribution model is predicted to occur when species arrive at an unsaturated habitat at regular intervals of time, and occupy fractions of remaining niche space.

A Log series pattern, by contrast, will result if the intervals between the arrival of these species are random rather than regular. The Log-normal model reflects a community normally distributed with few dominant and rare species. Finally, Zipf-Mandelbrot model has been interpreted as reflecting a successional process in which later colonist have more specific requirements than the first species to arrive (Magurran 2004). This assumes that the entry of species into a community is dependent upon changes caused by those species already present.

Furthermore, communities can be divided into two components: permanent members versus occasional species. The distribution of permanent species typically resembles a Log normal whereas occasional species tend to follow a Log series distribution and rare species a Zipf-Mandelbrot distribution of species abundance.

In this Thesis, the abundance was fitted to the following species distribution models (using the “vegan” package and “radlattice” function in R software) (Figure 14): Null model, Preemption model, Log-normal model, Zipf model and Zipf-Mandelbrot model. A number of different criterias have been used to compare species distribution models; among them, Akaike’s information criterion was widely used (Matthews and Whittaker 2014).

10.3. Heterogeneity index

Globally, a heterogeneity index, combining elements of richness and evenness, is the most popular method of diversity measurement. The so-called ‘heterogeneity measures’ have found particular application in environmental management and in monitoring the consequences of anthropogenic change (Magurran 2005). The heterogeneity measures can be divided into two categories: parametric indices, that are based on a parameter of species abundance model (such as Log series model) and non-parametric indices (such as Shannon index) that make no assumptions about the underling distribution of species abundances. Non-parametric measures can be also divided into those that use the species richness as component of diversity (Shannon index) and those (Berger-Parker, Simpson) that focus on the dominance/evenness component. Whereas the

Simpson index provides a good estimate of diversity at relatively small samples sizes, the Berger-Parker index provides a simple and easily interpretable measure of dominance (Magurran 2004).

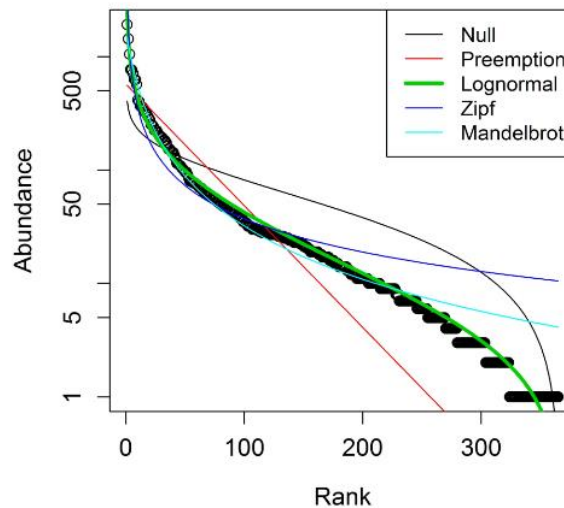


Figure 14. Rank/abundance plots illustrating the typical shape of some species abundance models: the Broken-stick model ("Null", black line), Geometric model ("Preemption", red line), Log-normal (green line), Zipf (dark blue line) and Mandelbrot (light blue line) (Source: Matthews and Whittaker, 2014).

Shannon index (Shannon and Weaver 1949) is widely used in biodiversity studies although there are some shortcomings associated to this index (for example, as it is difficult to interpret as don't separate richness and evenness values) (Magurran 2004). It assumes that individuals are randomly sampled from an infinitely large community (Pielou 1975) and that all species are represented in the sample. The Shannon index is calculated from the equation:

$$H' = - \sum p_i \cdot \ln \cdot p_i$$

,where p_i is the proportion of individuals found of the i th species. The value of the Shannon index usually ranges between 1.5 and 3.5 and rarely is higher than 4. Despite of great criticisms around this index, the Shannon index generally performs well with respect to five of the six criteria for biodiversity index developed by Buckland et al. (2005) (Magurran and McGill 2011). In this Thesis, the Shannon diversity index was used to compare diversity between areas and fishing modes (mean per set), as well as to model the habitat preferences of the by-catch communities.

10.4. Beta diversity

The choice of an index to study the similarity in species composition (Beta diversity) and their relationship with geographical or environment factors depend on the aims of the investigation and the form of the data (Magurran 2004). Species composition matters as much, or more, than species richness when is directly related with the environment and the structure of the assemblages. This is because changes in species composition can lead to a reduction of the resilience of the ecosystem.

Thus, Beta diversity is a measure of the extent to which the diversity of two or more spatial units differs in terms of their species composition (Magurran 2004). There are multiple methods of measuring Beta diversity. Among them, two different dissimilarity/similarity indexes were proposed in this work.

Firstly, the Simpson dissimilarity index or beta-sim index (based on presence-absence data) is defined as:

$$beta - sim = \frac{\min(b, c)}{[a + \min(b, c)]}$$

, where a is the number of species present in both samples and b and c are the numbers of species occurring in only one of the sample. Beta-sim index was calculated in the Atlantic and Indian Ocean. Their values range from 0 to 1 representing highest and lowest similarity.

Secondly, Bray-Curtis index, which provide accurately estimations about similarities in species composition (based on abundances) between areas was calculated in the Pacific Ocean. It is defined as:

$$BC = 2W/(A + B)$$

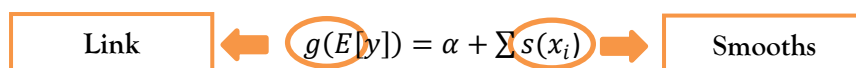
, where A and B are the sums of the abundances of all species at the two areas and W is the sum of minimum abundances of all common species (i.e. number of individuals) between two areas where the species were sampled (Irigoiien et al. 2011). The value of this index should be 1 when two samples are identical and 0 when samples have no species in common.

In addition to these measures, Mantel test determines the correlation between species similarity matrices and environmental and geographic distance. Concretely, the Mantel (1967) test is a non-

parametric test based on a bootstrap randomization of the matrices, to determine the frequency of the similarity observed by chance. This test (Legendre and Legendre 2012) computes a statistic “r” which measures the correlation (like a correlation coefficient) between two matrices (matrix of similarity with matrix of distance or matrix of similarity with matrix of environment) resulting from the cross product of the matrix elements (previously normalized). Since similarity and distance matrix entries are not independent, the Mantel statistic is tested by a non-parametric permutation test (999 permutations were computed for each test). The environmental distance and the geographical distance among sampling sites is measured with the Euclidean distance. The selection of the most relevant environmental variables to be included in the test is obtained from the “bioenv” function in R software.

10.5. Generalized Additive Models (GAMs)

Generalized Additive Models (GAMs) are models which can explain diversity patterns (response variable) in function of environmental, temporal and geographical variables (predictor variables). Such models, which are non-parametric generalizations of multiple linear regression techniques (Hastie and Tibshirani 1990), are useful for modelling continuous or categorical variables, by replacing the linear form by a sum of smooth functions (below). Furthermore, an exponential family distribution is specified for the response variable (for example normal, binomial or poisson distributions) along with a link function. In this Thesis, GAMs were proposed for modelling the habitat preferences (geographical, spatial and environmental) of the by-catch communities with reference to the species richness and Shannon diversity index in both fishing modes (FAD versus Free School) and in the three oceans. Specific methodology (i.e. selection of the family distribution, use of regression splines and selection of the covariates) is explained in detail in Chapter 1, 2 and 3.



10.6. Habitat distribution models

Willing to improve the understanding of the habitat modelling approach addressed in this PhD Thesis, this subsection aims to describe the theory, methods and the steps required to build a habitat model, together with their potential applications.

These models, called habitat distribution models or species distribution models (SDM) identify relationships between known species distribution data (presence or abundance) and environmental predictor variables to predict the potential suitable habitat for species, as in our case, in the marine system (Marshall 2012) (Figure 15).

They provide extensive information about the distribution of the species and allow the prediction of changes in their distribution (Guisan and Zimmermann 2000). Accurate knowledge of species distribution is a fundamental issue in ecology and conservation, and therefore, these models have become essential tools in biodiversity conservation and management (Elith and Leathwick 2009). Furthermore, they have been widely used to project the potential effects of anthropogenic global warming and climate change on species distributions and ecosystem properties (Franklin 2010).

While these modelling methods have been widely applied in terrestrial ecology, their application in marine ecosystems is more recent (Robinson et al. 2011). Thus, SDMs have been applied to address conservation and ecosystem management related issues such as the creation of marine protected areas (Valavanis et al. 2008), for predicting the commercial fish distribution (Jones et al. 2012) or the changes in distribution of marine biodiversity in response to climate change (Beaugrand et al. 2002; Cheung et al. 2009).

A correct model prediction depends of complete, reliable and non-biased data (Lobo 2008) of the species distribution and the main environmental variables. There are several techniques to build SDMs (Franklin and Miller 2009; Guisan and Zimmermann 2000), but the adequate selection of the modelling algorithm which is essential for habitat distribution modelling (P Anderson et al. 2006) depends on the objectives and the data available. The may be based on presence data (MaxEnt, Bioclim, etc) or based also on presence-absence data (GAMs, GLMs, etc).

In addition, there is another way to model species distribution when only presence data are available. This alternative approach is based on the generation of (i) background data or (ii) pseudo-absence data from the study area (Pearce and Ferrier 2000). Pseudo-absence techniques tend to perform better than presence-only models (Brottons et al. 2004; P Anderson et al. 2006) and can be generated randomly or according to a set of weighting criteria (Barbet-Massin et al. 2012). The main difference between both techniques is that background method generates automatically 10000 points over the study area and includes species occurrence sites within the background dataset (Pearson et al. 2007). In contrast, the pseudo-absence method doesn't include species occurrence within the set of pseudo-absences and allows to select the number of points based on the objective of the work or the position of other related-species.

Once the models are built and calibrated, the model is represented in the geographical space through the construction of habitat suitability maps. The evaluation of the model is the final step for assessing the accuracy of the predictions and informing about the applicability of the model (Pearce and Ferrier 2000). Different measures of prediction accuracy have been developed for evaluating the model, which will allow determining if the model is acceptable. Threshold dependent measures, for example, are mostly derived from the confusion matrix (Fielding and Bell 1997).

There are three main methods to address model evaluation (Araújo et al. 2005): resubstitution, data partitioning and external validation; however, data partitioning has become the most common strategy where the data is split into two random sets (one to calibrate or train the model and the other one to evaluate it) (Franklin 2010).

In this Thesis, the MaxEnt habitat distribution model was selected for studying the potential suitable habitat for *Carcharhinus falciformis* and *Canthidemis maculata* by-catch species in the Atlantic, Indian and Eastern Pacific Ocean (Chapter 4). We chose this model because it is considered one of the best modelling techniques (P Anderson et al. 2006) when no real absences are available, showing higher predictive accuracy than GLMs, GAMs, BIOCLIM or GARP distribution models (Franklin and Miller 2009). In addition, this type of model is useful to obtain an overall perspective of their habitat with different number of samples and few predictors.

By-catch data from this work was considered presence-only, as true absences were unknown because the absence of species in a set could be explained by three reasons: 1) the species was not captured by the net but was present nearby (i.e. was not circled by the PS), 2) the species was present but escaped from the net, and 3) the species was captured but it was not recorded by the observer. Therefore, a set of pseudo-absences with the same number as occurrences was randomly created inside the sampled area. The model with the generation of pseudo-absences was applied and evaluated through data partitioning method and through threshold dependent measures.

The different techniques, biodiversity measures (Alpha and Beta diversity) and Generalized Additive Models applied in this work are explained in Chapter 1, 2 and Chapter 3. The habitat model applied in this PhD Thesis which corresponds to the Maximum Entropy Modeling (MaxEnt) and the principal steps required to build and validate this model are explained in detail in Chapter 4.

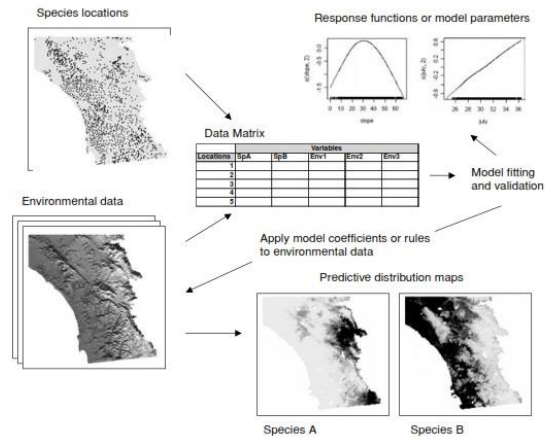


Figure 15. Example of habitat distribution model and its process (Source: Franklin, 2010).

STUDY AREA

Regional ocean processes such as circulation, environmental variables, or upwelling systems influence the habitat distribution of the by-catch species around the tropical area. Therefore, it is important to describe the oceanic characteristics of the study areas, because environment variations determine the patterns of diversity of these species.

The regions that will be investigated in this Thesis correspond to the Western Indian Ocean, the eastern tropical Atlantic and the Eastern Pacific Ocean, where the tropical tuna purse seine fleets operate respectively. The Atlantic and Pacific Oceans have many common climatological features (easterly trade winds, eastward thermocline, eastern cold tongue, and northerly Inter-Tropical Convergence Zone (ITCZ)) but also some climatic variability or differences between them. In contrast, the Western Indian Ocean seems to be the most different due to its monsoon system.

Western Indian Ocean circulation and Oceanographic conditions

The Indian Ocean is the smallest of all oceans. It has a north-south extent of 9600 km from Bay of Bengal to Antarctica and 7800 km in east-west direction between southern Africa and west coast of Australia. The continental shelves are narrow, averaging 200 km and the mean depth is 3800 m (Tomczak and Godfrey 2003). The Western Indian Ocean (WIO) has a surface area of about 30 million km². This part of the Indian Ocean is composed by several regions with distinct oceanographic conditions and fishery resources (Shotton 1997).

The variation of the sea surface salinity (SSS) in the IO follows the precipitation-evaporation distribution. The SSS in the eastern tropical region is quite uniform with values close to 34.5 that increase towards the African coast and towards the north into Arabian Sea (Tomczak and Godfrey 2003). It is in this northern region where maximum values of SSS are found around 36.

The Sea surface temperature (SST) is high in the entire Northern Indian Ocean with mean temperatures above 28°C. However, in the northern region, and especially in the Somali Current (SC) region, the temperature decreases below 28°C due to upwelling processes occurring in the area during the summer monsoon (Schott and McCreary Jr 2001; Tomczak and Godfrey 2003). There is no equatorial upwelling in this ocean, so the minimum sea surface temperature which is so prominent in the equatorial Pacific and also visible in the equatorial Atlantic is not found in the Indian Ocean.

The Western Indian Ocean surface circulation is regulated by wind monsoons, which describes a clear seasonal pattern (Figure 146). This winds system, characterized by surface winds which are seasonally reversed to the north of 10°S (Schott and McCreary Jr 2001), is considered one of the main characteristics of the Indian Ocean. The monsoon system dominates the ocean climate (e.g., heavy precipitations); however, south of 10° S, the ocean circulation does not reveal much seasonal variability (Wiggert et al. 2006).

The Northeast or Winter Monsoon determines the climate of the northern Indian Ocean during the northern hemisphere winter (December - March). It is characterized by high pressure over the Asian land mass and northeasterly winds over the tropics and northern subtropics (Tomczak and Godfrey 2003). The Intertropical Convergence Zone (ITCZ) and the Doldrums are located south of the equator (near 5°S) rather than north. In this period, due to northeast winds, the Arabian Sea water gets colder and salty, which contributes for supplying the upwelling zones (Schott and McCreary Jr 2001).

During the northern hemisphere summer (June-September) the South-west or Summer Monsoon (SM) determines the ocean circulation and climate. Southwest winds blow steadily along east African coast. In this situation, the South Equatorial Current (SEC) and the East African Coast Current (EACC) supply the Somalia Current (SC) which flows toward the north. In the northern hemisphere the Somali Current turns offshore into the Southern Gyre (SG) and Great Whirl (GW) gyre. Associated to SG and GW, strong upwellings take place around 3°-4°N and 5-12°N. Off the Arabian Peninsula and east and west of the Indian coasts also take place some weaker upwellings. These upwelled waters are carried far offshore (more than 500 km) and propagate southward by the Ekman circulation (Schott and McCreary Jr 2001).

The transition from Northeast to Southwest Monsoon (from April to June and from October to December) or inter-monsoon period is characterized by the presence of a unique wind forcing pattern (Schott and McCreary Jr 2001). The Equatorial Jet is climatically important because it carries warm upper-layer waters eastward, thereby increasing sea level and mixed-layer thickness in the east and decreasing them in the west. Furthermore, in this situation, the IO is characterized by the highest SST, a general stratification of its waters and a low productivity as the nutrients appear close to depletion (Veldhuis et al. 1997).

The subtropical gyre of the southern hemisphere is characterized by two western boundary currents, one along eastern Madagascar and one along the coast of Mozambique. The flow through the Mozambique Channel may occur by the Mozambique Current (MC) and by anti-

cyclonic eddies passing through the channel (de Ruijter et al. 2002; Schouten et al. 2003). The formation of these eddies may result by southward advection of anomalies generated by Rossby waves coming from the east. These anti-cyclonic eddies generate the upward movement of nutrient rich waters around their edge, contributing to the food chain in the Mozambique Channel (Tew-Kai and Marsac 2009).

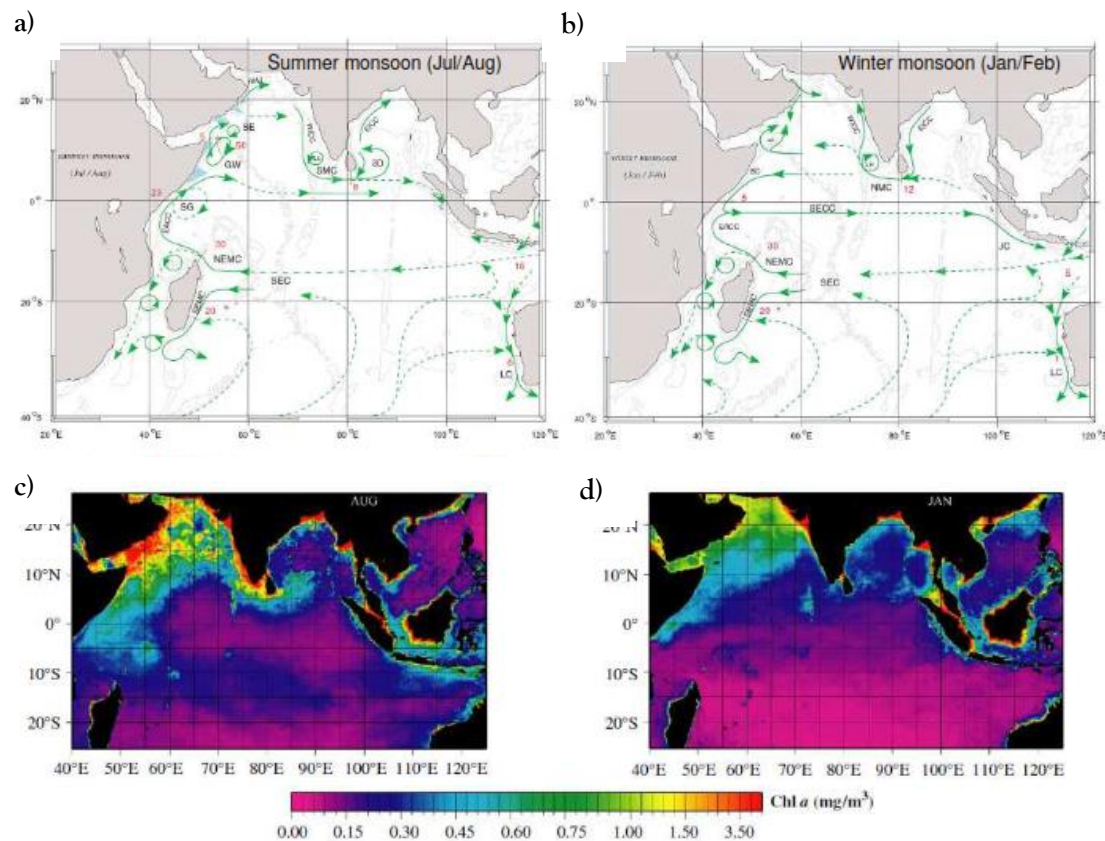


Figure 16. a-b: Horizontal and shallow meridional circulation of the Indian Ocean during the Summer monsoon (top-left) and Winter monsoon (top-right). The Currents branches: Southeast and Northeast Equatorial Mozambique Current (SEMC and NEMC), South Equatorial Current (SEC), South Equatorial Countercurrent (SECC), East African Coast Current (EACC), Somalia Current (SC), Southern Gyre (SG) and Great Whirl Gyre (GW), Southwest Monsoon Current (SMC), and Leeuwin Current (LC) (Source: Schott and McCreary, 2001). c-d: Seasonal climatology of Sea WiFs chlorophyll for August (bottom-left) and January (bottom-right) (Source: Wiegert et al. 2006; data obtained from Goddard DAAC (<http://daac.gsfc.nasa.gov/>)).

Eastern Pacific Ocean circulation and Oceanographic conditions

The Pacific Ocean is the largest of all oceans. In the tropics it spans a zonal distance of 20000 km from Malacca Strait to Panama. Its meridional extent between Bering Strait and Antarctica is over 15000 km. With all its adjacent seas it covers an area of $178 \cdot 106 \text{ km}^2$ and represents 40% of the surface area of the world ocean, equivalent to the area of all continents (Tomczak and Godfrey

2003). The Eastern Pacific Ocean (EPO), where this study was carried out, is located between 20°S-30°N and between 70°-150°W, from Baja California Peninsula in the North to the coast of Peru in the South and Hawaii on the West.

The ITCZ is always in the northern hemisphere and oscillates seasonally between $\sim 5^{\circ}\text{N}$ (in winter) and $\sim 10^{\circ}\text{N}$ (in summer), which significantly influences the oceanography of the EPO (Amador et al. 2006). Thus, the most direct effects are visible in the distributions of SST, sea surface salinity (SSS), the depth and strength of the thermocline, and the depth of the surface mixed layer (Fiedler and Talley 2006).

In the EPO the most important surface feature is situated on the west of Mexico and Central America, called Pacific “warm pool”. It is characterized by low salinity values, sea surface temperature values higher than elsewhere (above 27.5°C) and a shallow and strong thermocline. The development of the warm pool begins during the boreal spring in the eastern north Pacific, reaching the Eastern Pacific Ocean in May (Wang and Fiedler 2006). During winter, wind jets occur (the Tehuantepec Jet, the Papagayo Jet and the Panama Jet) in the warm pool, inducing thermocline lifting (Pennington et al. 2006).

The distribution of sea surface salinity is appreciated as a band of low salinity along $5^{\circ} - 10^{\circ}\text{N}$ (in parallel with ITCZ). Minimum salinities in the ITCZ system occur in the Gulf of Panama where salinity drops below 33.0 in the annual mean. This water originates from the North Equatorial Countercurrent, which crosses the Pacific Ocean eastward under the heavy rains of the ITCZ and arrives in the east with substantially reduced salinities (Pennington et al. 2006).

Thus, the water masses of the EPO have different characteristics (Figure 17). The equatorial surface water has moderate salinity and is over a shallow but relatively weak pycnocline (Tsuchiya and Talley 1998). In contrast, warm subtropical surface waters have high salinity values. The lowest SSS are observed in the coastal waters of Central America and Baja California, and it extends along the 10°N latitude. Finally, the eastern boundary currents transport cool and low salinity waters into the eastern tropical Pacific from the north and south (Fiedler and Talley 2006).

The most prominent circulation characteristic is the strong subtropical gyre in the northern hemisphere, consisting of the North Equatorial Current with strongest flow near 15°N , and the California Current. The circulation in the subtropics of the southern hemisphere is weaker. Thus, the major components of the southern subtropical gyre are the South Equatorial Current, centered on 15°S , and the Peru Current (Tomczak and Godfrey 2003).

It is seen that the equatorial system has a banded structure. The major westward components of the equatorial current system are the North Equatorial Current (NEC) and the South Equatorial Current (SEC). Both are directly wind-driven, strongly seasonal and reach their greatest strength during the winter of their respective hemispheres when the trades are strongest (Tomczak and Godfrey 2003).

In contrast, the most important eastward flow in the equatorial current system is the North Equatorial Countercurrent (NECC). In the termination region of the NECC is formed the Costa Rica Dome, with a minimum thermocline depth. The Costa Rica Dome (near 9°N, 88°E) is an upwelling region, with seasonal variation in size, being smaller in February-March and bigger in summer-fall (Fiedler and Talley 2006). Primary and secondary productions are relatively high at the Dome, supporting tuna and other fisheries (Ichii et al. 2002).

The NECC varies seasonally in strength and position. During February - April is restricted to 4 - 6°N with maximum speeds below 0.2 m s⁻¹; east of 110°W it disappears completely. During May - January the NECC flows between 5°N and 10°N with surface speeds of 0.4 - 0.6 m s⁻¹. Below the ITCZ at -10°N, the NECC eastward flow transports high concentration of nitrate and primary production (Kessler 2006; Pennington et al. 2006) and therefore, is an important physical feature for many top predators (e.g. tuna, dolphin, seabird) (Ballance et al. 2006).

In the eastern Pacific region, the main upwellings are located in the California Current, the Peruvian Current, along the equator, and around the eastern Pacific warm pool. Coastal upwelling regions are among the few regions of the world ocean where nutrients are returned to the surface layer and made available for phytoplankton growth and therefore, these systems are among the most important fishing regions of the world (Fiedler and Talley 2006).

The most productive coastal upwelling region of the world ocean is found in the Peru/Chile Current (Figure 18). This current is strong enough to lower sea surface temperatures along South America by several degrees from the zonal average. The Peru/Chile upwelling system extends from Southern Chile (-45°S) to northern Peru (-4°S), where cool-upwelled waters collide with warm tropical waters forming the Equatorial Front. The corresponding coastal upwelling region in the northern hemisphere is found in the California Current. In this current system, the winds along the coast are much more seasonal than along the coast of Peru. Coastal upwelling with equatorward surface flow prevails during spring and summer (Tomczak and Godfrey 2003).

On the other hand, the equatorial upwelling is created by the reversal of Coriolis acceleration to either side of the equator. This upwelling has a moderate seasonal variability; phytoplankton and zooplankton biomasses are largest in summer and autumn (Pennington et al. 2006).

El Niño-Southern Oscillation, ENSO

In the Pacific Ocean, the El Niño-Southern Oscillation (ENSO) is characterized by unusually warm temperature along the equator and the coast of Ecuador and Peru (Wang and Fiedler 2006). ENSO-related changes in winds, insolation, hydrography and circulation in the EPO are of sufficient magnitude and duration to affect organisms, populations and ecosystems. Thus, El Niño has a negative effect on primary productivity as consequence of the reversal of upwelling system, deepening of the thermocline and nutricline. This process has negative consequences on the productivity of the Peru/Chile current/waters and, hence, for the majority of the fisheries such as the collapse of the sardine fishery which took place during the warming of the 1972 El Niño (Fiedler et al. 1992; Pennington et al. 2006).

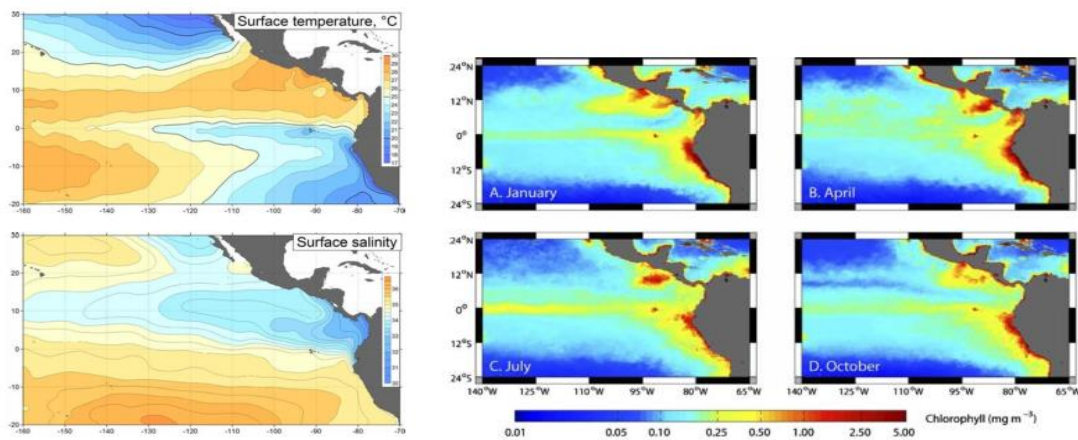


Figure 17. (left): Sea surface temperature (upper left) and sea surface salinity (bottom left) in the eastern tropical Pacific Ocean (Source: Fiedler and Talley 2006).

Figure 18. (right): Chlorophyll a concentration from SeaWiFS data (1997-2005) in the tropical Pacific from January (A-upper right), April (B-upper right), July (C-bottom right) and October (D-bottom right) emphasizing seasonal differences (Source: Pennington et al. 2006).

Eastern Atlantic Ocean circulation and Oceanographic conditions

The Atlantic Ocean extends both into the Arctic and Antarctic regions with a total meridional extent of over 21000 km, from Bering Strait through the Arctic to the Antarctic continent. Furthermore, the Atlantic Ocean has the largest number of adjacent seas, which influences the characteristics of its waters. When all its adjacent seas are included, the Atlantic Ocean covers an area of 106106 km². The average depth of the Atlantic Ocean is 3300 m, less than the mean depths of both the Pacific and Indian Ocean (Tomczak and Godfrey 2003). The Eastern Atlantic Ocean, where this study was carried out, is located between 35° W and 15° E and between 30° N and 15° S, bounded by the African continent with Senegal and Mauritania in the north, the Gulf of Guinea in the middle and Angola and Namibia in the South.

The Trade Winds are slightly stronger in winter (February north of the equator and August in the south) than in summer on both hemispheres. The Doldrum belt, or Intertropical Convergence Zone (ITCZ), is found north of the equator like in the Pacific Ocean. Thus, the thermal equator is at about 5°N and coincides with the ITCZ.

The distribution of sea surface temperature (SST) in the Gulf of Guinea varies between 27°C and 29°C outside of the upwelling seasons (Allersma and Tilmans 1993) to below 22°C at the coast during the major upwelling events (Binet and Marchal 1993). Furthermore, the depth of the tropical thermocline can vary seasonally between 10 and 60 m in this area (Hardman-Mountford and McGlade 2003) (Figure 19).

The highest sea surface salinities of the world ocean are found in the region of the Canary and North Equatorial Currents (Figure 20); the SSS maxima therefore are shifted westward with respect to the Precipitation-Evaporation maxima. In contrast, low salinity waters flow through the Gulf of Guinea driven by the high precipitation and the numerous rivers runoffs in the eastern part of the Gulf. The low SSS values along South Africa and Namibia, on the other hand, are the result of the introduction of water through the Agulhas Current from the Indian Ocean (Hardman-Mountford and McGlade 2003).

As in the Pacific Ocean, the tropical Atlantic surface circulation is bounded by the northern and southern subtropical gyres, and its equatorial currents system also presents a banded structure.

The North Equatorial Current (NEC) is a westward flow (north of 10°N) with speeds of 0.1 - 0.3 m·s⁻¹. The South Equatorial Current (SEC), again flows towards west with similar speeds, and extends from about 3°N to at least 15°S (Tomczak and Godfrey 2003). The Equatorial

Undercurrent (EUC) is the strongest, with maximum speeds exceeding 1.2 m s^{-1} and producing an east-west slope of the thermocline (Stramma and Schott 1999).

The eastward flowing North Equatorial Countercurrent (NECC) has similar speeds than the NEC and the SEC. However, it is highly seasonal and nearly disappears in February when the trades in the northern hemisphere are strongest. East of 20°W longitude, the NECC is permanent. The eastward extension of the NECC is the Guinea Current which is a shallow surface flow. One part of its flow combines with the North Equatorial Undercurrent to create a small cyclonic gyre centered at 10°N , 22°W . A similar small gyre, centered near 10°S , 9°E is driven by the South Equatorial Undercurrent. Cyclonic flow is accompanied by a sea surface depression, minimum oxygen concentrations and an elevation of the thermocline in the center of the gyre. Because of the predominant thermocline in summer the gyres are known as the Angola and Guinea Domes (Tomczak and Godfrey 2003).

The eastern tropical Atlantic contains 12% of Atlantic Ocean primary production (Longhurst 1995). The main upwellings are localized close to the Canary Current, the Benguela Current, the equator, and in the coasts of Côte d'Ivoire and Ghana.

In the northern hemisphere, the Canary current flows along the Moroccan and Mauritanian coasts, feeding the North Equatorial Current (NEC) around 20°N latitude.

During winter, the Canary Current upwelling reaches its most southern point. In contrast, during spring, the upwelling becomes semi-continuous with a maximum of chlorophyll *a* between 10°N latitude and 20°N latitude (Chavez and Messié 2009).

On the other hand, the NECC is extended through the Gulf of Guinea along the African coast by the Guinea Current. In this region, the upwelling along the coasts of Côte d'Ivoire and Ghana occurs from July to September (Binet and Marchal 1993). This upwelling is caused by the Kelvin waves generated off the coast of Brazil which reach the Gulf of Guinea about one month later, showing strong regular upwelling events (Tomczak and Godfrey 2003).

In the southern hemisphere the Benguela Current extends northward along the Namibia coast, and shifts to the west around 17°S . The Benguela Current upwelling is strongest in the south during boreal fall and winter. In contrast, during boreal summer (from June to September), it extends northward with high primary production concentrations (Tomczak and Godfrey 2003) (Figure 20). The Angola-Benguela Front is created by opposition of the northward movement of the Benguela Current.

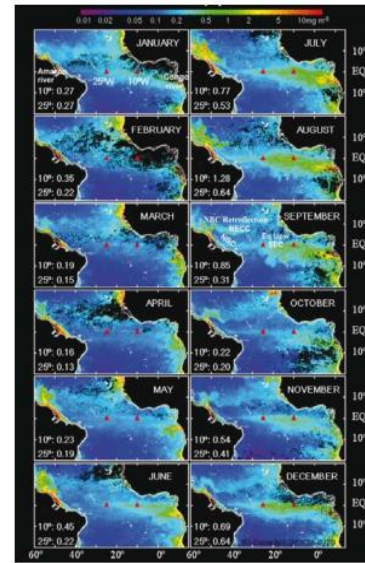
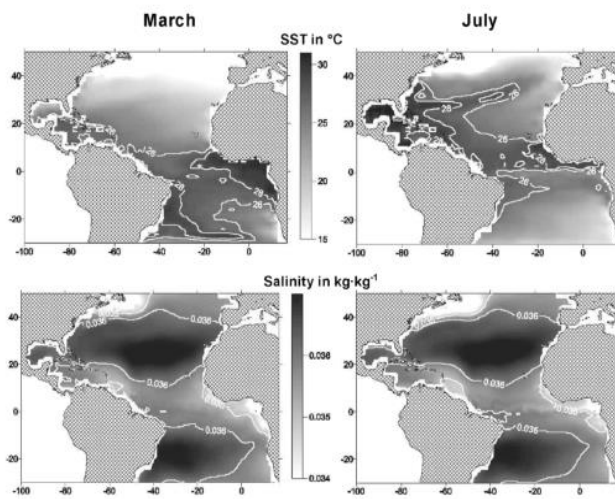


Figure 19. (left): Sea surface temperature (upper-left) and sea surface salinity (bottom-left) in the tropical Atlantic Ocean (Source: Maury et al. 2001).

Figure 20. (right): Monthly chlorophyll a concentration from SeaWiFS in the tropical Atlantic in 2001 (Source: Pérez et al. 2005).

CHAPTER 1

Biodiversity in the by-catch communities of the pelagic ecosystem in the Western Indian Ocean

Nerea Lezama-Ochoa¹ • Hilario Murua¹ • Guillem Chust¹ • Jon Ruiz¹ •

Pierre Chavance² • Alicia Delgado de Molina³ • Ainhoa Caballero¹ • Igor Sancristobal¹

¹Azti-Tecnalia. Herrera kaia, portualdea z/g, 20110, Pasaia, Spain.

²Institut de Recherche pour le Développement (IRD), Sète, France

³Instituto Español de Oceanografía (IEO), Tenerife-Canary Island, Spain

ABSTRACT

Diversity in the by-catch communities from the pelagic ecosystem in the tropical tuna purse seine fishery has been poorly studied. This study uses different biodiversity measures to compare Drifting Fish Aggregating Devices (FADs) and Free School sets (sets made on schools of tuna) of the Western Indian Ocean. Data was collected from observer programs carried out by the European Union (EU) between 2003 and 2010 on board Spanish and French fleets. Alpha (species diversity of a particular area) and Beta diversity (difference in species composition between different areas) was analyzed to assess differences in the number of species, abundances and the species composition between areas and fishing modes. Generalized Additive Models (GAM) were undertaken to explore which geographical/environmental variables explain the distribution of species richness index and Shannon diversity index in both fishing modes. Results showed that by-catch species in FAD communities may be used as observatories of surface pelagic biodiversity in combination with Free School communities. FAD communities were more diverse with higher number of species (74 species) and evenly distributed than Free School communities (56 species). However, environmental variables played a more important role in Free School communities. Somalia area and Mozambique Channel were the areas with highest biodiversity

rates in both fishing modes. This work contributed for the future implementation of the EAFM to manage the pelagic ecosystem in a holistic and more integrated way.

Keywords: By-catch · Diversity · Purse seine fishery · Western Indian Ocean · Ecosystem Approach to Fishery Management

1. INTRODUCTION

Biodiversity loss has been identified by international organizations as a major human threat, which may hamper sustainability for future generations by impacting ecosystem processes and reducing the provision of their services (Sala and Knowlton 2006). Similarly, the impact of human activities has been identified as a main player of diversity loss in the marine ecosystem, where changes in biodiversity are directly caused by exploitation, pollution, introduction of new species and habitat destruction (Fontaubert et al. 1997; Worm et al. 2006). Thus, biodiversity studies are important as they provide essential baseline data for detecting changes caused by human factors or climate changes between past and present conditions.

Fishing may be also considered as an important source of marine biodiversity loss, especially when non-selective fishing methods generate high levels of by-catch and discards (Hall 1996), which may affect the species composition of the community in the ecosystem (Botsford et al. 1997; Hutchings and Baum 2005; Jackson et al. 2001; Myers and Worm 2005). In that sense, few studies have been conducted to understand the impact of the by-catch generated by various fisheries on diversity, and the role of these species in the pelagic ecosystem. Most studies have traditionally focused on the biodiversity of by-catch communities primarily in the trawling (Fraser et al. 2008; Tavares and Arocha 2008; Zhu et al. 2011). Gaertner et al. (2008) showed the application of different diversity indexes in by-catch species using visual census in FADs in the Indian Ocean; and recently, other biodiversity study about the by-catch communities in the tropical tuna purse seiner fisheries in the Atlantic Ocean has been published (Torres-Irineo et al. 2014). By-catch and discard practices are considered to be responsible for economic loss and have ecological effects on keystone species which are important for ecosystem performance and structure (Alverson 1994).

In the tropical area, 60% of tuna global catches are performed by purse seine gear (Scott and Lopez 2014). This type of fishery is focused on yellowfin (*Thunnus albacares*), skipjack (*Katsuwonus pelamis*), and bigeye tuna (*Thunnus obesus*). Although the by-catch in the tropical tuna purse seine fishery is relatively low in comparison to other fishing strategies (Amandè et al. 2010), it can be

distinguished based on the strategy used for finding tunas (Dagorn et al. 2013). The two most important strategies are related to how the set is performed: Free School sets are normally mono or paucispecific schools of tuna detected by sonar marks, jumpers or breezes in surface waters; whereas Drifting Fish Aggregating Devices (FADs) sets are done on natural or man-made floating objects used to attract tuna and other species. FADs have a submerged structure and a satellite buoy transmitting its position (Delgado de Molina et al. 1999).

In the Indian Ocean, the total annual catch of tropical tunas has increased significantly since the early 1980s with the introduction of the purse-seine fishery in this area and the use of Fishing Aggregating Devices (FADs) (Miyake et al. 2010). Some studies revealed that FAD sets have higher levels of by-catch (Amandè et al. 2010) and higher number of species (Torres-Irineo et al. 2014) than Free School sets. The capture of these non-target species associated with floating objects could negatively impact biodiversity either by removing by-catch species in unsustainable quantities or by affecting the balance of the species composition in the community of the ecosystem (Hall 1996).

One of the objectives the Convention on Biological Diversity, signed in 1992, is to conserve the biological diversity in the seas, establishing protected areas or reducing the catch of the non-target species. To reach this objective, Regional Fishery Management Organizations have implemented several measures to regulate and control the levels of by-catch and protect specific areas in the ocean to avoid diversity loss (Cullis-Suzuki and Pauly 2010). To date, fisheries management has generally focused on the protection of a single target species with a substantial economic cost included. However, the advantage of considering not only few species but the habitat or characteristics of the ecosystem, where fisheries are totally integrated, is that their effects on marine diversity can be widely recognized (Cury et al. 2005). For that reason, the study of the by-catch communities will be valuable towards the practical application of the Ecosystem Approach to Fishery Management (EAFM) to conserve biodiversity and, hence, to improve the fishery management (Garcia and Cochrane 2005).

One of the EAFM objectives is to reduce the levels of by-catch species, by using indicators to evaluate ecosystem impacts and changes of marine biodiversity (Gascuel et al. 2012; Shin et al. 2010). In that sense, the Marine Strategy Framework Directive adopted by the European Commission in 2008, developed a set of 11 descriptors and indicators to achieve a Good Environmental Status (GES) of the ocean and to contribute to an ecosystem-based management of marine waters (Bourlat et al. 2013). For applying those indicators, observer programs of ecosystem monitoring are necessary steps to establish a baseline of current status as demonstrated by several studies (Babcock et al. 2003; Butterworth and Punt 1999).

Therefore, the main aim of this study is to characterize the diversity patterns of the epipelagic ecosystem, based on the by-catch communities of the tropical tuna purse seine fisheries in the Western Indian Ocean and to explore the relation among those patterns with environmental variables. In order to address this, and with the objective to identify the most diverse areas for future conservation issues, diversity as the number of species and their abundance (species richness and evenness) was measured in both fishing modes (Free School vs. FAD) used by tropical tuna purse seine fishery. Differences in biodiversity between by-catch communities in both fishing modes were investigated as well as the contribution of each environmental variable in diversity patterns. Moreover, the study also discusses the different biodiversity metrics investigated in relation with GES indicators in the light of the application of the Ecosystem Approach to Fishery Management (EAFM).

2. MATERIAL

2.1. Study area

The Western Indian Ocean surface circulation is regulated by wind monsoons, which describes a clear seasonal pattern (Figure 21a). It is characterized in the northern hemisphere by the North Equatorial Current (NEC) which is prominent in January and March when the Northeast Monsoon is fully established, and extends with variations approximately between 5°N and 2°S. On the southern hemisphere the South Equatorial Current (SEC) is predominant and occupies the region south of 8°S. Between these two main westwards flows (NEC and SEC) runs the Equatorial Counter current flowing eastwards. The changes produced in current directions as a consequence of the monsoons produces semi-annual variations in the thermocline depth, the sea level and the position of the Intertropical Convergence Zone that is located south of equator (5°S). A strong upwelling takes place in coastal waters of Somalia and Arabia during Summer Monsoon (Tomczak and Godfrey 2003). Besides the coastal upwellings there are other mesoscale processes that increase the primary production in the eastern Indian Ocean: eddies, filaments, fronts and whirls. In the Mozambique Channel the chlorophyll distribution, abundance and variability are significantly affected by eddies and filaments (Tew-Kai and Marsac 2009). With regard to the Somalian coast, the offshore flow of the low-latitude Somali current, during summer, generates two main gyres, the “Southern gyre” and the “Great whirl” and in certain summers a third gyre, the “Socotra eddy”, appears (Schott et al. 2009). These structures have a great impact on the productivity of the western Indian Ocean.

2.2. By-catch data

With the aim of estimating the amount of by-catch in EU fleets, the European Union, in support to its Common Fishery Policy, established a mandatory sampling program in 2003 to collect by-catch data under the EU Data Collection Regulations (EC) No 1543/2000, 1639/2001 and 199/2008. The observer program of tropical tuna purse seine fisheries in the Atlantic and Indian Oceans, sampling approximately 10% of fishing trips (Amandè et al. 2010), are run by French (Institut de Recherche pour le Développement (IRD) and Spanish scientific institutes (Instituto Español de Oceanografía (IEO)- and AZTI) .

The data recorded by observers includes information about the trip and fishing activities (set type, position of the set, day and hour of the set, total catch), the environment conditions (sea surface temperature and wind speed) and the catch of the by-catch species groups. By-catch species groups were divided in billfishes, sharks, bony fishes, rays, turtles and mammals. The entire by-catch species were identified to species level in general, or to genus or family level in some cases (see selection of taxonomic categories section). A subsample of the catch for each by-catch species was also measured in weight and length. Six areas were selected to carry out biodiversity analysis based on the ET zones (ET is related to the European Community (EC) research program “Echantillonnage thonier”) defined by Pallarés and Hallier (1997) and Pianet et al. (2000): North of Somalia (2x01N), South of Somalia (2x01S), NW Seychelles (2x02), SE Seychelles (2x03), Mozambique Channel (2x04) and Maldives Chagos archipelagos (2x05) (Figure 19b). These statistical areas were defined based on the similarity of target tuna species catch and size composition.

The fishing set was considered as the sample unit and was categorized into Drifting Fish Aggregating Devices (FADs) and Free-School sets. A total of 1802 sets were observed between 2003 and 2010 in Spanish and French purse seine fleet, from which 326 were done in the Free School sets and 1475 in the FAD sets. The numbers of sets in both fishing modes for each area are presented in Table 4.

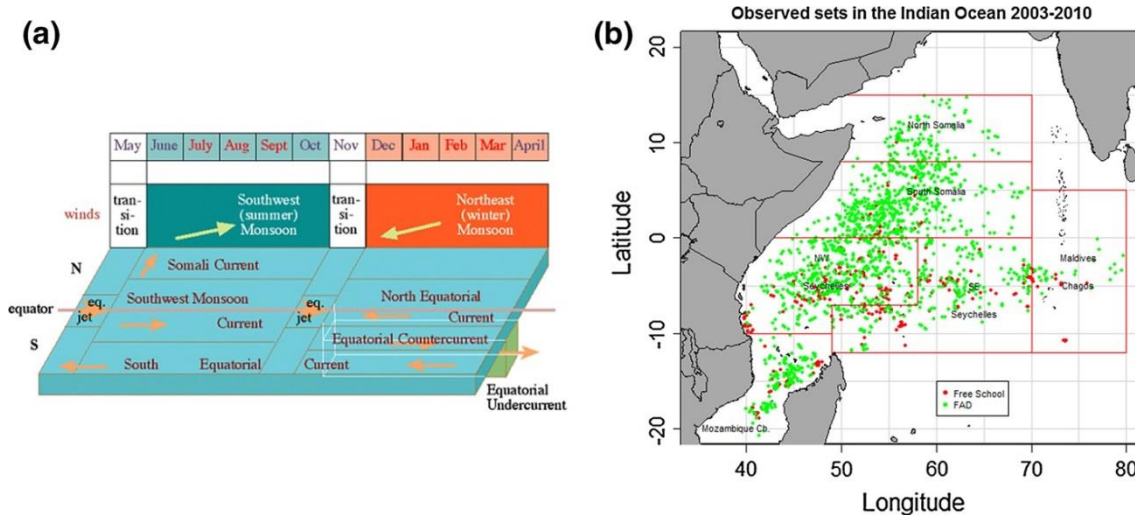


Figure 21. (a) Monsoon system in the Indian Ocean: winds cycle and main surface oceanic currents in response to the Monsoons (courtesy of Tomczak and Godfrey 2003). (b) Different ZET areas or fishing zones (red rectangles) and Free School (red points) and FAD catches (green points).

2.3. Selection of taxonomic categories

A total of 31 sets (22 FAD sets and 9 Free School sets) only defined species to the by-catch species group level so they were removed from any subsequent analyses. Furthermore, 19 mislabeled Free School sets were deleted for avoid the introduction of bias in sampling methodology.

In the case of records of higher level taxa (genus, family, order and other levels), the number of species and their abundance was assigned using the species composition of the same group (e.g., genus, family) in the same area for that particular year (Amandè et al. 2008a). As species level identification for Exocoetidae, Bramidae, and Serranidae families, and Etmopterus genus was not possible, they were considered as morphospecies -taxa that are distinguishable on the basis of the morphology (Oliver and Beattie 1996a; Oliver and Beattie 1996b) and treated as species in species richness estimates.

Abundance of species in each set was not always available because the observer recorded only the total weight of the by-catch species and the mean size or weight. In those cases, the number of individuals was calculated dividing the total estimated weight by the mean weight or size converted to weight by the corresponding length weight relationship. The list of species selected comprised a total of 77 species (7 billfish species, 12 sharks, 44 fishes, 5 turtles, 2 species of marine mammals and 7 species of rays) (see S1. Table 1 in Supplementary material-Chapter 1).

2.4. Environmental data

For each fishing set (date and position), which covered the period December 2005- February 2010, values of oceanographic variables were obtained from ocean models and satellites.

Temperature at 20, 30, 50 and 75 m depth (S20, S30, S50, and S75; in °C); Depth of the Thermocline (Therm. Depth; in m); Gradient of the Thermocline (Therm. Grad; in °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) came from ocean models with a spatial resolution of 25 km and a frequency of 2/3 days.

Sea Surface Temperature (SST; in °C) was measured from AVHR and MODIS sensors and have 4 km resolution. Chlorophyll concentration the same day of the fishing set and 18 days before (Cl and Cl-18 in mg m⁻³) had a 4 km resolution and came from measurements of MODIS and MERIS satellite sensors. Sea Level Anomaly (SLA; in cm) and geostrophic current speed (WG; in kn) presented 25 km resolution. These altimetry products came from different combinations of satellites ERS², Topex/Poseidon, Jason¹/2, ENVISAT/GFO and CRYOSAT. This information was processed and provided by the CLS (Collecte Localisation Satellite, France, <https://www.cls.fr>).

3. METHODS

Diversity was estimated using Alpha diversity measures including species richness, evenness and Shannon diversity index, and Beta diversity measures. Alpha diversity measures the species diversity of a particular and heterogeneous community, whereas Beta diversity measures the change in the composition of species between different communities (Magurran 2004).

3.1. Alpha diversity

Species richness index (the total observed and the mean per set) was calculated for each area and trimester in both fishing modes. Species accumulation curves were also constructed for each fishing mode and by areas. It seems 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). For that reason, Chao2 non-parametric estimator (Chao 1984) based on the incidence or frequencies of species was also calculated to obtain the estimated total species richness.

Evenness is a measure of the relative abundance of the different species of an area. Log-rank abundance curves were constructed for each fishing mode (FAD vs. Free School) for obtaining the 10 most abundant species (Kindt and Coe 2005). The mean of Pielou's J-evenness index, a Shannon evenness index, was also calculated for the estimation of Evenness by areas for both fishing modes. Pielou's J-evenness is calculated as: $H / \ln(S)$ where H is the Shannon diversity index and S the Species richness. The shape of the log-rank abundance can be explained by species abundance models as Geometric, Log-series, Log-normal and Broken stick models (Magurran 2004) and is used to describe the structure of the community. The data was fitted to different models and the best model fit, according to the lowest AIC value (Akaike's Information Criterion), represents best the community structure (Kindt and Coe 2005).

Diversity indices combines species richness and evenness information (Magurran 2004), such as Shannon diversity index (Shannon and Weaver 1949). If Shannon index (H) increases, diversity increases. Thus, the mean Shannon diversity index was calculated for each area and trimester for each fishing mode (FAD vs. Free School).

On the basis of the species richness and Shannon index, biodiversity maps were constructed by interpolation to a grid of 40 x 40 degrees. Data was aggregated by fishing set and thin plate spline regression was applied, using the "Tps" function from the "fields" package (Furrer et al. 2009) in R software.

3.2. Beta diversity

Simpson dissimilarity index based on presence-absence data was calculated for both fishing modes to analyze similarities in species composition between areas. Beta-sim or Simpson dissimilarity index, proposed by Simpson (1943) and later introduced by Lennon et al. (2001), is defined as $\text{beta-sim} = \min(b,c)/[a+\min(b,c)]$, where a is the number of species present in both samples and b and c are the numbers of species occurring in only one sample or the other sample. Values range from 0 to 1 representing highest and lowest similarity, respectively. As there are differences in the number of samples by area and, therefore, in species richness, Beta-sim was chosen because is independent of species richness (Lennon et al. 2001). Results were showed by hierarchical cluster analysis with the "complete" linkage method and the function "hclust" from the R software. Furthermore, we used Mantel tests (Legendre and Legendre 2012) to determine the correlation

between species similarity matrices and environmental and geographical distance. Bray-curtis index was used to measure the compositional similarity between pairs of fishing sets. The distance matrix for environmental variables and the geographical distance was measured with the Euclidean distance. For environmental variables, “bioenv” function from the vegan package (Oksanen et al. 2007) implemented in the R language was used to select the best subset of environmental variables.

3.3. Geographical and habitat preferences of by-catch communities

Generalized Additive Models (GAM) are a non-parametric generalization of multiple linear regression (Walsh and Kleiber 2001) to fit nonlinear relationships between response and smoothed explanatory variables (Guisan et al. 2002; Leathwick et al. 2006). GAMs were constructed to determine which geographical and environmental variables explain the distribution of species richness and Shannon diversity index for each fishing mode in the Western Indian Ocean between 2005 and 2010; for which environmental data was available. Oceanographic variables, geographic variables (latitude and longitude) and trimesters were included in the analysis.

Relationships between environmental variables were analyzed to find possible collinearities between them. In case of high correlation between two variables, only one of them was included in the final model. Each GAM was fitted using thin plate regression splines to model nonlinear covariate effects. Species richness index was modeled with Poisson family and logit-link function to find relationships between the number of species and geographical/environmental variables.

To relate Shannon diversity index with geographical/environmental variables, a Gaussian error distribution with identity-link function was used. Best GAM model was obtained using backward stepwise procedure selecting significant p-values for each geographical/environmental variable.

The by-catch data organization was carried out following the structure suggested in Kindt and Coe (2005) and the R packages (describe below) for biodiversity analysis. All the analyses were carried out based on both datasets and analyzed in R software using mainly “vegan”, “BiodiversityR”, “maps” and “mgcv” packages of R free software (Team 2013)-version 2.14.0.

4. RESULTS

4.1. Alpha diversity

The Chao2 non-parametric estimator and species accumulation curves showed differences in species richness estimated for both fishing modes (Table 4). The species richness index showed that the total number of species observed in FAD sets (74) was higher than in Free School sets (56). Furthermore, Chao2 estimator showed that species accumulation curves in FAD sets nearly reached the asymptote with 86 species caught (Figure 22a), which means that almost all species appeared in this type of fishing mode. However, in Free School sets the asymptote is not reached (70), and thus, more sampling would be needed to encounter all species (Figure 22b).

In FAD sets, the Chao2 index estimated a maximum of 25.3 species in Maldives-Chagos, 51.0 in Mozambique Channel, 46.1 in North Somalia, 64.7 in NW Seychelles, 44.4 in SE Seychelles, and 65.3 in South Somalia (Table 4). The shape of the rarefaction curve reaching the asymptote suggested that by-catch species were frequently caught in NW Seychelles and South Somalia, (Figure 23a). By contrast, in Free School sets, the Chao2 index estimated a maximum of 16.9 species in Maldives-Chagos, 25.4 in Mozambique Channel, 9.3 in North Somalia, 50.1 in NW Seychelles, 60.2 in SE Seychelles and 31.0 in South Somalia (Table 4). By-catch species were frequently caught in NW Seychelles and SE Seychelles, when the asymptote was more or less close to be reached (Figure 23b).

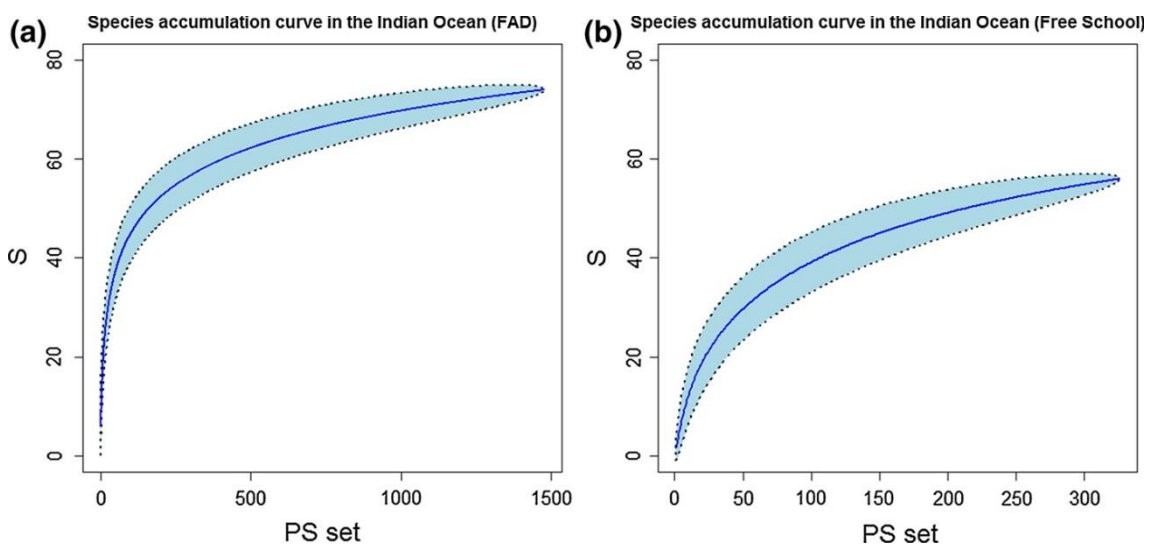


Figure 22. Species accumulation curves in FAD (a) and (b) Free School sets.

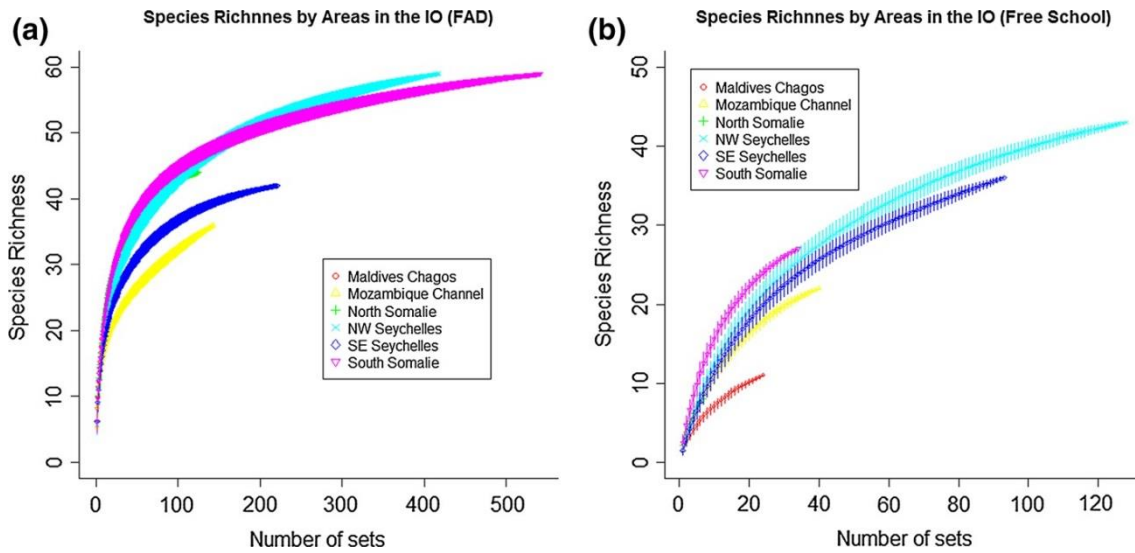


Figure 23. Species accumulation curves in FAD (a) and (b) Free School sets.

Mean species richness index estimated by areas showed that SE Seychelles and Maldivas Chagos were the areas with highest species richness observed in FAD sets, with 6.2 and 8.2 species respectively, and North Somalia and South Somalia in Free School sets, with 2.1 and 2.5 species, respectively (Table 4).

Mean species richness index by trimester (Table 5) showed the highest values in the third (7.0) and fourth (5.7) trimester in FAD sets and in the third (2.8) and fourth (1.6) trimester in Free School sets.

With respect to the evenness measures, Mozambique Channel is the area with largest species evenness values in FAD and Free School sets. Thus, areas from most to least evenness were ordered as follows: Mozambique Channel > South Somalia > North Somalia > NW Seychelles > SE Seychelles > Maldives-Chagos in FAD sets, and Mozambique Channel > North Somalia > South Somalia > SE Seychelles > Maldives-Chagos > NW Seychelles in Free School sets (Table 4).

Based on Log-rank abundance data, the first ten most abundant species are shown in Table 6, forming 93.3% with respect the total species in FAD sets and 97% in Free School sets. The most abundant species in FAD sets was the *Canthidermis maculata* (244873 individuals) and *Elagatis bipinnulata* (12959 individuals) in Free School sets.

Table 4. Distribution of sets (N), Overall Observed Species richness by Area (Obs. SR), Mean species richness per set (Richness), Chao2 non-parametric estimator, Mean Evenness index per set (Evenness) and Mean Shannon diversity index per set (Shannon) by areas in FAD and Free School sets.

Area	FAD						Free School					
	N	Obs. SR	Richness	Chao2	Evenness	Shannon	N	Obs. SR	Richness	Chao2	Evenness	Shannon
Maldives Chagos	27	25	8.2	25.3	0.27	0.94	24	11	1.4	16.9	0.35	0.22
Mozambique Ch.	143	36	5.4	51	0.56	1.18	40	22	1.6	25.4	0.7	0.28
North Somalia	125	44	6.2	46.1	0.51	1.01	7	8	2.1	9.3	0.69	0.41
NW Seychelles	418	59	5.7	64.7	0.46	1	128	43	1.7	50.1	0.11	0.27
SE Seychelles	221	42	6.2	44.4	0.45	0.99	93	36	1.5	60.2	0.46	0.21
South Somalia	542	59	6.1	65.3	0.51	1.03	34	27	2.5	31	0.65	0.49
Total estimation	1476	74	5.97	86	0.47	1.02	326	56	1.69	70	0.24	0.27

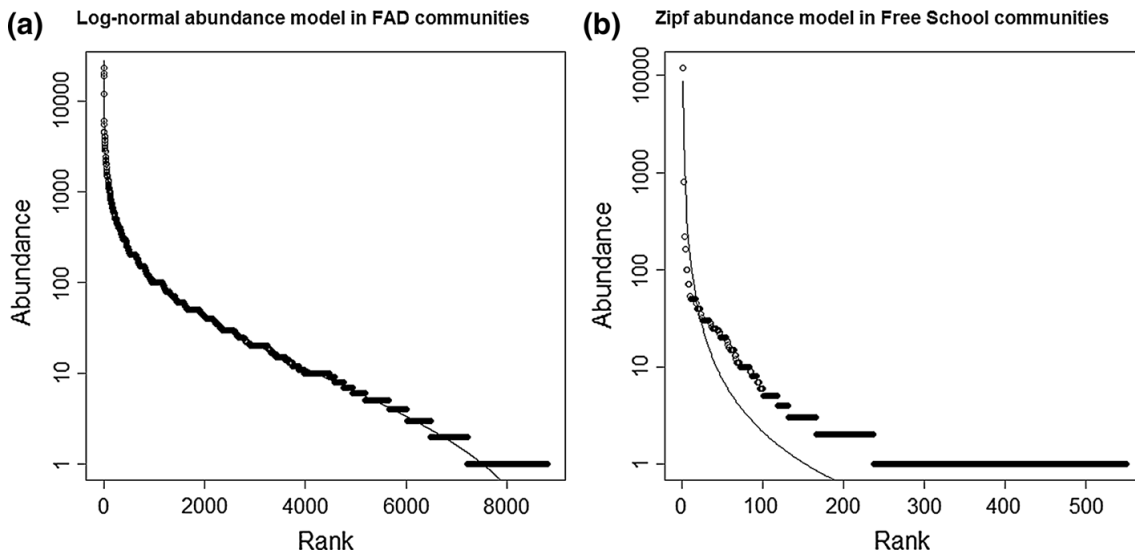
Table 5. Distribution of sets (N), Overall Observed Species richness by Trimester (Obs. Richness), Mean species richness per set (Richness), Chao2 non-parametric estimator, Mean Evenness index per set (Evenness) and Mean Shannon diversity index per set (Shannon) by trimester in FAD and Free School.

Trimester	FAD						Free School					
	N	Obs. Richness	Mean Richness	Chao2	Evenness	Shannon	N	Obs. Richness	Mean Richness	Chao2	Evenness	Shannon
1	196	45	5.4	45	0.5	1.1	48	32	1.6	40	0.7	0.3
2	268	53	5.1	59	0.4	0.9	116	38	1.5	64	0.7	0.2
3	486	63	7	96	0.5	1.2	36	27	2.8	29	0.1	0.6
4	526	60	5.7	80	0.4	1	126	36	1.6	48	0.5	0.2

Table 6. Species abundance in FAD and Free School sets.

FAD				Free School			
Species	Rank	Abundance	Proportion	Species	Rank	Abundance	Proportion
<i>Canthidermis maculata</i>	1	244873	36.4	<i>Elagatis bipinnulata</i>	1	12959	79.3
<i>Elagatis bipinnulata</i>	2	156894	23.3	<i>Canthidermis maculata</i>	2	1173	7.2
<i>Decapterus macarellus</i>	3	63588	9.4	<i>Coryphaena hippurus</i>	3	640	3.9
<i>Abalistes stellatus</i>	4	50483	7.5	<i>Carcharhinus falciformis</i>	4	358	2.2
<i>Coryphaena hippurus</i>	5	43481	6.5	<i>Acanthocybium solandri</i>	5	204	1.3
<i>Aluterus monoceros</i>	6	31374	4.7	<i>Exocoetidae</i>	6	123	0.8
<i>Acanthocybium solandri</i>	7	10911	1.6	<i>Abalistes stellatus</i>	7	88	0.5
<i>Uraspis secunda</i>	8	10079	1.5	<i>Pteroplatytrygon violacea</i>	8	80	0.5
<i>Carcharhinus falciformis</i>	9	9622	1.4	<i>Istiophorus platypterus</i>	9	73	0.4
<i>Kyphosus vaigiensis</i>	10	6875	1	<i>Lobotes surinamensis</i>	10	68	0.4

Furthermore, the application of the different species abundance models to rank abundance curves in both fishing modes showed that by-catch species communities in FAD sets followed a Log-normal distribution, and the by-catch species communities in Free School sets a Zipf distribution based on the lowest AIC values (see S1. Table 2 in Supplementary material-Chapter 1). Slopes of the curve in Free School sets were steeper than in FAD sets, where the curve reached larger values in the x axis (Figure 24).

**Figure 24.** Models selected to fit log-rank abundance curves in FAD (a) and (b) Free School sets.

Shannon index (Table 4) showed highest diversity in FAD sets in South Somalia (1.03) and Mozambique Channel (1.18). In Free School sets, on the other hand, the Shannon index showed the highest diversity in North Somalia (0.41), Mozambique Channel (0.28) and South Somalia (0.49).

Shannon index, classified by trimester (Table 5) showed the maximum diversity in the first and third trimester in FAD sets (1.1 and 1.2, respectively). In Free School sets, Shannon index by trimester (Table 5) showed the highest values also in the first and third trimester (0.3 and 0.6).

Biodiversity maps (Figure 25), by using thin plate spline regression technique showed the areas with major richness and diversity indexes.

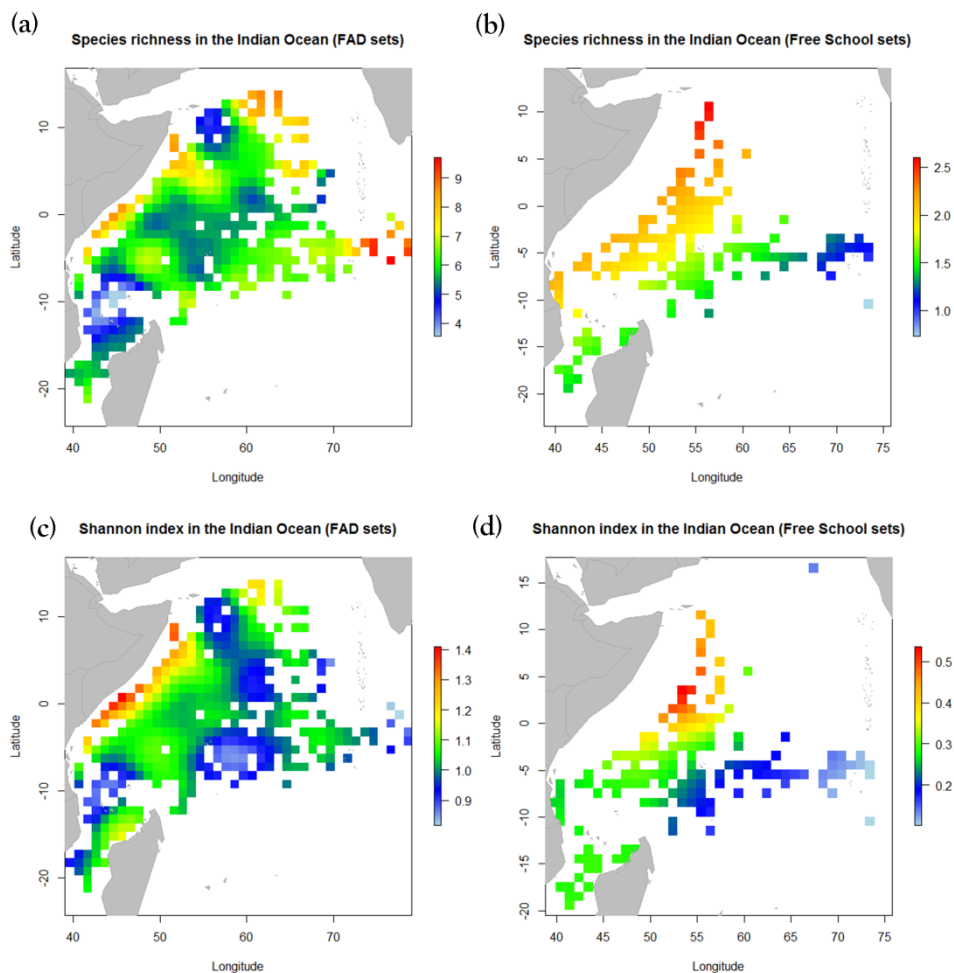


Figure 25. Richness index between 2003-2010 in (a) FAD sets and (b) Free School sets. Shannon index between 2003-2010 in (c) FAD sets and (d) Free School sets.

4.2. Beta diversity

FAD sets were characterized by high similarity in species composition between NW Seychelles and Maldives-Chagos (0.00) and between South Somalia and Mozambique Channel (0.02). The largest dissimilarity was found between Mozambique Channel and NW Seychelles (0.22) (Figure 26a).

The Simpson dissimilarity index showed the lowest values in Free School sets between Maldives Chagos and NW Seychelles/SE Seychelles (0.09); which implies that those areas are represented by communities with similar species composition (Figure 26b). High values were found between Maldivas Chagos and North Somalia (0.37), which means that both areas are characterized by different species composition. In general, higher dissimilarity values were found between areas in Free School (higher value of 0.37) sets than in FADs sets (higher value of 0.22).

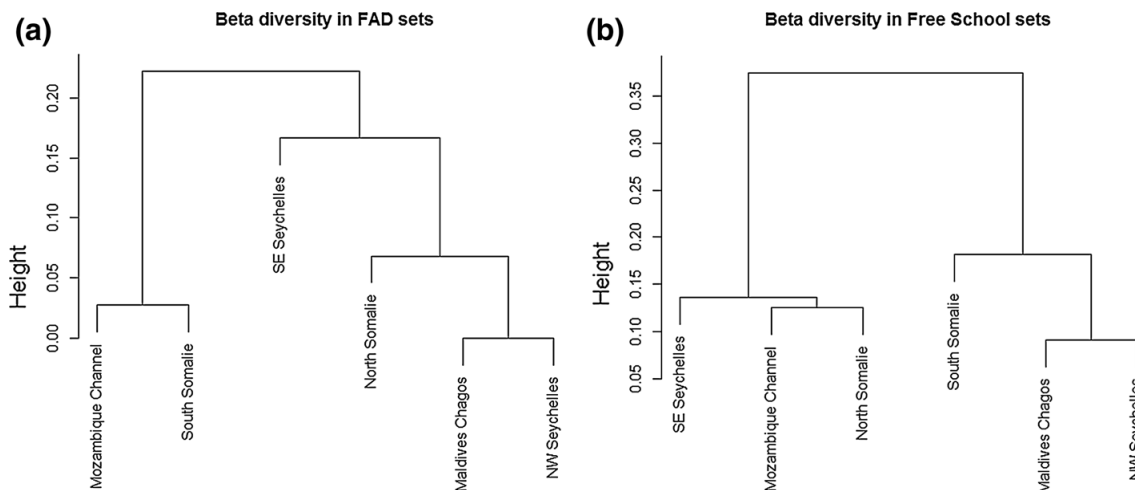


Figure 26. Simpson dissimilarity index in FAD (a) and (b) Free School sets.

In general, coastal upwelling areas (South Somalia and Mozambique Channel) and equatorial areas (Seychelles and Maldives Chagos) showed similar species composition in FAD sets. On the other hand, equatorial areas showed similar species composition in Free School sets. The results of the Mantel test showed there is not a correlation between species similarity and environmental factor (0.07) and geographical distance (0.1) for Free School communities. FAD communities, on the other hand, only showed correlation with environmental factors (0.001) (Table 7).

Table 7. Mantel correlation test between species similarity and environmental variables and geographical distance in FAD and Free School sets.

FAD communities	Mantel r	p-value	Environmental variables selected
Bray x distance	0.003	0.608	latitude, longitude
Bray x environment	0.04	0.001	SST, SLA, Cl, Cl.18, Therm.Prof, WG, WT
Free School communities	Mantel r	p-value	variables
Bray x distance	0.01	0.105	latitude, longitude
Bray x environment	0.01	0.074	SST, SLA, Therm.Prof, Therm.Grad, Sal20, WG

4.3. Geographical and habitat preferences of by-catch communities

Generalize Additive Models (GAM) were constructed to relate species richness distribution with geographical and environmental variables. In the case of FAD sets, the final model includes species richness as a response variable; trimester as a factor variable and longitude, sea level anomaly, chlorophyll and velocity of the geostrophic current as geographical/environmental variables. The estimated parameters for species richness data and p-values are listed in Table 8 and Figure 27. The model explained 13.4 % of the variance with a R² of 0.12 with 1152 samples. The results showed that the highest number of species was observed in the third trimester between 60-80°E, in areas with low concentrations of chlorophyll (< 0.2 mg/m³), negative sea levels and geostrophic velocities higher than 2 knots.

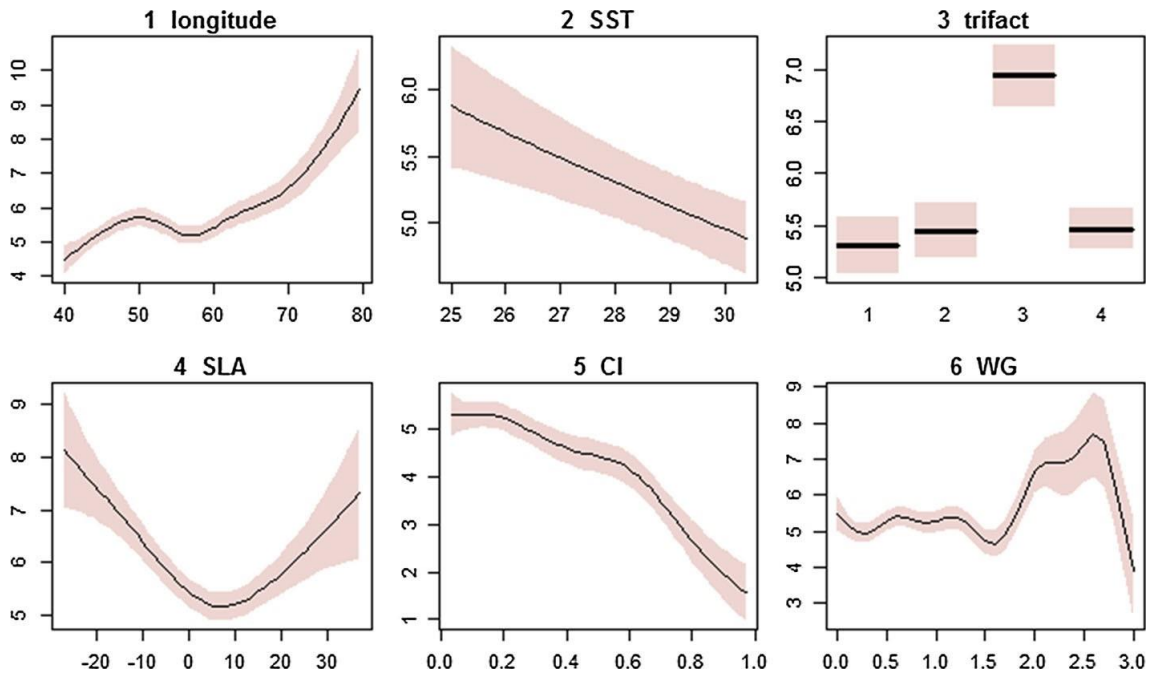


Figure 27. Smoothed fits of covariates modelling the species richness index: 1) Longitude, 2) SST (Sea surface temperature), 3) Trimester, 4) SLA (Sea level anomaly), 5) Chlorophyll and 6) WG (Geostrophic speed current) in FAD fishing mode. The y-axis represents the spline function. Dashed lines indicate approximate 95% confidence bounds.

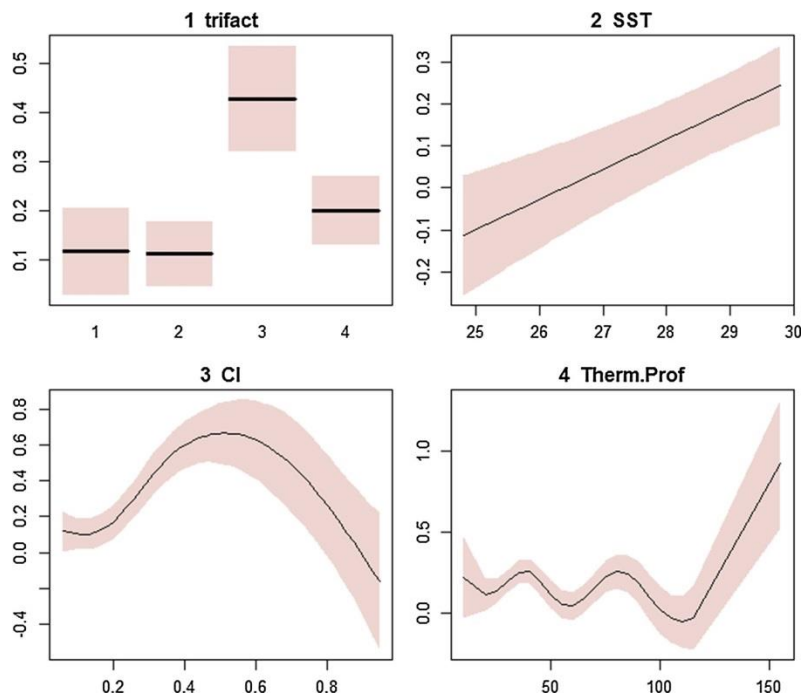


Figure 28. Smoothed fits of covariates modelling the species richness index: 1) Trimester, 2) SST (Sea surface temperature), 3) Depth of the thermocline and 4) Chlorophyll variables in Free School fishing mode. The y-axis represents the spline function. Dashed lines indicate approximate 95% confidence bounds.

Table 8. Summary results for the optimal GAMs selected for species richness index and Shannon diversity index in FAD and Free School sets.

	FAD				Free School			
	Species richness		Shannon index		Species richness		Shannon index	
Family	Poisson		Gaussian		Quasipoisson		Gaussian	
Link function	Log		Identity		Log		Identity	
Adjusted R2	0.12		0.09		0.29		0.2	
Deviance explained	13.4		10.6		34.7		24.6	
	Estimate	p-value	Estimate	p-value	Estimate	p-value	Estimate	p-value
Trimester 1	-	-	-	-	-	-	-	-
Trimester 2	-	-	-	-	-	-	-	-
Trimester 3	0.26887	4.51E ⁻⁰⁷	0.31794	6.10E ⁻⁰⁸	0.72737	2.35E ⁻⁰⁵	0.29358	0.0193
Trimester 4	-	-	-	-	-	-	-	-
SST	-0.0345	0.03	-	-	0.11756	0.0102	0.07013	0.0192
Chlorophyll	4.176	0.00012	-0.40836	0.00533	5.039	9.61E ⁻⁰⁵	3.453	0.00033
Longitude	5.456	1.16E ⁻⁰⁷	4.465	0.0051	-	-	-	-
Latitude	-	-	-	-	-	-	-	-
SLA	3.231	4.09E ⁻⁰⁸	2.328	5.50E ⁻⁰⁶	-	-	-	-
Sal20	-	-	6.627	0.00295	-	-	-	-
Therm.Grad	-	-	-0.06098	0.03437	-	-	-	-
Therm.Prof	-	-	-	-	6.403	0.00964	6.371	0.02896
WG	8.323	0.00249	1	0.00557	-	-	-	-

With regard to Free School sets, species richness was explained with trimester, chlorophyll, thermocline depth and sea surface temperature variables. Results showed that the model explained 34.7% of the variance with a R2 of 0.29 with 243 samples (Table 8, Figure 28). Species richness was higher in the third trimester with concentrations of chlorophyll between 0.4 and 0.6 mg/m³, high sea surface temperature (> 28°C) and depth of the thermocline at 40 and 80 meters.

In order to relate Shannon diversity index with environmental and geographical variables in FAD sets, a GAM was constructed with Shannon diversity index as response variable; with trimester as a factor, and longitude, sea level anomaly, chlorophyll, salinity, velocity of the geostrophic current and gradient of the thermocline as geographical/environmental variables.

Gaussian model for Shannon diversity index explained 10.6% of the variance with a R2 of 0.09 with 1156 samples (Table 8, Figure 29). The results showed that diversity was higher in the third trimester between 40-50°E with negative values of SLA and low values of salinity. Furthermore, the thermocline gradient and chlorophyll showed a negative linear relationship with diversity,

indicating that diversity decreased with increasing the thermocline gradient and concentrations of chlorophyll. Positive linear relationship occurred between the diversity and velocity of the geostrophic current, with higher diversity at higher velocity.

For Free School sets, the Gaussian model was constructed with trimester as a factor and chlorophyll, thermocline depth and sea surface temperature as environmental variables. Results showed that the model explained 24.6% of the variance with a R² of 0.2 with 243 samples (Table 8, Figure 30). Diversity was higher in the third trimester with a positive linear relationship with sea surface temperature, increasing diversity at higher temperatures, and with chlorophyll concentrations between 0.4 and 0.6 mg/m³. Higher number of species was found at 40 and 80 m depth of the thermocline.

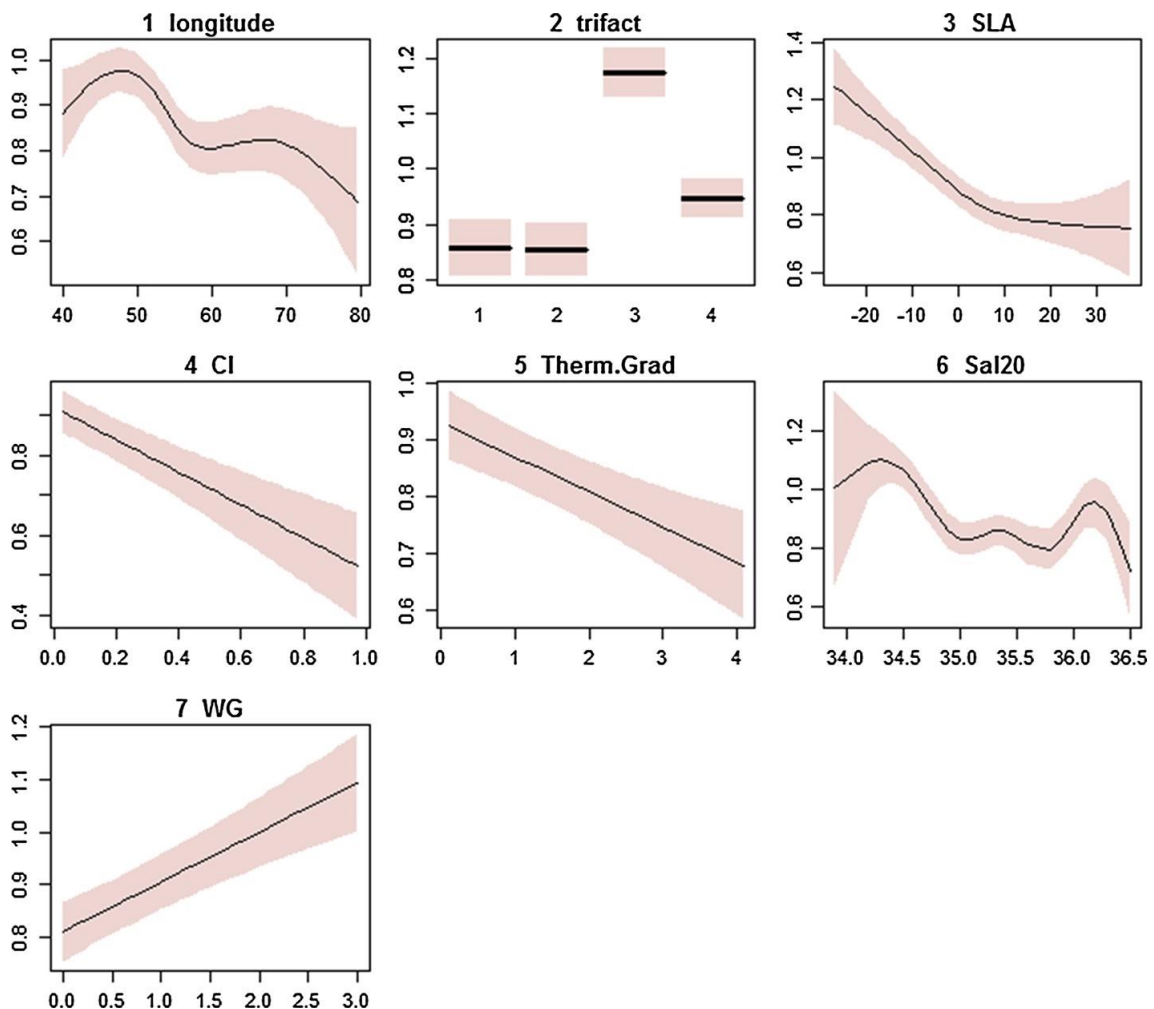


Figure 29. Smoothed fits of covariates modelling the Shannon diversity index: 1) Longitude, 2) Trimester, 3) SLA (Sea level anomaly), 4) Chlorophyll, 5) Gradient of the thermocline, 6) Salinity at 20 meters depth and 7) Geostrophic speed current in FAD fishing mode. The y-axis represents the spline function. Dashed lines indicate approximate 95% confidence bounds.

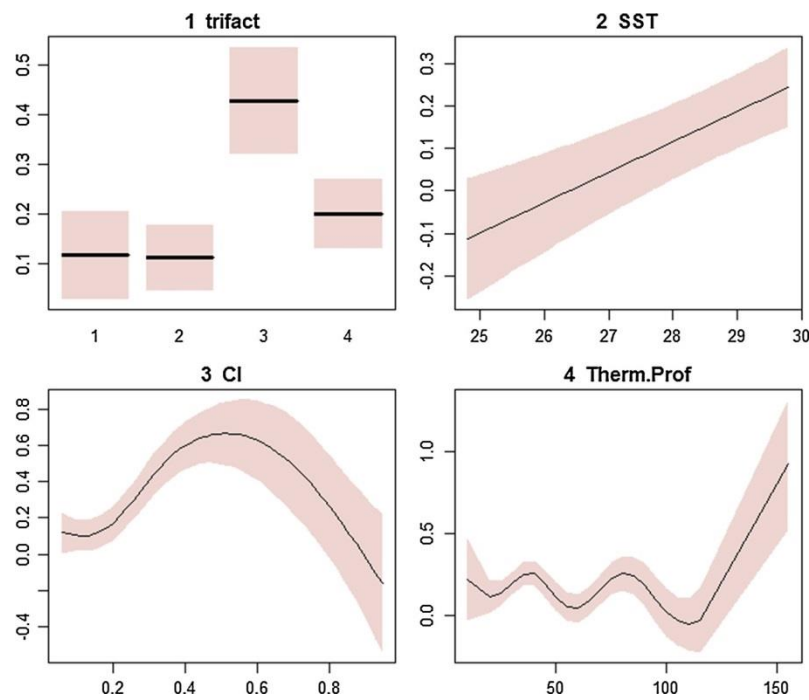


Figure 30. Smoothed fits of covariates modelling the Shannon diversity index: 1) Trimester, 2) SST (Sea surface temperature), 3) Depth of the thermocline and 4) Chlorophyll in Free School fishing mode. The y-axis represents the spline function. Dashed lines indicate approximate 95% confidence bounds.

5. DISCUSSION

It is important to understand Indian Ocean circulation pattern because this will affect the mechanisms regulating the number, abundance and spatial distribution of species (He and Legendre 2002). This information about environment conditions combined with diversity patterns will be very valuable for understanding the ecosystem functioning and, thus, for a correct management of the fisheries and the ecosystems of the area. Gaertner et al. (2008) assessed pelagic fish diversity from visual census data on FADs and they proposed the analysis of several components of pelagic fish diversity to better capture the complexity of the diversity of the open-ocean communities. Thus, based on that work, and including new methods, the present study tried to apply different biodiversity indices and techniques with the aim of better understanding the diversity patterns and habitat preferences of the by-catch communities from the tropical tuna purse seine fishery in the Western Indian Ocean in FADs and Free School sets.

5.1. Alpha and Beta diversity

This study found that higher number of species appeared in by-catch communities in FAD sets than in Free School sets. This result was consistent with Torres-Irineo et al. (2014) who studied the total species richness between both fishing modes in the Atlantic Ocean for the “EU Research Bigeye program” from 1997 and 1999 and DCR sampling program between 2005 and 2008. For both periods the total species richness based on Chao non-parametric estimator was higher in FAD sets than in Free School sets. Furthermore, those findings are similar to those from Amandè et al. (2010) and Taquet et al. (2007) who described the species composition of the by-catch of the purse seine fishery.

Based on the use of Chao2 non-parametric estimator and species accumulation curves the necessary sampling effort to observe the total species richness of the community can be evaluated. Among the different species richness estimators, we used Chao2 (Chao 1984) because is known to provide a better estimate of true species richness than observed species richness (Torres-Irineo et al. 2014). Furthermore, Hortal et al. (2006) showed that incidence based estimators (such as Chao2) are accurate and less sensitive to sample coverage or variability in the probability of capture especially for small sample numbers (Colwell and Coddington 1994). These indices are considered to be more rigorous in sampling theory than parametric estimators or curve extrapolations (Gotelli and Colwell 2011) to estimate total species richness with precision (Chao 1984). This is because it does not require a predetermined abundance distributions or the application of a priori or ad hoc models (Colwell and Coddington 1994; Chao et al. 2005). These techniques widely used by ecologists to improve faunal inventories and as an indicator of biodiversity (Colwell 2009; Gotelli and Colwell 2001), can be considered a useful measure to obtain an overall view of the communities. As new species are added, the curve moves from left to right (Magurran 2004) until the rarest species appeared and the asymptote is reached (Colwell 2009). Thus, by-catch communities in FAD sets need lower sampling effort to observe the total species richness compared with Free School sets, where normally all the possible species are not found. This is explained by the fact that FAD sets aggregate higher number of species than Free School sets (Amandè et al. 2010), so the asymptote is closer and the inventory is more complete. The group of species captured incidentally in Free School sets is considerably lower as not all species can maintain the cruising speed of the tuna schools (Hall and Roman 2013).

In that sense, FAD sets, in contrast to tuna Free School sets, may be a better indicator of the surface pelagic biodiversity because their by-catch almost represents the total number of species of the pelagic ecosystem. However, the sampling effort needs to be large enough to find the total species richness of the habitat.

In addition to the number of species, the species composition for each by-catch group was also similar to previous work published in the literature (Amandè et al. 2008a; Romanov 2002). The most abundant species caught in FAD and Free School sets were *Canthidermis maculata* and *Elagatis bipinnulata*, respectively. Although these species are normally discarded at sea, are not considered vulnerable by the exploitation of the fishery. In contrast, the *Carcharhinus falciformis*, which always appears between the most species caught in FAD sets, is considerable vulnerable by this and mostly by other types of fishery (Gilman et al. 2008); and therefore, it must be considered for future conservation plans and individual managements.

Thus, the species richness can be used as a tool to have a good inventory and baseline of the community composition; which will allow a comparison in the future if new species (dis)appear due to anthropogenic or climate induced changes. Although species richness is the most frequently used diversity measure in ecology, this diversity measure should be used in conjunction with other indices accounting for species relative abundance. This is because of the essential role that abundances play to explain distribution patterns and to manage the non-target species from the purse seiners. For that reason, the number of species in relation to evenness (Robinson et al. 2014) was calculated in FAD and Free School sets and differences between both fishing modes were found. In general, a higher number of species evenly distributed and, hence, higher diversity was found in by-catch species in FAD sets in comparison with Free School sets. Therefore, FAD communities were better indicators of biodiversity in the surface pelagic ecosystem.

The selection of the indicators to describe species diversity should depend on the objective of the study and the nature of the available data (Gaertner et al. 2008). In this work, biodiversity indicators such as species richness index, evenness and Shannon diversity index that analyze and combine both, the number of species and their abundance, were used to describe the by-catch communities in both fishing modes. Gaertner et al. (2008) described in his work 11 diversity indices describing 4 different components of diversity which can be used to address different questions. Nonetheless, our results suggest that the biodiversity indicators selected in this work were useful tools to describe by-catch communities in the surface pelagic ecosystem in both fishing modes. A single index, such as the species richness or Shannon index cannot provide a complete description of the pelagic species (Magurran 2004). The pelagic diversity is formed by different components and therefore, the use of several complementary indices is necessary in order to describe accurately the species diversity of this marine ecosystem (Gaertner et al. 2008).

FAD communities were formed by higher number of species than Free School, represented by smooth curves (Log-normal models) with aggregated species which remain close to the FAD in the same habitat and evenly distributed (Magurran 2004), in large communities in the same areas. On

the contrary, Free School communities were formed by few and rare (Zipf models) by-catch species, represented by steep curves, that move across oceans with migratory species such as tunas for reproductive activities or suitable environment gradients for feeding activities (Maguire 2006; Magurran and Henderson 2003). Thus, the structure of the by-catch communities based on species abundance models let us to infer that FAD communities are more stable and easy to study in the open ocean with permanent species in the same habitat than Free School communities. However, this affirmation must be taken with precaution because FADs sets can act as an "ecological trap" (Marsac et al. 2000). This theory suggested that FADs may alter the natural movements of tuna and by-catch species from biological productive areas towards less productive areas where FADs are deployed and accumulated. These changes can modify the habitat and the behavior and biology of tuna and by-catch species. This could explain why some coastal and rare species appear in the pelagic zone giving the false appearance of belonging to offshore communities and be permanent in this area.

In addition to this, the suggestion to consider Drifting Fish Aggregating Devices sets as possible observatories of diversity hot spots in the Western Indian Ocean was reinforced with Beta diversity analysis. If species accumulation curves showed that FAD sets may represent the total by-catch species in the surface pelagic ecosystem, their similitude in species composition around the tropical areas help to consider them as a good reference of biodiversity indicators. The areas with major diversity index in this study were also the equatorial and coastal upwellings, where the same species composition was found (mainly in South of Somalia and Mozambique Channel) in by-catch communities in FAD sets. It seems that these areas, with similar environmental conditions, aggregate species with similar ecological niche. Based on the high number of species found in this fishing mode and the suggestion that there is a very high level of similarity in the species composition of those communities in all oceans of the world (Hall and Roman 2013), FAD sets may be used to investigate the biodiversity in the surface pelagic ecosystem. Furthermore, the results of the Mantel test and the low values of dissimilarity index found in this fishing mode in comparison with Free School sets reinforce this assumption.

5.2. Geographical and habitat preferences of by-catch communities

Based on the results obtained from GAMs, we suggest that larger percentage of variability of diversity is explained by environment parameters in Free School sets in comparison with FAD sets. Thus, species richness and Shannon diversity indices were better explained (34.7% and 24.6%, respectively) by geographical and environmental factors in Free School communities than

in FAD communities (13.4% and 10.6%), despite the low number of samples in Free School sets. This is evident in the Free School communities where chlorophyll explained a high proportion of the variability in species richness and Shannon indices.

On the other hand, environmental variables had a lower contribution to the diversity distribution in FAD communities. Sea surface temperature and its relation with Somalia and Mozambique Channel upwelling systems (Schott and McCreary Jr 2001) was the most important variable but with low percentage of the species richness index explained. High geostrophic velocities could be related with eddies which stimulate the primary productivity around the Mozambique Channel and therefore, have higher concentration of predators such as tunas around this area (Kai et al. 2009). Sea level anomaly and salinity, related to upwelling areas, were the most important environmental variables to explain Shannon diversity index, but also with very low explanation power. The diversity found at low chlorophyll concentrations and the low contribution of the environmental variables to explain diversity distribution of FAD communities can be interpreted as the environmental variables being less important explanatory variables than in Free School communities; which could be explained as the FADs drift with currents and are less affected by environmental conditions. On the contrary, more diverse (i.e. higher species richness and Shannon indexes) Free School communities were found at higher chlorophyll concentrations, low depths of the thermocline (typical in the Western Indian Ocean area) and high sea surface temperatures in relation with the typical fishing areas for this fishing mode.

Another relevant finding of this study is that the associated behavior of tunas around FADs could be the reason for the lower variance explained by the environmental parameters. The same biodiversity and species composition was found in different habitat conditions in FAD which explain why environmental factors do not explain the diversity patterns. In that sense, the diversity on by-catch communities in FAD communities could be explained by other components than environment which have not yet been investigated; which could be related to the behavior of by-catch species. Various hypothesis about the associative behavior of tuna and by-catch species to objects can be found in the literature (Forget 2010; Fréon and Dagorn 2000), with the "meeting point" hypothesis the most accepted. This hypothesis suggests that tuna and other species (in our case, by-catch species) could make use of FADs to increase the chance of encounters between conspecifics (Soria et al. 2009), helping individuals to form larger schools. The study of the social behavior of these species is important because the relationships created around these devices could modify the ecological niche or habitat of the surrounding areas, affecting the diversity patterns of these by-catch communities.

Furthermore, in terms of diversity indexes, the species richness index explained more percentage of variance than the Shannon index in both fishing modes. The high variability of Shannon diversity index may complicate to model the geographical/environmental parameters in comparison to species richness index, where the patterns are better defined.

5.3. Implications for fisheries management

Fisheries management is changing from a single-based regime towards an ecosystem-based fishery management (EBFM), where the management of the by-catch species is essential to maintain biodiversity of the ecosystem (Torres-Irineo et al. 2014). In that sense, observer programs carried out by EU in the tropical tuna purse seine fishery can be a useful scientific tool to estimate diversity indicators of by-catch data to be used as a health indicator of the ecosystem. Thus, biodiversity metrics related with those indicators and investigated in this work can help towards the application of the EAFM.

This work led us to infer that FAD set seems to be a good biodiversity measure in the surface pelagic ecosystem based on the large number of species associated with them in a wide area. Furthermore, although a comparatively the low number of species are found in Free School communities, this fishing mode which seems to be more related to surrounding environment conditions, can contribute to understanding the oceanographic processes that determine diversity patterns. For that reason, the combination and integration of information obtained by observers in both fishing modes is fundamental to support an ecosystem-based fisheries management. The low observer coverage of around 10% agreed by various international tuna commissions only permit to obtain a precision between 10 and 40% in the by-catch estimations (Lennert-Cody 2001; Sánchez et al. 2007). For that reason, in spite of the high cost of the observer programs, an appropriate level of observer coverage is needed for biodiversity studies, which will allow examining the real benefits of collecting observer data to satisfy the management objectives of the EAFM. According to Gaertner et al. (2008) and despite the low sampling effort, our results suggest that, as the work with visual censuses around FADs, data from observer programs may provide a representative picture of species diversity for the area and period studied. In that sense, our work addresses a larger area and period and includes the Free School sets. For that reason, this work provides new information and perspectives on diversity of the by-catch communities.

In this sense, biodiversity studies in marine habitats have been difficult to accomplish, compared to plant or animal terrestrial communities, due to the difficulty of sampling marine habitats. Thus, open sea biodiversity studies are more difficult and costly to be carried out because the

areas tend to be much larger, the impact of the human activity is more diffuse and the delimitation for such studies is more complex (Hall and Roman 2013). Moreover, the spatiotemporal variability of the oceans and the wide movement patterns of these animals, may hamper biodiversity studies (Tyberghein et al. 2012).

Nonetheless, some open sea biodiversity studies, such as those carried out by Gaertner et al. 2008, showed that visual censuses by divers efficiently estimate the species diversity of fish around FADs. The only problem associated with this type of study is that visual censuses cannot provide a complete and exhaustive measure of pelagic fish diversity in the open ocean at an ecosystem level. For that reason, fishery observer's data, as used in this work, may be used to sample by-catch diversity and complement data from visual surveys. Although it is difficult to estimate the diversity of surface pelagic populations, which are moving in space and time (Dempster and Taquet 2004), the use of routine observer programs could be seen as an alternative to investigate the diversity of the marine communities under exploitation and to assess the effect that fishing and other human disturbances may have on those populations. The data from these programs are easier to collect and can provide larger data sets than fishery independent sampling techniques. Concretely, purse seiners can sample a wider variety of circumnatanant species but miss all the small individuals that escape through the mesh (Gaertner et al. 2008). In addition, data is limited to commercial fishing areas. For that reason, it is important to develop projects which combine fishery-dependent and fishery-independent data to monitor the diversity efficiently (Gaertner et al. 2008) and therefore, to improve and obtain more complete diversity studies in the open ocean.

Other drawback for diversity studies based on fishery observers is that it depends largely on the knowledge and experience of the observers in species identification, which determines the quality of inventories. Although some progress has been achieved through observer training, identification guides, and setting of minimum standards, more work is necessary to improve the observer programs (Hall and Roman 2013). However, advances in species identification have been conducted to improve the quality of the data (Taquet et al. 2007) in the Indian Ocean. Alternative tools as electronic monitoring to improve the coverage and species identification would be very valuable for a correct monitoring and observation system of the surface pelagic ecosystem.

6. CONCLUSION

All the analysis led us to infer that FAD sets can aggregate higher and more diverse number of by-catch species than Free School sets, in agreement with previous studies by Romanov (2002), Amandè et al. (2010), and Torres-Irineo et al. (2014). Furthermore, Somalia area and Mozambique Channel are mainly the most diverse areas in both fishing modes, so it is important to take them into account for future biodiversity studies or conservation plans. By-catch communities in FAD sets may be used as observatories of the biodiversity in the surface pelagic ecosystem; whereas by-catch communities in Free School sets may provide information about the relation between biodiversity and environment. Our findings contribute to understand the biodiversity of the surface pelagic ecosystem in the Western Indian Ocean based on the two fishing modes employed by tropical tuna purse-seiners. These results could be considered as a step for the future implementation of the EAFM to manage the pelagic ecosystem in a holistic manner, leaving behind the idea of the management of single species with the aim to focus on biodiversity studies towards integration in the ecosystem.

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CHAPTER 2

Biodiversity and habitat preferences of the by-catch communities from the tropical tuna purse-seine fisheries in the Eastern Pacific Ocean

Nerea Lezama-Ochoa¹ • Hilario Murua¹ • Martin Hall² • Jon Ruiz¹ •

Nick Vogel² • Ainhoa Caballero¹ • Igor Sancristobal¹

¹Azti-Tecnalia. Herrera kaia, portualdea z/g, 20110, Pasaia, Spain.

² Inter-American Tropical Tuna Commission, 8901 La Jolla Shores Drive, CA 92037, USA

ABSTRACT

This study examined diversity patterns and habitat preferences for by-catch communities from different areas in the Eastern Pacific Ocean between 1993 and 2011 using biodiversity metrics and Generalized Additive Models (GAMs). The by-catch information was based on data collected by onboard observers covering more than 80% of the purse seine fishing trips. The species accumulation curves showed that the total number of species observed in the purse seiners was similar in Drifting Fish Aggregating Devices (FADs) and School sets (sets made on school of tunas) and the samples available allowed to find all the possible species in both cases. Diversity was higher in the north equatorial area and around the Gulf of Panama than in the permanent coastal upwelling areas of Peru and California. Concretely, diversity was directly related with the equatorial upwelling, the front system and the Costa Rica Domo in FAD sets and with the coastal upwelling of Panama induced by wind jets in School sets. Generalized Additive Models and biodiversity metrics showed that diversity patterns and differences in species composition were explained by oceanographic conditions of each area. Variables, such as temperature, salinity,

chlorophyll and depth of the thermocline play an essential role in the habitat distribution of the by-catch communities; with around 22% of deviance explained by the model in FAD sets and 12% in School sets. This work has investigated multiple indicators related to the by-catch communities and their habitat, which could be helpful for the development of an Ecosystem Approach to Fishery Management.

Keyword: By-catch · Bycatch · Species diversity · Purse seine · Eastern Pacific Ocean · Ecosystem Approach to Fishery Management

1. INTRODUCTION

Open oceans cover much more of the Earth's surface than does land; however, the patterns and trends of species diversity in the pelagic ocean are not well known because of the complexity of the marine ecosystem (Irigoiien et al. 2004; Worm et al. 2005). In order to fill this knowledge gap, studies of marine biodiversity are critical for oceans conservation as marine biodiversity contributes to maintain the sustainability and functioning of ecosystems (Hammer et al. 1993). The impact of the human activities that are performed on marine ecosystem is not always easy to measure; however, fishing is one of the most recognized causes of marine biodiversity loss, especially when the excessive fishing pressure alters marine ecosystems by removing predators and species with low reproductive rates (Dayton et al. 1995). Furthermore, fishing activity can affect 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 the most over-fished species (Cullis-Suzuki and Pauly 2010). However, to date fisheries management has often been ineffective because it is generally focused on the protection of a single target species with a substantial economic cost included. 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 sustain a healthy marine ecosystem, the fisheries they support and protect specific areas in the ocean to avoid diversity loss (Pikitch et al. 2004). However, as stated above describing and measuring the effects of a fishery on an ecosystem is difficult (Gerrodette et al. 2012) and therefore, EAFM requires metrics that provide information about those effects (Rochet and

Trenkel 2003). Many different types of indicators have been developed to reflect a variety of aspects of ecosystems in simple terms, including biological, chemical and physical (Smeets et al. 1999). One of the most basic but important ecological indicators is species diversity, which is closely related to the concept of biodiversity (Zhu et al. 2011). Evaluating the spatial-temporal variability of species diversity can provide important information to facilitate the implementation of EAFM (Greenstreet and Rogers 2006).

In the Eastern Pacific Ocean, the tropical tuna purse seine fishery is one of the most important fisheries for the tuna cannery industry targeting skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*) and bigeye (*Thunnus obesus*) (Arrizabalaga et al. 2012). 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 made on objects (encountered natural objects or objects deployed by the fishers themselves, called fish-aggregating devices (FADs)). For more detailed descriptions of the fishery and the gear there is a recent review (Allen et al. 2010).

By-catch, defined as the part of the capture which is formed by non-target species, whether retained and sold or discarded, has become one of the most important issues in fishery management. The general worldwide increase of FAD sets during the 1990s has led to higher by-catches and the ecological problems associated (Allen et al. 2010). For example, by-catch of particular species, such as sharks (*Carcharhinus falciformis*) or billfishes (*Makaira nigricans*), which are vulnerable because of their life histories, may have impacts on the ecosystem and biodiversity.

Monitoring the species diversity of the by-catch species in space and time can provide insights into changes in ecosystem structure (Symstad et al. 2003). In that sense, some literature has been published about the biology and habitat preferences of the tuna and by-catch species in the Eastern Pacific Ocean (Duffy et al. 2015; Olson et al. 2010; Olson et al. 2014; Scott et al. 2012). In addition, the tropical tuna purse seine fishery has been used recently as an effective sampling tool for studying by-catch species diversity and community structure in the Atlantic and Indian Oceans (Lezama-Ochoa et al. 2015; Torres-Irineo et al. 2014); but not yet in the Eastern Pacific Ocean. Understanding the habitat and diversity patterns of these species in the eastern tropical Pacific purse-seine fishery is an effective way of assessing biodiversity and to support the conservation and the fisheries management.

The main objectives of this work were to 1) study the structure and diversity patterns of the by-catch communities using biodiversity metrics and 2) investigate the geographical and habitat preferences of the by-catch species in the Eastern Pacific Ocean in FAD and School fishing mode.

Finally, we will also discuss about the importance of applying ecosystem indicators in the by-catch communities to achieve a good environmental status under the EAFM. We hypothesize that the diversity patterns of by-catch communities caught by both fishing modes (FAD vs. School sets) could vary according to the specific oceanographic characteristics of the Eastern Pacific Ocean.

2. MATERIAL

2.1. Study area

The study area lies between latitudes 20°S-30°N and between longitudes 70°-150°W, from the Baja California Peninsula in the North, to the coast of Peru in the South and reaching the longitude of the Hawaiian Islands in the West.

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 S2. Figure 1 in Supplementary material-Chapter 2). Both equatorial currents (NEC and SEC) 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. The trades and the westerly winds are stronger in winter than in summer in the two hemispheres (Fiedler et al. 1992; Pennington et al. 2006). California and Peru-Chile currents are eastern boundary currents (Fiedler et al. 1992; Pennington et al. 2006), 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).

Besides the seasonal variability the coupled ocean-atmosphere system of Pacific Ocean is affected by the El Niño Southern Oscillation (ENSO). This climate event, with an irregular interannual cycle, significantly modifies winds and surface currents in the Eastern Pacific Ocean. The warm/cold phases of the ENSO cycle, called El Niño/La Niña are characterized by the presence of unusual warm/cold waters in the west coast of South America, which cause changes in the oceanographic processes (deepening/shoaling of the thermocline, for example) and therefore, to the distribution and abundance of some species (Ballance et al. 2006; Fiedler and Talley 2006).

2.2. By-catch data

By-catch data were collected from the Inter-American Tropical Tuna Commission observer program (1993-2011) conducted in large purse seine vessels (> 363 t carrying capacity). Since 1992 the observer coverage of the trips on large vessels by the combined IATTC and national observer programs has been more than 80% (Roman-Verdesoto et al. 2005).

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 by-catch in biomass or number for the different species groups. In this study, the numbers of individuals was used to perform the analysis. By-catch species groups were divided in billfishes, sharks, bony fishes, rays, turtles and marine mammals. By-catch was identified to species level in general and to genus or family level in some cases (see “Selection of taxonomic categories” 2.3 section).

Five broad areas were selected to carry out the analysis based on the distribution of fishing effort (Figure 31a): Area 1 (20-30°N/110-150°W), Area 2 (10-20°N/85-150°W), Area 3 (0-10°N/80-150°W), Area 4 (0-10°S/80-150°W), and Area 5 (10-20°S/70-150°W).

The fishing set was considered as the data unit for the analysis and was categorized into FAD sets and School sets. Few log sets (sets on natural drifting objects) (around 8% with respect to the total of sets) were observed throughout the studied period, and therefore, they were included as FAD sets. A total of 105241 sets were observed between 1993 and 2011, from which 20649 were School sets and 84592 were FAD sets. The number of sets in both fishing modes for each area is presented in Table 1.

2.3. Selection of taxonomic categories

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. The years were divided in two periods: Period 1 (before 2000) where there was a worst species identification and Period 2 (2000 and onwards) where there was a better one. When it was not possible to assign species within specific high level taxa into the first period, it was done based on the proportions in the second period.

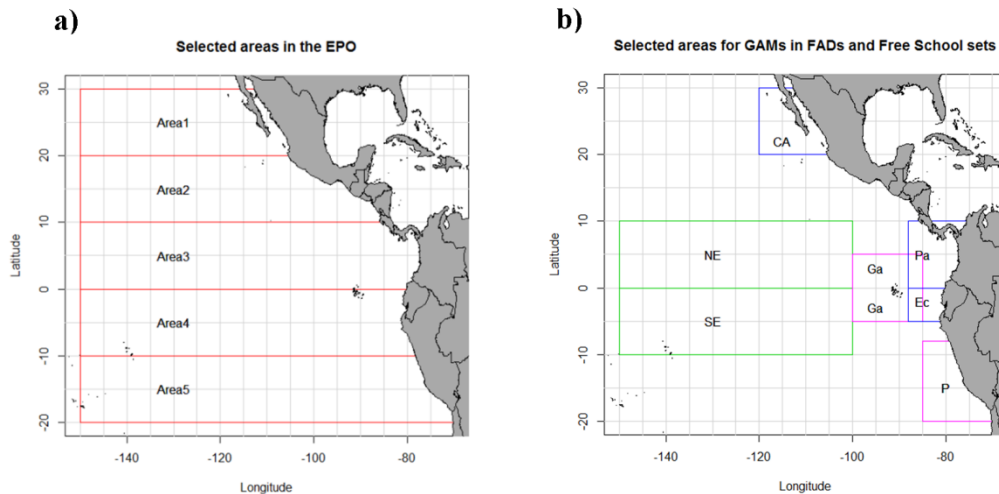


Figure 31. (a) Selected areas for the study in the Eastern Pacific Ocean and (b) Selected areas for GAM analysis in FAD (green and blue) and School sets (pink and blue). NE (North Equator), SE (South Equator), Ga (Galapagos), P (Peru), CA (California), Pa (Panama) and Ec (Ecuador).

As species level identification for the Families Belonida, Diodotidae and Myliobatidae, and the Genus *Sphyrna* were not possible, they were considered as morphospecies -taxa that are distinguishable on the basis of the morphology (Oliver and Beattie 1996b) - and treated as species in species richness estimates (Lezama-Ochoa et al. 2015).

The list of species selected comprised a total of 83 species (6 billfish species, 28 sharks, 36 fishes, 5 turtles and 8 species of rays) (see S2. Table 1 in Supplementary material-Chapter 2).

2.4. Environmental data

For each fishing set (date and position), which covered the period December 2005- February 2010, values of oceanographic variables were obtained from ocean models and satellite data. Temperature at 20, 30, 50 and 75 m depth (S20, S30, S50, and S75; in °C); Depth of the Thermocline (Therm. Depth; in m); Gradient of the Thermocline (Therm. Grad; in °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 ocean models with a spatial resolution of 25 km and a frequency of 2/3 days.

Sea Surface Temperature (SST; in °C) was measured from AVHRR and MODIS sensors and have 4 km resolution. Chlorophyll concentration the same day of the fishing set and 18 days before (Cl

and Cl-18 in mg m^{-3}) had a 4 km resolution and came from measurements of MODIS and MERIS satellite sensors. Sea Level Anomaly (SLA; in cm) and geostrophic current speed (WG; in kn) were available with 25 km resolution. These altimetry products came from different combinations of satellites ERS², Topex/Poseidon, Jason-1/2, ENVISAT/GFO and CRYOSAT. This information was processed and provided by the CLS (Collecte Localisation Satellite, France, <https://www.cls.fr>).

3. METHODS

3.1. Alpha diversity

Biodiversity is a concept with multiple meanings, and with attributes that can be measured in many different ways (Buckland et al. 2005). Alpha diversity measures the species diversity of a particular community, expressed by two components: the number of species present and how even their numerical participation in the community is (Magurran 2004).

Species richness index (the total observed and the mean per set) was calculated for each area in both fishing modes. Species accumulation curves with 100 permutations were also constructed for each fishing mode and by areas. 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). For that reason, Chao2 non-parametric estimator (Chao 1984) based on the incidence or frequencies of species were also calculated to obtain the estimated total species richness (which represents the asymptote of the species accumulation curve) vs. total observed species richness. Chao2 non-parametric estimator was selected as is considered to be more rigorous in sampling theory than parametric estimators or curve extrapolations (Gotelli and Colwell 2011) to estimate total species richness with precision (Chao 1984). This is because it does not require a predetermined abundance distributions or the application of a priori or ad hoc models (Colwell and Coddington 1994; Chao et al. 2005).

Evenness is a measure of the relative abundance of the different species of an area. 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. Thus, log-rank abundance curves were constructed for each fishing mode (FAD vs. School) for obtaining the abundance of the first 10

species. The mean of Pielou's J-evenness index, a Shannon evenness index, was also calculated for the estimation of Evenness by areas for both fishing modes. Pielou's J-evenness is calculated as: $H/\ln(S)$ where H is the Shannon diversity index and S the Species richness. The shape of the log-rank abundance for each fishing mode can be explained by species abundance models as Geometric, Log-series, Log-normal and Broken stick models (Magurran 2004) and it is used to describe the structure of the community. The data were fitted to different models and the best model fit, according to the lowest AIC value or Akaike's Information Criterion (1974), represents best the community structure (Kindt and Coe 2005).

Diversity indices such as species richness provide information about the number of species of the community. In contrast, other index such as Shannon diversity index (Shannon and Weaver 1949) also provides information about the relative abundance of them (Magurran 2004). If Shannon index (H) increases, diversity increases.

Thus, species richness and Shannon diversity index were calculated for each FAD and School fishing set (total and by trimester) and are shown in biodiversity maps. These maps were constructed by aggregating the sets in $1^{\circ} \times 1^{\circ}$ grids. The mean species richness was represented for squares containing more than 30 FAD sets. In the case of School sets, the index was represented for squares containing more than 10 sets. In the case of Shannon index, diversity (as the average Shannon index value per set) was represented in squares which contain more than 20 FAD sets and more than 5 School sets. The mean Shannon diversity index was also calculated by year in both fishing modes to relate diversity patterns with the ENSO phenomenon.

3.2. Beta diversity

Beta diversity measures the change in the composition of species between different communities. The Bray - Curtis similarity index (1 minus dissimilarity index) (Legendre and Legendre 2012) was calculated in both fishing modes to find similarities in species composition between areas. It is defined as $2W/(A+B)$, where A and B are the sums of the abundances of all species at the two areas and W is the sum of minimum abundances of all common species (i.e. number of individuals) between two areas where the species were sampled (Irigoiien et al. 2011). Values range from 0 when all species are common between 2 areas to 1 when communities do not share species. Abundance data were log-transformed ($\log n + 1$) to reduce the effect of the most

abundant species. Results were showed by hierarchical cluster analysis with the “complete” linkage method and the function “hclust” from the R software.

3.3. Geographical and habitat preferences of by-catch communities

GAMs (Guisan et al. 2002; Hastie and Tibshirani 1990) were constructed to identify the spatial and habitat preferences of the by-catch species in relation with species richness and Shannon diversity index for each fishing mode. The period 2006-2010 was used for which environmental data was available. The areas selected for constructing the models (Figure 31b) were chosen based on the most diverse areas observed with the diversity maps. Spatial (latitude and longitude), temporal (month) and oceanographic variables were included in the analysis. These models were chosen over generalized linear models due to their ability to deal with non-linear relationships between the response and explanatory variables and smooth functions were used to fit the variables.

All environmental covariates were considered initially for both parts of the model, except those highly correlated between them to avoid overfitting (Wood 2006). The degrees of freedom of the smooth functions were determined for each explanatory variable as part of the model fitting process. 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.

A GAM with a QuasiPoisson error distribution and logistic-link function was used to model the number of species (species richness) in both fishing modes.

A GAM with a Gaussian error distribution with identity-link function was used to model the Shannon diversity index in FAD sets and with Gamma error distribution with inverse-link function (+0.05 applied to response data to correct the model) in School sets. 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.

All the analyses were carried out following similar methodology as in Lezama-Ochoa et al. (2015) and using “vegan” (Oksanen et al. 2013), “BiodiversityR” Kindt and Kindt (2015) and “mgcv”

(Wood and Wood 2007) packages of R-2.14.0 free software (Team 2013). Geographic Information System (GIS) software (Quantum 2011) was used to create biodiversity maps.

4. RESULTS

4.1. Alpha diversity

The Chao2 estimator and species accumulation curves showed that FAD and School sets nearly reached the asymptote with 86 and 75 species respectively (Table 9, Figure 32), which means that almost all species of the study area appeared in both fishing modes and the sample size was enough for obtaining the total by-catch estimates.

In general, both fishing modes showed similar species richness (or number of species) (Table 9), with slightly higher number of observed species in FAD sets (78) in comparison with School sets (74). However, FAD sets seem to need more sample size to find the same number of species than School sets (Figure 32a). A simulation (see S2. Figure 2 in Supplementary material-Chapter 2) was done (5 replicates) of species accumulation curves for both fishing modes in which the same numbers of sets for FADs than for School sets were selected to estimate the total species richness. In all the cases, and with the same number of sets in both fishing modes, FAD sets needed more sample size to find the same number of species than School sets.

Different number of species for each area was found. Species richness estimated by areas showed that Area 3 and Area 4 were the areas with highest number of species observed in FAD and School sets; with 70 and 66 observed species, respectively in the first one and 61 and 57 species in the second one. The area with lowest species richness in FAD sets was the Area 1 with 26 species and Area 5 with 40 species for School fishing mode (Table 9, Figure 33).

Table 9. Distribution of sets (N), Overall Observed Species richness (Obs. SR), Mean species richness per set (Richness), Richness standard error (Rich. se), Chao2 non-parametric estimator, Chao2 standard error (Chao se), Mean Evenness index per set (Evenness), Evenness standard error (Ev. se), Mean Shannon diversity index per set (Shannon) and Shannon standard error (Sh. se) by areas in FAD and School sets.

Area	FAD										School									
	N	Obs. SR	Richness	Rich. se	Chao2	Chao se	Evenness	Ev. se	Shannon	Sh. se	N	Obs. SR	Richness	Rich. se	Chao2	Chao se	Evenness	Ev. se	Shannon	Sh. se
Area 1	211	26	2.47	1.1	29	3.66	0.58	0.3	0.45	0.38	3279	52	1.32	0.61	55	3.49	0.8	0.26	0.16	0.3
Area 2	1766	52	3.54	1.88	53	1.31	0.62	0.26	0.69	0.48	2437	51	1.38	0.7	53	2.51	0.77	0.27	0.17	0.31
Area 3	39040	70	4.24	2.02	79	10.17	0.63	0.25	0.82	0.47	5849	61	1.49	0.81	63	2.65	0.76	0.27	0.22	0.34
Area 4	30915	66	3.27	1.63	74	11.66	0.66	0.24	0.69	0.43	6371	57	1.32	0.63	62	4.84	0.78	0.25	0.16	0.3
Area 5	12660	54	2.55	1.28	60	7.55	0.63	0.27	0.5	0.38	2713	40	1.21	0.51	42	2.16	0.73	0.27	0.1	0.24
Total	84592	78	3.62	1.89	86	8.28	0.64	0.25	0.72	0.45	20649	74	1.36	0.68	75	1.01	0.77	0.27	0.17	0.31

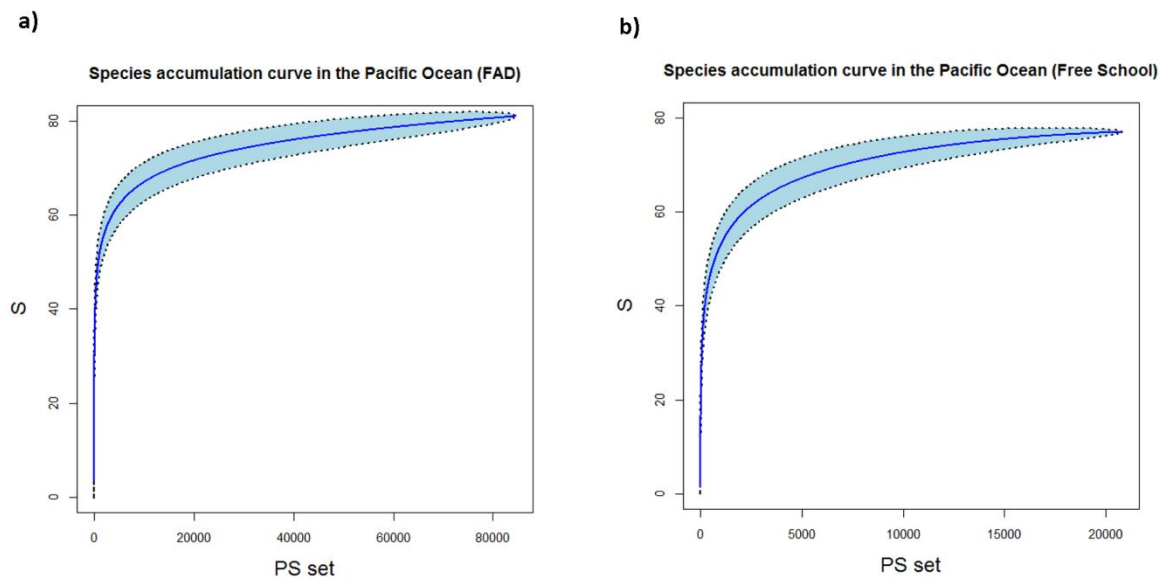


Figure 32. Species accumulation curves in FAD (a) and (b) School sets. PS=purse seine set; S=Species richness.

In FAD sets, the Chao2 index estimated a maximum of 79 species in Area 3 and 74 species in Area 4 (Table 9). The shape of the accumulation curve reaching the asymptote suggested that by-catch species were frequently caught in Area 3 and Area 4 (Figure 31a). By contrast, in School sets, a maximum of 63 species could be caught in Area 3 and 62 in Area 4 (Table 9, Figure 33b).

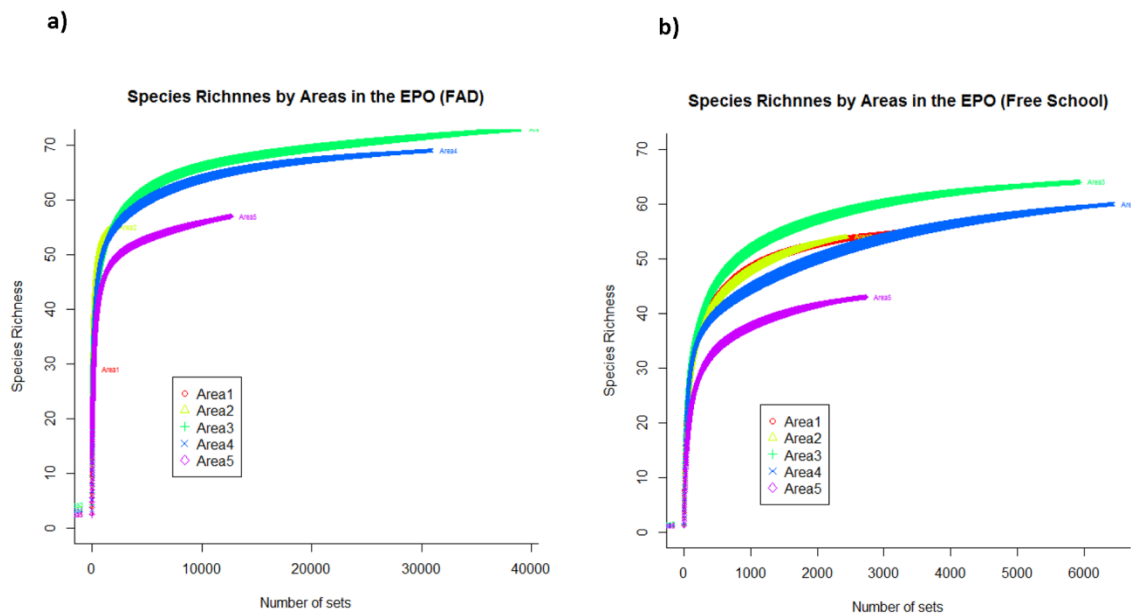


Figure 33. Species accumulation curves by areas in FAD (a) and (b) School sets. PS=purse seine set; S=Species richness.

With respect to the evenness measures, Area 4 is the area with largest species evenness values in FAD sets and Area 1 in School sets. Thus, areas from most to least evenness were ordered as follows: Area 4>Area 3=Area 5>Area 2>Area 1 for FAD sets, and Area 1>Area 4>Area 2>Area 3>Area 5 for School sets (Table 9).

Table 10. Species abundance in FAD and School sets.

FAD				School sets			
Species	Rank	Abundance	Proportion	Species	Rank	Abundance	Proportion
<i>Canthidermis maculatus</i>	1	16983197	46.2	<i>Seriola lalandi</i>	1	231807	21.7
<i>Coryphaena hippurus</i>	2	6589668	17.9	<i>Sectator ocyurus</i>	2	173652	16.3
<i>Acanthocybium solandri</i>	3	3885018	10.6	<i>Coryphaena hippurus</i>	3	131939	12.4
<i>Sectator ocyurus</i>	4	3333164	9.1	<i>Caranx sexfasciatus</i>	4	93892	8.8
<i>Elagatis bipinnulata</i>	5	1482598	4	<i>Canthidermis maculatus</i>	5	89783	8.4
<i>Aluterus scriptus</i>	6	1222902	3.3	<i>Carcharhinus falciformis</i>	6	66943	6.3
<i>Coryphaena equiselis</i>	7	990409	2.7	<i>Acanthocybium solandri</i>	7	62226	5.8
<i>Aluterus monoceros</i>	8	881017	2.4	<i>Sphyrna spp.</i>	8	55523	5.2
<i>Carcharhinus falciformis</i>	9	468542	1.3	<i>Elagatis bipinnulata</i>	9	20634	1.9
<i>Seriola lalandi</i>	10	256284	0.7	<i>Mobula thurstoni</i>	10	17602	1.6

Based on Log-rank abundance data, the abundance of the first 10 species is shown in Table 10. The ten most abundant species formed 98.1% with respect the total species in FAD sets and 88.4% in School sets. The most abundant species in FAD sets was the *Canthidermis maculata* (16983197 individuals) and *Seriola lalandi* (231807 individuals) in School sets.

Furthermore, the application of the different species abundance models to rank abundance curves in both fishing modes showed that by-catch communities in FAD sets followed a Log-normal distribution, and the by-catch communities in School sets a Zipf distribution based on the lowest AIC values (see S2. Table 2 in Supplementary material-Chapter 2).

Finally, the mean species richness and Shannon diversity index were calculated and results are shown in Figs. 35-38. In general, diversity showed latitudinal and longitudinal gradients. Species richness and Shannon index showed highest diversity in FAD sets in Area 3 and Area 4 at both sides of Equator, followed by the area situated around Galapagos Islands and finally along the Peru and California coast with lowest diversity values (Figs. 35 and 36). Diversity increased from North and South towards the Equator and westward from the coast.

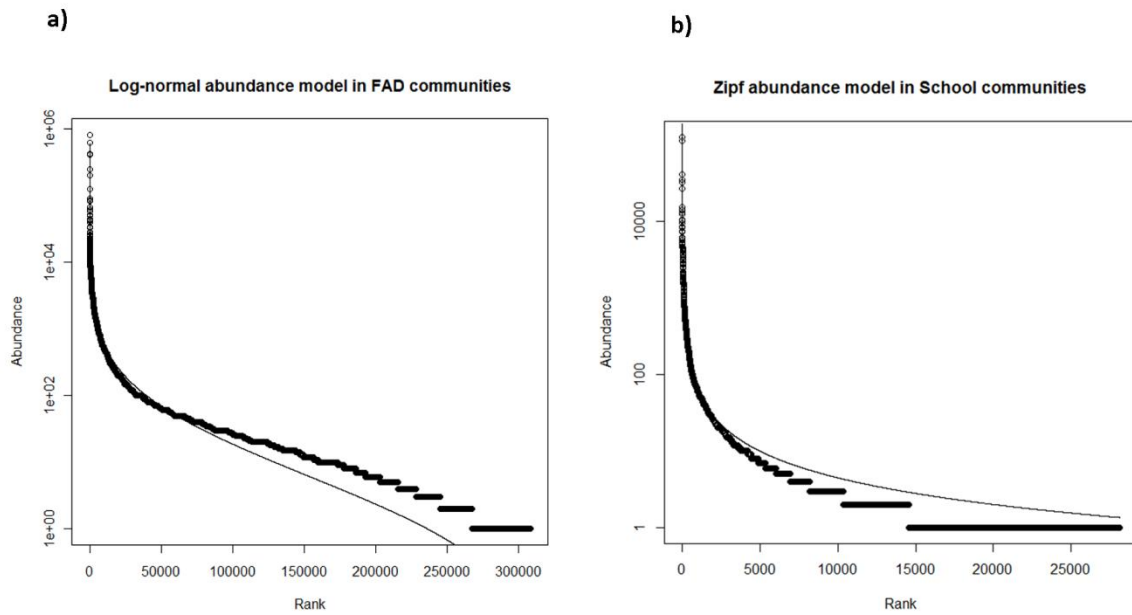


Figure 34. Species distribution model selected in FAD (a) and (b) School sets.

In contrast, in School sets, the mean species richness and Shannon index showed the highest diversity around Panama, Costa Rica and Nicaragua (Area 3), followed by the area situated around Ecuador and with the lowest values around the coastal upwelling of Peru (Figure 37 and Figure 38). Mean richness and Shannon index, stratified by quarters in FAD sets showed the maximum diversity in the third and fourth quarter. A progressive increase of diversity by quarter from the coast of Peru towards the Equator was observed (Figure 35 and Figure 36). In School sets, there was no diversity pattern by quarters, with highest values observed in the first and second quarter (Figure 37 and Figure 38).

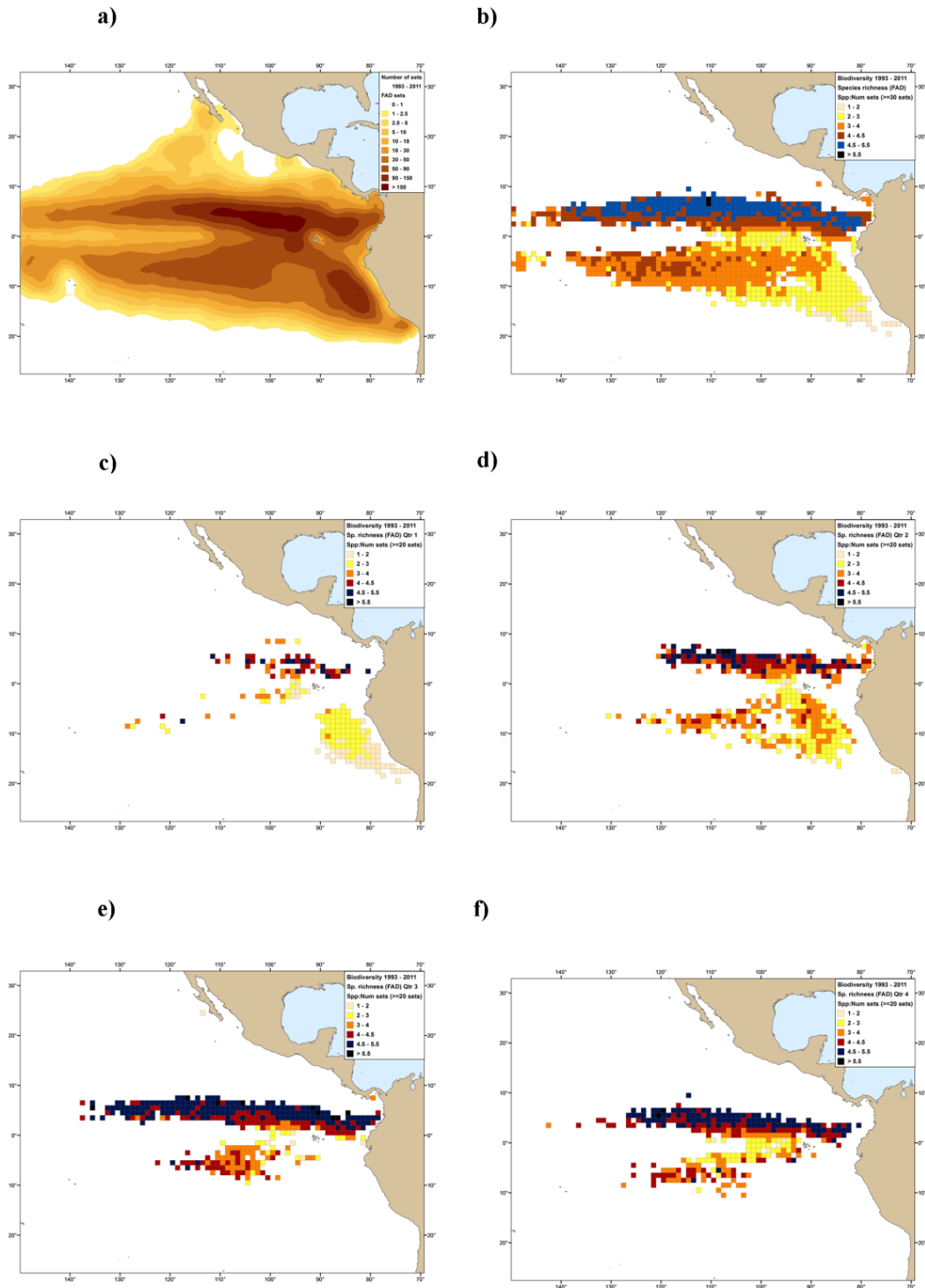


Figure 35. (a) Distribution of sets in FAD fishing mode. (b) Average number of species (species richness index) per set in squares with > 20 sets: (c) First quarter, (d) second quarter, (e) third quarter and (f) last quarter.

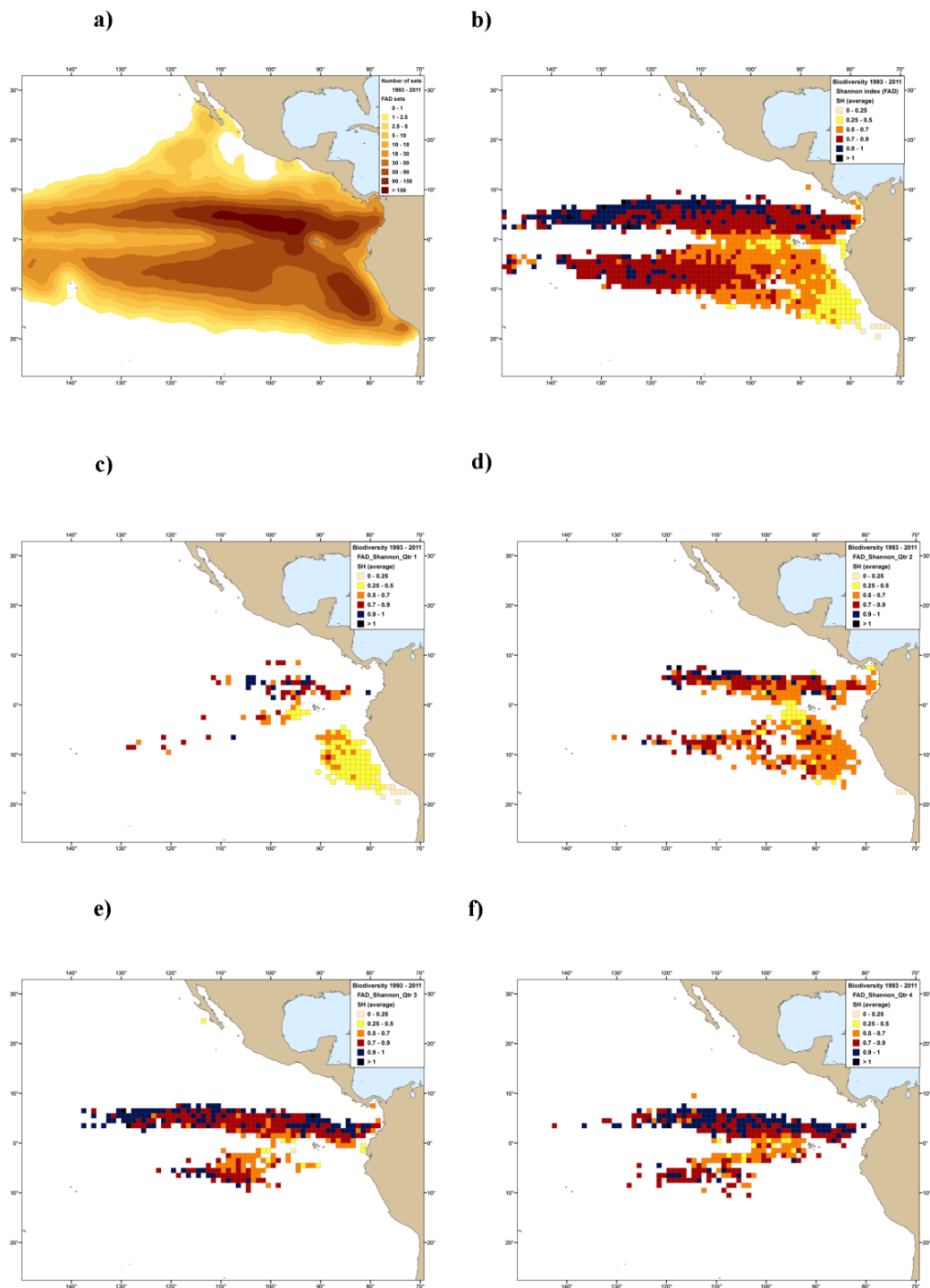


Figure 36. (a) Distribution of sets in FAD fishing mode. (b) Average diversity (Shannon index) per set in squares with > 20 sets: (c) First quarter, (d) second quarter, (e) third quarter and (f) last quarter.

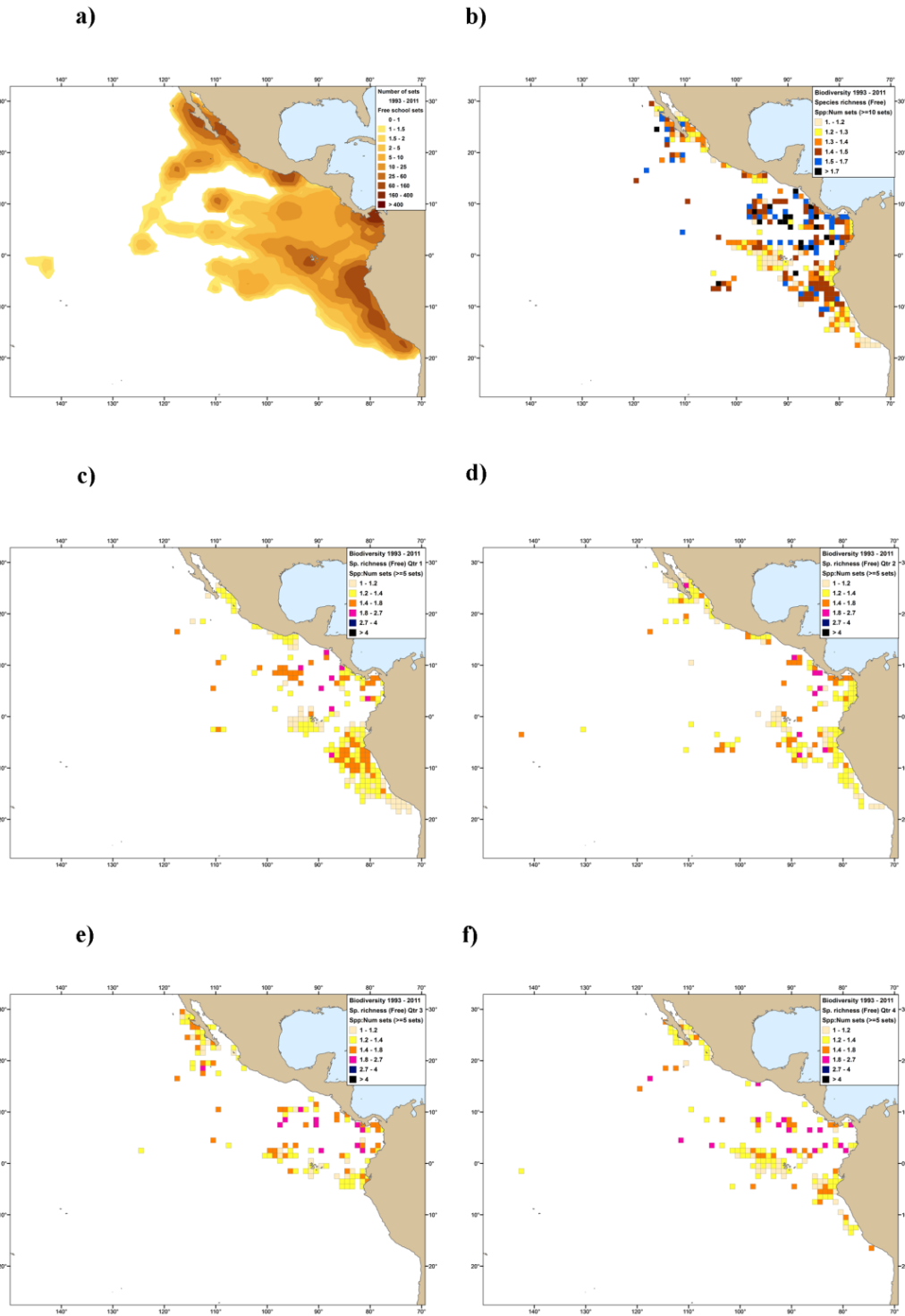


Figure 37. (a) Distribution of sets in School fishing mode. (b) Average number of species (species richness index) per set in squares with > 10 sets. Species richness in (c) first quarter, (d) second quarter, (e) third quarter and (f) last quarter in quadrants with > 6 sets.

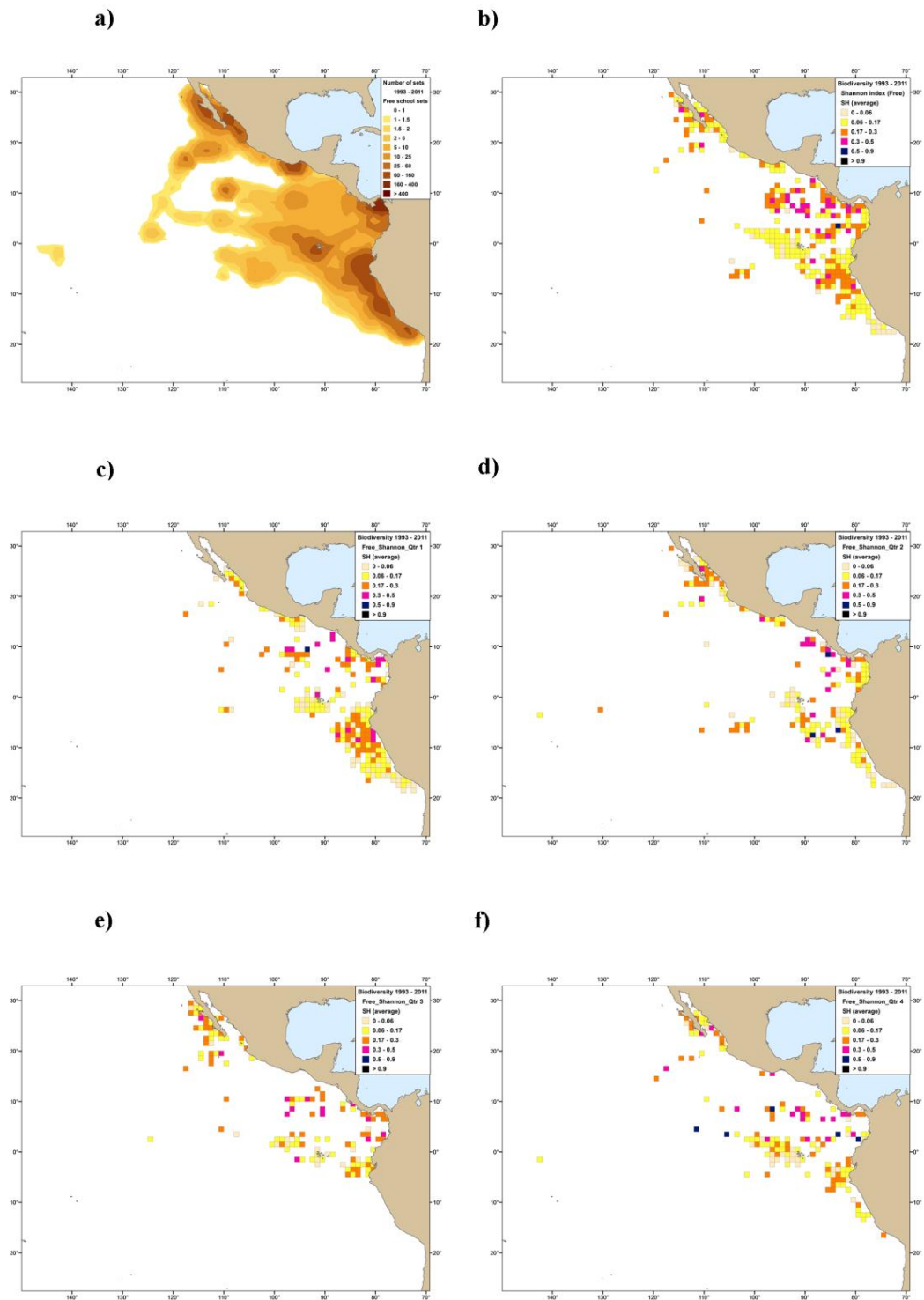


Figure 38. (a) Distribution of sets in School fishing mode. (b) Average diversity (Shannon index) per set in squares with > 10 sets. Shannon diversity index in (c) first quarter, (d) second quarter, (e) third quarter and (f) last quarter in quadrants with > 6 sets.

Diversity (based on observed Shannon index) was analyzed by years and differences between both fishing modes were found. Diversity decreased in School sets since 2000 and in FAD sets since 2005. In addition, diversity was better related with the ENSO phenomenon in FAD sets than in School sets. Changes in diversity in FAD sets match up with the major El Niño (1997-1998 and 2009-2010) and La Niña events (1994, 1999-2000 and 2007-08) (Figure 39).

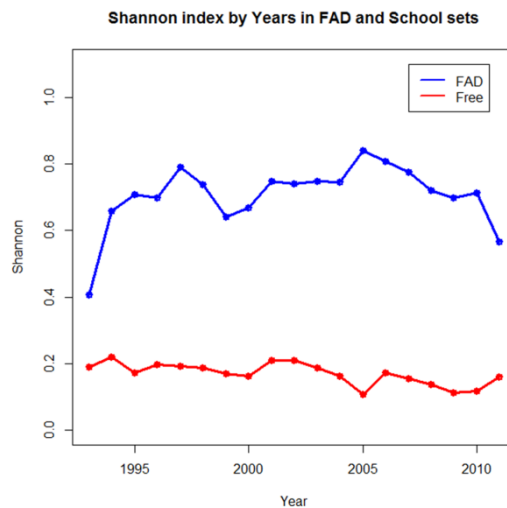


Figure 39. Shannon diversity index (mean per set) by years and fishing mode related with El Niño and La Niña phenomenon.

4.2. Beta diversity

FAD sets were characterized by high similarity in species composition between Area 3 and Area 4 (0.13). The larger dissimilarity was found between Area 1 and Area 3 (0.63) and between Area 1 and Area 4 (0.59) (Figure 40, see S2. Table 3 in Supplementary material-Chapter 2).

The Bray-Curtis similarity index showed lowest values in School sets between Area 3 and Area 4 (0.2); which implies that those areas are represented by communities with similar species composition. Area 1 showed some similar species composition with Area 5 (0.29) but the highest values were found between Area 2 and Area 5 (0.39) for School sets (Figure 40, see S2. Table 3 in Supplementary material-Chapter 2).

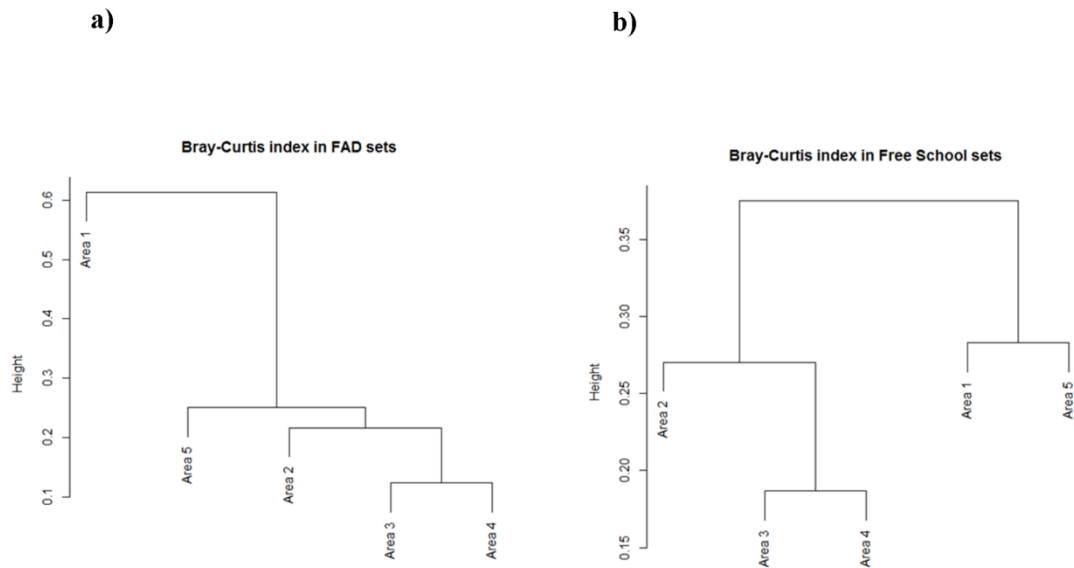


Figure 40. Bray-Curtis similarity index in (a) FAD and (b) School sets.

Overall, equatorial areas (Area 3 and Area 4) showed similar species composition between them in FAD sets. On the other hand, areas which support coastal upwelling systems (Area 1 and Area 5) showed similar species composition in School sets. Nevertheless, the area which supports the coastal upwelling of California (Area 1) seems to be the most different compared with others in FAD sets.

4.3. Geographical and habitat preferences of by-catch communities

In the case of FAD sets, the final model for species richness included as explanatory variables spatial variables (latitude-longitude interaction), temporal factors (month), and environmental variables (sea surface temperature, depth of the thermocline, salinity, chlorophyll and current speed).

The estimated parameters for species richness data and p-values are listed in Table 11 and Figure 41. The model explained 22.1% of the variance with a R^2 of 0.2 with 26412 samples. The results showed that the highest number of species was observed north of the Equator (0-10°N) around 120-140°W during September-October. Furthermore, highest richness values were found in areas with high sea surface temperatures, deep thermoclines, low salinities, low concentrations of chlorophyll ($< 0.2 \text{ mg/m}^3$), and velocities of the total current higher than 2 knots.

Table 11. Summary results for the optimal GAMs selected for species richness index and Shannon diversity index in FAD and School sets.

	FAD				School			
	Species richness		Shannon index		Species richness		Shannon index	
Family	Quasipoisson		Gaussian		Quasipoisson		Gamma	
Link function	Log		Identity		Log		Inverse	
Adjusted R ²	0.2		0.19		0.12		0.09	
Deviance explained	22.1		19.5		13.4		11.9	
	Estimate	p-value	Estimate	p-value	Estimate	p-value	Estimate	p-value
Latitude * Longitude	27.114	< 2e ⁻¹⁶	27.564	< 2e ⁻¹⁶	25.826	< 2e ⁻¹⁶	23.349	< 2e ⁻¹⁶
Month	7.494	< 2e ⁻¹⁶	7.667	< 2e ⁻¹⁶	2.299	2.42e ⁻⁰⁷	2.266	1.32e ⁻⁰⁷
SST	6.72	< 2e ⁻¹⁶	5.667	< 2e ⁻¹⁶	1.287	7.91e ⁻⁰⁷	1.816	6.09e ⁻⁰⁸
Chlorophyll-18	-	-	-	-	-	-	-	-
Chlorophyll	7.738	3.66e ⁻¹¹	7.81	2.40e ⁻⁰⁷	3.867	0.01033	7.94	0.000714
SLA	-	-	-	-	-	-	-	-
Sal20	6.2	1.78e ⁻¹³	6.257	6.68e ⁻⁰⁷	-	-	-	-
Therm.Grad	-	-	-	-	1.002	0.02	-	-
Therm.Prof	5.151	0.000128	1	0.00177	-	-	-	-
WG	-	-	-	-	4.333	0.00717	-	-
WT	7.015	1.21e ⁻⁰⁹	7.301	0.00079	-	-	-	-

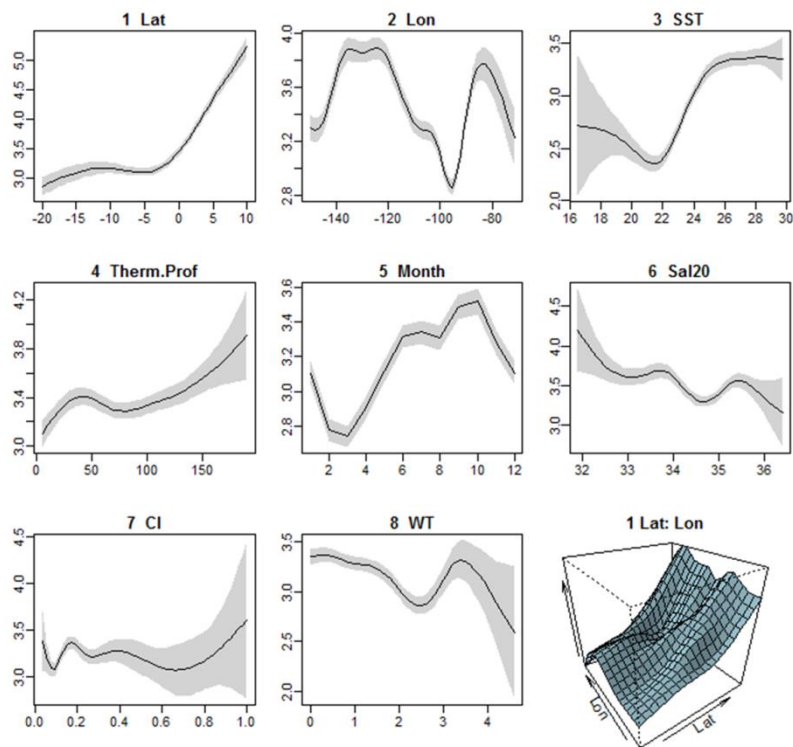


Figure 41. Smoothed fits of covariates modelling the species richness index:: 1) Lat (Latitude), 2) Lon (Longitude), 3) SST (Sea surface temperature), 4) Therm. Prof (Depth of thermocline), 5) Month, 6) Sal20 (Salinity and 20 meters

depth), 7) CI (chlorophyll) and 8) WT (Total speed current) variables and interaction of latitude with longitude (1 Lat : Lon) in FAD fishing mode. The y-axis represents the spline function. Dashed lines indicate approximate 95% confidence bounds.

With regard to School sets, species richness was explained with spatial interaction (latitude-longitude), month (as factor), sea surface temperature, chlorophyll, gradient of the thermocline and geostrophic velocity variables. Results showed that the model explained 13.4% of the variance with a R2 of 0.1 with 3525 samples (Table 11, Figure 42). Species richness was higher between 0°-10°N and 90°-100°W during the first and the last quarter. High values were found in warm areas with high concentration of chlorophyll (>5 mg/m³), low thermocline gradients and geostrophic velocities between 0.8-1 knots.

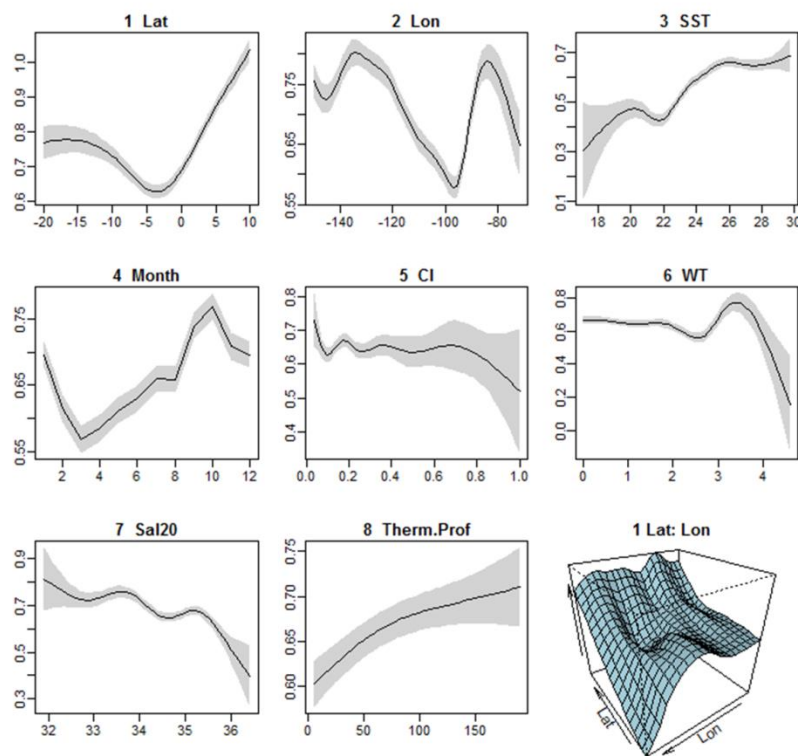


Figure 42. Smoothed fits of covariates modelling the species richness index:: 1) Lat (Latitude), 2) Lon (Longitude), 3) SST (Sea surface temperature), 4) Month, 5) CI (Chlorophyll), 6) WT (Total speed current), 7) Sal20 (Salinity at 20 meter depth) and 8) Therm.Prof (Depth of thermocline) variables and interaction of latitude with longitude (1 Lat : Lon) variables in School fishing mode. The y-axis represents the spline function. Dashed lines indicate approximate 95% confidence bounds.

In order to relate Shannon diversity index with environmental variables in space and time in FAD sets, the final GAM includes Shannon diversity index as response variable, latitude and longitude as geographical variables, month as temporal-factor variable and sea surface temperature, chlorophyll, salinity, depth of the thermocline and velocity of the current as environmental variables. Gaussian model for Shannon diversity index explained 19.5% of the variance with a R² of 0.1 with 26412 samples (Table 11). Results showed similar diversity patterns as with species richness and therefore, only models with species richness were represented.

Finally, for School sets, the final GAM model for Shannon index was constructed with latitude and longitude as geographical variables, month as temporal-factor variable and sea surface temperature and chlorophyll as environmental variables. Results showed that the model explained 11.9% of the variance with a R² of 0.09 with 4163 samples (Table 11). High diversity was found between 0°-10°N, between 10°-20°S, and around 90° W. Diversity was higher in the first and the last quarter with a positive linear relationship with sea surface temperature, increasing diversity at higher temperatures, and with chlorophyll concentrations between 0 and 0.1 mg/m³ and between 5 and 7 mg/m³ (two different diversity peaks). As the GAM model with Shannon index showed the same patterns as with richness index, only the model of richness was represented. The relative percentage of deviance explained for the most important variables in all the models are showed in the supplementary material (see S2. Table 4 in Supplementary material-Chapter 2).

5. DISCUSSION

Diversity patterns in the pelagic ecosystem are not well known and need to be considered in developing an Ecosystem Approach to Fisheries Management (Zhu et al. 2011). The implementation of EAFM requires extensive information not only about the by-catch species but also about the environmental conditions, which influence the species diversity patterns of those species.

This study examined the diversity of the by-catch communities with a variety of relatively simple but comprehensive metrics based on data collected by observer programs from tropical tuna purse seine fishery in FAD and School sets. Results showed a variety of diversity patterns on by-catch communities, with associated changes on the number and abundances of the species as a function of the area, time of year and fishing mode. Furthermore, they provided new information about the habitat preferences of the species communities in the Eastern Pacific Ocean. We suggest that

diversity and habitat preferences of by-catch communities in both fishing modes vary according to the specific oceanographic characteristics of the Eastern Pacific Ocean.

5.1. Alpha and Beta diversity

Marine biodiversity in the pelagic ecosystem has been under threat and in that sense, species diversity is an important ecological parameter to study the changes of the by-catch communities because of its sensitivity to ecosystem properties (Tolimieri 2007).

Species diversity can be measured in different ways and levels of organization, but in regard to its use in conservation biology, diversity at the species level and with a good sample size is necessary. Our results showed that the sample size used in this study nearly to 100% coverage rate was enough to find all species in FAD and School sets using accumulation curves. In contrast with previous work about biodiversity of the by-catch species in the Indian Ocean (Lezama-Ochoa et al. 2015), the number of species observed in this work were similar in both fishing modes. In fact, although it is known that the by-catch number of species and weight found usually in each FAD set is higher than in each School set (Amandè et al. 2010; Torres-Irineo et al. 2014), our work suggests that the total number of possible by-catch species caught in the tropical tuna purse seiners depends on the sample size and the coverage rate, and not on the fishing mode like in previous estimation (Amandè et al. 2010). A good sample size is necessary to estimate the species richness with precision to carry out any biodiversity study. For that reason, the low sample size and coverage rate (around 10%) used in the Indian (Lezama-Ochoa et al. 2015) and Atlantic Ocean (Lezama-Ochoa et al. 2015, submitted) could explain the differences found in the total richness estimation in comparison with the Pacific Ocean.

Most of the actual works use richness as the sole measure of diversity, ignoring community evenness and species' relative abundances (Connolly et al. 2013). In that sense, the species accumulation curves and the log-abundance curves provide information, based on the shape of the curve, about the species richness and relative abundance of the by-catch species. For example, areas with high diversity such as equatorial areas (Area 3 and Area 4) had steeper initial slopes in their species accumulation curves, plateau quickly and provided accurate estimate of species richness (Thompson and Withers 2003). In addition, in this work, the most abundant species (*Canthidermis*, *Coryphaean*, *Elagatis*, etc) match with the work published by Taquet et al. (2007) about the fish communities associated with FAD sets in the Western Indian Ocean using underwater visual surveys.

A community with evenly distributed species abundance (as in our study around equatorial areas) appears more diverse than a community with the same number of species that is dominated by few species (Stirling and Wilsey 2001). Furthermore, 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 relation with the species abundance models. In general, the Zipf model assumes a larger fraction of rare species than the Log-normal distribution model does (Magurran and McGill 2011). The structure of the by-catch communities in FAD sets (Log-normal model) and School sets (Zipf or Mandelbrot model) let us to infer that both fishing modes represent different communities and therefore, the environment conditions and the areas where the species are found are also different.

Analysis of dissimilarity or Beta diversity indicated that the by-catch communities have different species composition depending of the area where they were observed. The composition of the species was similar between the equatorial areas (with low dissimilarity values between Area 3 and Area 4) and between the areas which support coastal upwelling systems (Area 1 and Area 5). Therefore, environment conditions could be the cause of the different species composition and behavior of the species.

General differences in diversity and species composition between the equatorial and the coastal upwelling areas (considered as different biomes (Hardman-Mountford et al. 2008)) are clear and the environmental conditions in each area seem to be the reason for that. On the other hand, biodiversity maps showed that in general, species diversity is distributed with a longitudinal gradient in the equatorial area in FAD sets and with a latitudinal gradient around the coast in School sets; which could be explained by the environment but also by the fishing strategy: fishing in FAD sets is usually in offshore following the surface currents and travelling thousands of miles whereas in the case of School sets, fishing takes place near to the coast.

It is clear that climatic variability can have major effects on the population dynamics of exploited fish stocks (Bakun 2010). Thus, for example, ENSO variability is most pronounced along the equator and along the coast of Peru and influence fishery production (Wilson and Adamec 2001). Thus, based on this work, we suggest that diversity in FAD sets is more influenced by ENSO phenomenon around the equatorial area, where important variability also occurs along the countercurrent thermocline ridge north of the equator (Fiedler 2002). The most important events of the El Niño and La Niña are consistent with the highest and lowest values of Shannon diversity index in FAD sets; therefore, this area could be considered as a perfect place to study the consequences of ENSO over biodiversity issues.

5.2. Geographical and habitat preferences of by-catch communities

Latitudinal gradient in diversity (diversity increases from the poles to the equator) is an evident phenomenon of biodiversity at the global scale (Hillebrand 2004). However, it is not always clear in the open ocean when environmental and physical conditions are considered (Zhu et al. 2011). Studies of oceanic biogeography have consistently shown that the distributions of pelagic communities match the distribution of water masses (Angel 1993), but determination of the dominant factors influencing the distributions of these communities is difficult. GAMs can be a useful tool to relate diversity of the by-catch communities with the geographical and environmental conditions in the Eastern Pacific Ocean.

We observed two general diversity patterns on by-catch communities in both fishing modes. Firstly, we observed that by-catch communities are more diverse in equatorial areas in FAD sets and in warm coastal areas in School sets. In contrast, the permanent coastal upwelling areas of California and Peru showed high productivity rates but low species diversity. These patterns, described by Irigoien et al. (2004) and Sala and Knowlton (2006) confirm that diversity in general in the open oceans and particularly in the tropics is lower at high disturbance levels and high productivity rates. High diversity can be maintained at intermediate levels of natural disturbance by enabling the coexistence of potential competitors and stress tolerant species (Kimbrow and Grosholz 2006). In general, areas with high disturbance and nutrients level such as permanent coastal upwelling areas of California and Peru have high density of organism with short trophic chains and high primary productivity rates (Huston 1979). For that reason, these areas usually have low species diversity; they are formed by few but abundant species in unstable systems. The equatorial areas and coastal upwelling systems induced by wind forces, in contrast, are stable systems with intermediate productivity rates and therefore, high species diversity.

Secondly, higher diversity was found in the western side of the Eastern Pacific Ocean in FAD sets than in the east side. This result also coincides with work published by Briggs (2007) and Sala and Knowlton (2006), who suggested that there is a positive relationship between species diversity and geographical area because of the major oceanic currents, decreasing diversity in general from west to east in the tropical Pacific and Atlantic.

Our models contributed to explain diversity patterns of the by-catch communities. Thus, the geographical position and the seasonal variability seem to play an important role in the habitat distribution of these species. In the case of the environmental variables, the sea surface temperature and salinity were the parameters that better explained diversity patterns in FAD sets and chlorophyll in School sets (see S2. Table 4 in Supplementary material-Chapter 2).

Diversity patterns of by-catch communities in both fishing modes in the eastern tropical Pacific are in good agreement with the principal characteristics of its oceanography, hydrography and circulation (Fiedler and Talley 2006; Kessler 2006; Lavin et al. 2006). Concretely, the higher values of diversity are related to water masses associated with coastal and oceanic upwelling processes. Thus, diversity patterns from the models clearly indicated that by-catch communities in FAD sets are highly associated with the equatorial tongue (from August to October) which is developed when the southeast trade winds are strongest during southern Winter (Wyrtki 1981) and with the North Equatorial Countercurrent and with three physical features particularly significant in the Tropical Surface Water (TSW): the Equatorial Front, the Costa Rica Dome within the warm pool (Fiedler and Talley 2006) and the countercurrent thermocline ridge (along 10°N) (Hoegh-Guldberg and Bruno 2010).

All these sites are characterized by warm waters with low-salinity and intermediate productivity concentrations, strong currents and with great biological significance, where marine predators and prey may aggregate during September-October. The north equatorial area is influenced by the thermocline, which is shallow and strong in the eastern region of the eastern tropical Pacific and deepest in the west. Variations in thermocline depth and surface temperature are often associated with variations in salinity and therefore, also in primary production (Pennington et al. 2006). In accordance with Fiedler and Talley (2006), the thermocline decreases significantly along the equator and along the countercurrent ridge, which induces to tuna and by-catch species to aggregate near the surface around this area, thereby becoming readily in areas of high diversity.

In the case of the by-catch communities in School sets, the models indicate that highest species diversity is associated with coastal upwelling regions around Costa Rica and Panama in the equatorial area (Gulf of Papagayo and Gulf of Panama). 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 (Change 2007), induce upwelling of colder and nutrient-rich waters to the surface, giving place to cool and very productive surface waters.

In general, the diversity patterns found in the models in relation to environmental variables in both types of fishing modes coincide with the oceanographic characteristics of the work published by Pennington et al. (2006).

Furthermore, whereas diversity in FAD sets seems to be related with total speed of the main currents in the equatorial area, in School sets diversity could be explained by geostrophic currents and eddy circulation (Bakun 2006) around the Mexican coast (around 5°N). However, further

analyses around this hypothesis are needed before to conclude any strong relationship. Likewise, the largest zone of low oxygen in the world's ocean is found between the American coast and the NEC and SEC, clearly as a result of lack of ventilation within the warm pool (Pennington et al. 2006). This property determines the distribution and diversity of most by-catch species that inhabit this area. For that reason, the inclusion of different environmental covariates such as dissolved oxygen (oxycline) and nutrients such as phosphate or nitrate might improve the results.

5.3. Implications for fisheries management

The impacts of fisheries in many regions of the world have contributed to overfishing. The lack of ability to apply the Ecosystem Approach to Fisheries Management shows that management has failed to assure the sustainability of the entire ecosystem in the world (Botsford et al. 1997; Hutchings and Baum 2005; Jackson et al. 2001; Myers and Worm 2005).

Biodiversity indices can be used to characterize the ecosystems and provide empirical measures for assessing any ecological change towards an implementation of the EAFM (Buckland et al. 2005). These measurements provide information on trends in biodiversity 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 potential ecological indicators of the pelagic ecosystem. However, some changes can be detected with these indicators whereas others not. For that reason, the application of those indices by size categories, for example, could detect specific changes. As such, improved knowledge of the spatial distribution and the habitat of the by-catch communities would allow considering spatial and temporal management measures for the conservation of marine biodiversity in the pelagic realm.

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 sometimes can be explained by the fact that some species are more detectable in some places than others as consequence of the different fishing effort, time of year or many other possible factors such as environmental events (ENSO cycle).

In the Atlantic and Indian Oceans, the European Union employs observers to record by-catch, but observers effort is low relative to the total fishing effort (around 10% of coverage rate) (Lewison et al. 2004) and, thus, observations and analysis can be biased (Lennert-Cody 2001). In

contrast, a 100% of coverage rate applied in 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 communities and impacts of commercial fisheries on the most vulnerable species.

Although observer programs provide important information about by-catch data, these programs are time-consuming, costly and require well trained observers for a correct identification of the species (Lewison et al. 2004). For that reason, a holistic Ecosystem Approach to Fishery Management requires the integration of different disciplines from species identification and levels or organization to ecological process (Botsford et al. 1997; Hutchings and Baum 2005; Jackson et al. 2001; Myers and Worm 2005).

Moreover, recent publications in fisheries management and ecology (Rochet and Benoît 2011; Zhou et al. 2010) suggest that selective fishing might change the biodiversity by altering species evenness, hindering rather than helping achieve the goals of EAFM (Garcia 2011). An integrated spatial-temporal management to protect the habitats, not only the species, and an effective fishing strategy that harvest in a sustainable manner all ecosystem components is essential for the conservation of the entire marine biodiversity (Garcia 2011).

6. CONCLUSION

This work has improved our understanding of diversity and habitat preferences of the by-catch communities 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. Although the FADs can aggregate higher and more diverse number of by-catch species in each set, in agreement with previous studies by Romanov (2002), Amandè et al. (2010), Torres-Irineo et al. (2014) and Lezama-Ochoa et al. (2015), all the analysis led us to infer that the total number of species observed in the purse seiner was similar in both fishing modes and the sample size necessary to find all the possible species was enough in both cases. Moreover, diversity was explained in both fishing modes according to the specific oceanographic characteristics of the Eastern Pacific Ocean.

This study contributed to the understanding and integration of different components and diversity measures to help to implement an ecosystem-based fishery management.

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CHAPTER 3

Biodiversity and habitat preferences of the by-catch communities from the tropical tuna purse-seine fisheries in the Eastern Atlantic Ocean

Nerea Lezama-Ochoa¹ • Hilario Murua¹ • Jon Ruiz¹ • Pierre Chavance² • Alicia Delgado de Molina³ • Ainhoa Caballero¹ • Igor Sancristobal¹

¹Azti-Tecnalia. Herrera kaia, portualdea z/g, 20110, Pasaia, Spain.

²Institut de Recherche pour le Développement (IRD), Sète, France

³Instituto Español de Oceanografía (IEO), Tenerife-Canary Island, Spain

ABSTRACT

The impact of human activities such as fishery has been identified as a main player of diversity loss in the open ocean. This paper studies the diversity patterns and habitat preferences of the by-catch communities in Fish Aggregating Devices (FADs) and Free School sets (sets made on school of tunas) from the tropical tuna purse-seine fishery in the tropical Atlantic Ocean (35° W-15° E and 20° N-15° S). Alpha diversity (species diversity of a particular area), Beta diversity (differences in species composition between areas) and Generalized Additive Models (GAMs) were calculated and developed for this purpose. Data were collected from scientific observer programs carried out between 2003 and 2011 on board Spanish and French fleets. Results showed that by-catch communities in FADs have slightly higher number of species (64 species) than Free School communities (60 species). Diversity patterns between both fishing modes varied according to the specific oceanographic characteristics of the Atlantic Ocean. The north equatorial surface current and thermal systems, such as Guinea and Angola Domes, could play an important role in the distribution of diversity of the by-catch communities associated to FAD sets around the equatorial

band (10°N-10°S). In contrast, diversity is related to coastal upwelling systems around the Senegal area and based on seasonal sampling in Free School sets. These results confirm the importance of integrating different components of the marine ecosystem towards the correct implementation of the Ecosystem Approach to Fishery Management (EAFM).

Keyword: By-catch · Bycatch · Species diversity · Purse seine-fishery · Generalized Additive Models · tropical Eastern Ocean · Ecosystem Approach to Fishery Management

1. INTRODUCTION

Human exploitation of marine resources, which has resulted in high levels of fishing or harvesting intensity, is one of the most important causes of diversity loss (Coll et al. 2010). The ten most productive species accounted for about 24% of world marine capture fisheries production in 2011, whereas 28.8% of fish stocks were estimated as overfished (FAO 2014).

In the tropical area, 60% of global tuna catches are performed by purse seine gear (Scott and Lopez 2014). This type of fishery in the tropical Atlantic is focused on yellowfin (*Thunnus albacares*), skipjack (*Katsuwonus pelamis*), and in a lesser extent on bigeye tuna (*Thunnus obesus*). Nevertheless, fisheries exploitation affects not only target species populations (such as tunas) but can also affect the structure, functionality and diversity of ecosystems by removing non-target species (Davies et al. 2009). By-catch or the “part of the capture formed by non-target species, which are accidentally caught” (Hall and Roman 2013) comprised of a large variety of species such as turtles, marine mammals, elasmobranchs and other bony fish species. Some of these species are especially rare or vulnerable due to their long life spans, slow growth rates, and low reproductive potential (Amandè et al. 2008a; Romanov 2002).

The by-catch in the purse seine fishery is normally discarded dead by their low economic value or due to breach of the regulatory measures. However, they can be also retained on board as by-product or be landed and sold in local markets (Amandè et al. 2010). In any case, by-catch may have ecological effects on keystone species which are important for ecosystem performance and structure (Alverson 1994).

Tropical tuna purse seine fishery can be distinguished based on the strategy used for finding tunas (Dagorn et al. 2013). Two strategies are related to how the set is performed in the Atlantic Ocean: Free School sets are normally mono or paucispecific schools of tuna detected by sonar marks,

jumpers or breezes in surface waters; whereas Fish Aggregating Devices (FADs) are sets done on floating objects and used to attract tuna and other species around them. FADs have two components; a floating raft and a submerged structure. A satellite buoy, attached to the raft, transmits its position (Delgado de Molina et al. 1999).

The by-catch in the tropical tuna purse seine fishery is relatively low in comparison to other fishing strategies (Amandè et al. 2010). Annual average by-catch for the tropical tuna purse seine fleet is estimated at 7.5% of the total catch (EU fleet in the AO) (Amandè et al. 2010). By-catch generated by both fishing modes is different with different species composition. FAD sets have higher by-catch rates (Amandè et al. 2010) and higher number of species (Lezama-Ochoa et al. 2015; Torres-Irineo et al. 2014) than Free School sets.

Fisheries management to date has often been ineffective because they are generally focused on the protection of a single target species with a substantial economic cost included. 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 (Bourlat et al. 2013), it has been not implemented very often to fisheries management. However, describing and measuring the effect of a fishery on an ecosystem is difficult (Gerrodette et al. 2012) and therefore, qualitative and quantitative metrics that provide information about those changes are necessary (Rochet and Trenkel 2003). One of the most basic but important ecological indicators is species diversity (Zhu et al. 2011). There is, however, little basis for defining optimum fishing by using related metrics such as diversity indices (Murawski 2000). To date, some studies concerning the effects of tuna purse-seine fishing modes on biodiversity estimates of the by-catch species groups have been performed (Lezama-Ochoa et al. 2015; Torres-Irineo et al. 2014); however, more results on the structure and patterns of diversity of these communities in the Eastern Atlantic Ocean are needed. The increase of FAD's use from the 1990s increased the purse seine catches of tropical tunas by nearly 60%, as well as the ecological problems associated with the by-catch managed by the International Commission for the Conservation of Atlantic Tunas (ICCAT) (Torres-Irineo et al. 2014). Thus, a better understanding of the interactions between pelagic species and their environment must be developed towards the correct implementation of an ecosystem-based fishery management, before performing any conservation plan.

The main objectives of this work were to 1) study the structure and diversity patterns of the by-catch communities in both purse seiner fishing modes using biodiversity metrics and 2) investigate the geographical and habitat preferences of the by-catch species in the Eastern Atlantic Ocean. We hypothesize that the diversity patterns of by-catch communities between both fishing

modes could vary according to the specific oceanographic characteristics of the Eastern Atlantic Ocean. Finally, we will also discuss about the importance of applying ecosystem indicators in the by-catch communities to progress to an integration of the species with the ecosystem (Ecosystem Approach to Fishery Management).

2. MATERIAL

2.1. Study area

The study area is located in the southeastern Atlantic Ocean between 35° W and 15° E and between 20° N and 15° S (Figure 43).

The Atlantic waters are characterized by high values of salinity and dissolved oxygen. The distribution of sea surface temperature in the Gulf of Guinea varies between 27°C and 29°C outside of the upwelling seasons to below 22°C at the coast during the major upwelling (Binet and Marchal 1993). The Intertropical Convergence Zone (ITCZ), the area where the northeast and southeast trade winds converge, is localized at north of the equator (at approximately 5° N) as in the Pacific Ocean. It is associated with low sea surface salinity and high surface temperatures. The North and South Equatorial Currents describe a westward flow at around 10°N and 3°N/15°S, respectively. The North Equatorial Countercurrent is an eastward flow showing high seasonality, its highest intensity and transport is reached during boreal summer.

The equatorial upwelling, describe a seasonal pattern as a consequence of the trade winds evolution; the equatorial upwelling begins in the boreal spring, reaching maximum chlorophyll concentrations during summer. Three different upwelling systems take place along the African coast as consequence of eastern boundary currents: Canary Current upwelling system (20°N); a coastal upwelling in the equatorial area (Ghana and Ivory Coast); and the Benguela upwelling system on Namibia's coast.

Furthermore, another important ocean processes that impact in the ecosystem, are the Guinea and Angola thermal Domes centered at around 12°N-11°W and 10°S-9°E, respectively. These are characterized by an elevation of the thermocline as a consequence of a dome of cold waters from deeper waters that take place at both sides of the equator during summer (Angola Dome) and winter (Guinea Dome). A cyclonic gyre is observed in both domes as a consequence of the sea surface depression (Tomczak and Godfrey 2003).

2.2. By-catch data

The EU scientific observer program on tropical tuna purse seine fisheries in the Atlantic and Indian Oceans, which covers approximately 10% of fishing trips (Amandè et al. 2010), is run by French (Institut de Recherche pour le Développement (IRD)) and Spanish scientific institutes (Instituto Español de Oceanografía (IEO) and AZTI) .

The data recorded by observers includes information about the trip, fishing activities (set type, position of the set, day and hour of the set), and the catch information (including both target and by-catch species). By-catch species were divided in groups; billfishes, sharks, bony fishes, rays, turtles and mammals. By-catch species were identified to species level in most cases, or to genus or family level in some cases (see selection of taxonomic categories section). A subsample of the catch for each by-catch species was also measured in weight and length. Seven areas were selected to carry out biodiversity analysis based on the ET zones (ET is related to the European Community (EC) research program “Echantillonnage thonier”) defined by Pallarés and Hallier (1997) and Pianet et al. (2000) (Figure 41): Senegal (1x01), Piccolo NW (1x02), Piccolo (1x03), Coastal (1x04N), Equator NE (1x04S), Cape Lopez (1x05) and South Equator (1x06) (Figure 29). These statistical areas were defined based on the similarity of target tuna species catch and size composition.

The fishing set was considered as the sample unit and was categorized into Fish Aggregating Devices (FADs) and Free School sets. Sets made under whale sharks were considered as FADs and sets made under whales (mysticetes) were considered as Free School sets (Pallarés and Hallier 1997). A total of 1591 sets were observed between 2003 and 2011 in Spanish and French purse seine fleet, from which 561 were done in Free School sets and 1030 in FAD sets.

2.3. Selection of taxonomic categories

A total of 9 sets (5 FAD sets and 4 Free School sets) only defined species to the by-catch species group level, so they were removed from any subsequent analyses. Furthermore, 6 mislabeled Free School sets (not correctly identified) were deleted for avoid the introduction of bias in sampling methodology.

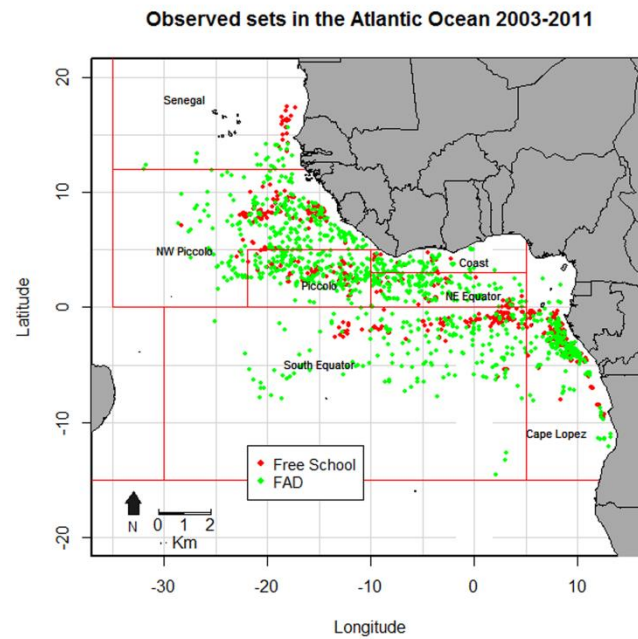


Figure 43. Different ZET areas or fishing zones (red rectangles) and distribution of sets in Free School (red points) and Fish Aggregating Device (FAD) catches (green points).

In the case of records of higher level taxa (genus, family, order and other levels), the number of species and their abundance was assigned using the species composition of the same group (e.g., genus, family) in the same area for that particular year; following the same method as in Lezama-Ochoa et al. (2015). As species level identification for Exocoetidae, Bramidae, and Torpedinidae families, Odontoceti suborder and Squaliformes order was not possible, they were considered as morphospecies -taxa that are distinguishable on the basis of the morphology (Oliver and Beattie 1996a; Oliver and Beattie 1996b) and treated as a single species in species richness estimates.

Abundance of species in each set was not always available because observers recorded total by-catch by species in numbers or weight. Additionally mean length or weight was also collected. This way, when by-catch estimates were recorded in weight, abundance by species was calculated based on the mean individual length or weight. The list of species selected comprised a total of 74 species (8 billfish species, 10 sharks, 37 fishes, 6 turtles, 5 species of marine mammals and 8 species of rays) (see S3. Table 1 in Supplementary material-Chapter 3).

2.4. Environmental data

For each fishing set (date and position), which covered the period December 2005- February 2010, values of oceanographic variables were obtained from ocean models and satellites. Temperature at 20, 30, 50 and 75 m depth (S20, S30, S50, and S75; in °C); Depth of the Thermocline (Therm. Depth; in m); Gradient of the Thermocline (Therm. Grad; in °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) came from ocean models with a spatial resolution of 25 km and a frequency of 2/3 days. Sea Surface Temperature (SST; in °C) was measured from AVHR and MODIS sensors and have 4 km and a daily spatial and temporal resolution. Chlorophyll concentration the same day of the fishing set and 18 days before (Cl and Cl-18 in mg m⁻³) had a 4 km resolution, a frequency of 2/3 days and came from measurements of MODIS and MERIS satellite sensors. Sea Level Anomaly (SLA; in cm) and geostrophic current speed (WG; in kn) presented 25 km and a 2/3 days spatial and temporal resolution, respectively. These altimetry products came from different combinations of satellites (depending on the date): ERS², Topex/Poseidon, Jason^{1/2}, ENVISAT/GFO and CRYOSAT. This information was processed and provided by the CLS (Collecte Localisation Satellite, France, <https://www.cls.fr>).

3. METHODS

3.1. Alpha diversity

Species richness index (the total observed and the mean per set) was calculated for each area in both fishing modes. Species accumulation curves were also constructed for each area and fishing mode. However, it seems 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). For that reason, Chao2 non-parametric estimator (Chao 1984) (which represents the asymptote of the species accumulation curve), based on the incidence or frequencies of species, was also calculated to obtain the estimated total species richness vs. observed species richness.

Evenness is a measure of the relative abundance of the different species in an area. The log-abundance curves represent the relative abundance of the species from the most abundant to the rarest one. Thus, the 10 most abundant species were obtained from the log-abundance curves (Kindt and Coe 2005) for each fishing mode (FAD vs. Free School). The mean of Pielou's J-

evenness index, a Shannon evenness index, was also calculated for the estimation of Evenness by areas for both fishing modes. Pielou's J-evenness is calculated as: $H / \ln(S)$ where H is the Shannon diversity index and S the species richness.

The shape of the log-rank abundance for each fishing mode can be explained by species abundance models as Geometric, Log-series, Log-normal and Broken stick models (Magurran 2004) and is used to describe the structure of the community. The data was fitted to different models and the best model fit, according to the lowest AIC value (Akaike's Information Criterion), represents best the community structure (Kindt and Coe 2005).

Diversity indices such as species richness index provide information about the number of species of the community. In contrast, other index such as Shannon diversity index also provides information about the relative abundance of them (Magurran 2004); such as Shannon diversity index (Shannon and Weaver 1949). If Shannon index (H) increases, diversity increases. Thus, the mean Shannon diversity index, which is defined as " $H' = -\sum p_i \ln p_i$ ", where p_i is the proportional abundance of each species, was calculated for each area and for each FAD and Free School fishing set.

As the data was insufficient to study diversity by quarters, statistical tests were performed to compare the diversity between areas. Thus, the Kruskal-Wallis test was performed to assess the differences among areas based on Shannon diversity index and the Wilcoxon test (post hoc test) to compare values between areas by pairs.

Finally, on the basis of the species richness and Shannon index, biodiversity maps were constructed by interpolation to a grid of 30 x 40 degrees. Data was aggregated by fishing set and thin plate spline regression was applied, using the "Tps" function from the "fields" package (Furrer et al. 2009) in R software.

3.2. Beta diversity

Beta diversity measures the change in the composition of species between different communities. Simpson dissimilarity index based on presence-absence data was calculated for both fishing modes to analyze similarities in species composition between ET areas (described above). Beta-sim or Simpson dissimilarity index (Lennon et al. 2001; Simpson 1943), is defined as $\text{beta-sim} = \min(b,c)/[a+\min(b,c)]$, where a is the number of species present in both samples and b and c are

the numbers of species occurring in only one sample or the other sample. Values range from 0 to 1 representing highest and lowest similarity, respectively. Results were showed by hierarchical cluster analysis with the “complete” linkage method and the function “hclust” from the R software. We used Mantel tests (Legendre and Legendre 2012) to determine the correlation between species similarity matrices and environmental and geographical distance. Bray-curtis index was used to measure the compositional similarity between pairs of fishing sets. The distance matrix for environmental variables and the geographical distance was measured with the Euclidean distance. For environmental variables, “bioenv” function from the vegan package (Oksanen et al. 2007) implemented in the R language was used to select the best subset of environmental variables.

3.3. Geographical and habitat preferences of the by-catch communities

GAMs (Hastie and Tibshirani 1990) were constructed to determinate the spatial, temporal and habitat preferences of the by-catch species in relation with species richness and Shannon diversity index for each fishing mode in the Eastern Atlantic Ocean between 2006 and 2010; for which environmental data was available. Spatial (latitude, longitude and area), temporal (month) and oceanographic variables were included in the analysis. The areas selected for constructing the models were chosen based on the following criteria: the Senegal area (see S3. Figure 1 in Supplementary material-Chapter 3) was delimited in agreement with the work published by Sancristobal and Sagarminaga (2006). They found similar oceanographic characteristics around the area of Senegal and Sierra Leone and therefore, this area was considered as only one. The other areas were chosen based on the oceanographic characteristics of the area and concretely, on the equatorial currents flow (North Equatorial Counter Current and South Equatorial Under Current) and the upwelling which takes place around Angola and Gabon.

Relationships between oceanographic variables were analyzed to find possible collinearities between them. In case of high correlation between two variables (Pearson correlation $r > 0.6$), only one of them was included in the final model. Each GAM was fitted using thin plate regression splines to model nonlinear covariate effects, except for monthly variation, where a cyclic cubic regression spline was used (Wood 2006).

Species richness index was modeled with Quasipoisson family and log-link function to find the relationship between the number of by-catch species and the geographical and habitat preferences of them. To relate the geographic and oceanographic variables with Shannon diversity index, a Gaussian error distribution with identity-link function was used for FAD sets and a Gaussian

error distribution also with identity-link function (+0.05 applied to the response variable to assure normality) for Free School sets. Best GAM model was obtained using backward stepwise procedure selecting significant p-values for each geographical, temporal and oceanographic variable.

The methodology used in this study was based on the work published by Lezama-Ochoa et al. (2015). By-catch data was analyzed in R software using the “vegan” (Oksanen et al. 2007) and “BiodiversityR” (Kindt and Kindt 2015) packages. Biodiversity maps were constructed using the packages “geoR” (Ribeiro Jr et al. 2015) and “maps” (Becker et al. 2013). Environmental data was analyzed using “mgcv” (Wood and Wood 2007) package.

4. RESULTS

4.1. Alpha diversity

Chao2 estimator and species accumulation curves showed that FAD and Free School sets could reach the asymptote with 84 and 72 species respectively (Table 12, Figure 44); however, the shape of the curve for both fishing modes was not completely flat. In general, both fishing modes showed similar species richness (Table 12), with slightly larger number of observed species in FAD sets (64) in comparison with Free School sets (60). Moreover, the mean species richness was higher in FAD sets (4.84) compared with Free School sets (1.47) (Table 12).

Different numbers of species by areas for each fishing mode were found. In FAD sets, the Chao2 index estimated a maximum number of species in Cape Lopez (57) and Piccolo NW (57) (Table 12, Figure 45a and Figure 47a). Despite of the high number of species observed in these two areas, the shape of the both accumulation curves is far to reach the asymptote, so more sample size is needed. In contrast, South Equator area is nearly to reach the asymptote with lower number of species (39), suggesting that all possible by-catch species were caught in this area.

By contrast, in Free School sets, a maximum of 104 species could be caught in Cape Lopez and 62 species in South Equator (Table 12, Figure 45b and Figure 47b). A larger sampling size is needed to find all the possible bycatch species in those areas.

Mean species richness index estimated by areas showed that Senegal and Piccolo NW were the areas with highest species richness observed in FAD (5.46 and 5.37 species) and Free School sets

(1.74 and 1.56 species). The ET Coastal area showed the lowest species richness in Free School (1.08) sets and the Cap Lopez area in FAD sets (3.57) (Table 12).

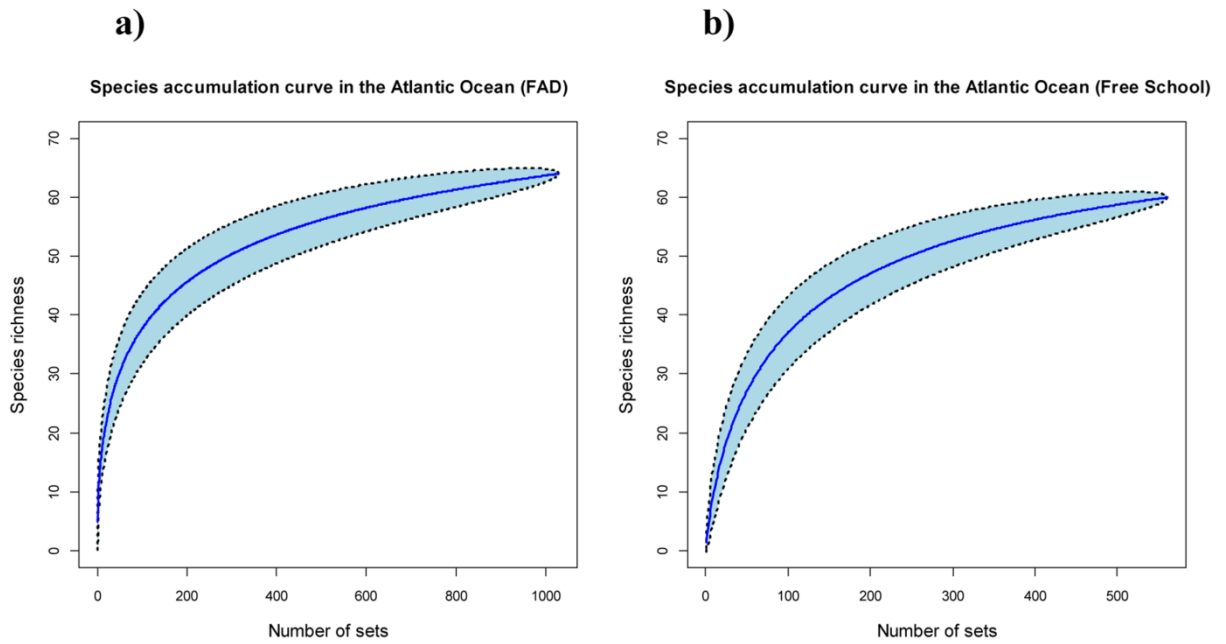


Figure 44. Species accumulation curves in Fishg Aggregating Device (FAD) (a) and (b) Free School sets.

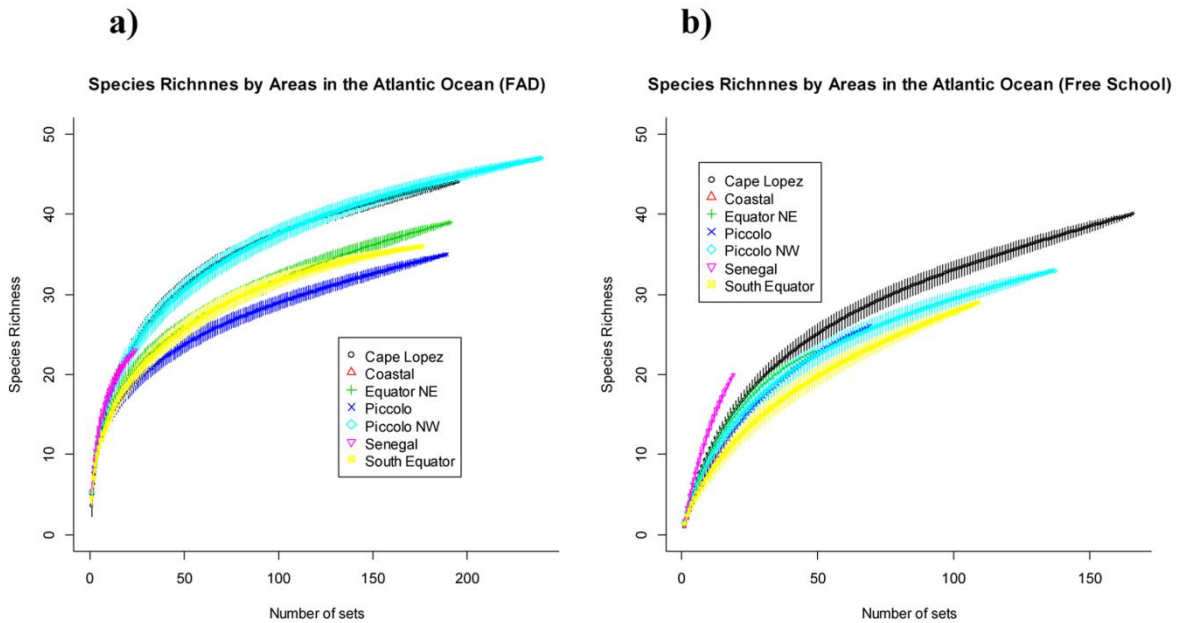


Figure 45. Species accumulation curves in Fish Aggregating Device (FAD) (a) and (b) Free School sets by areas.

With respect to the evenness measures, (Table 12) Senegal (0.63) and South Equator (0.63) showed the highest evenness values in the case of the FAD sets. In contrast, Equator NE (0.93) and the Coast (0.70) ET area showed the highest evenness values for Free School sets (Table 12). Based on Log-rank abundance data, the first ten most abundant species are shown in Table 13, forming 97.3% with respect the total species in FAD sets and 81.6% in Free School sets. *Canthidermis maculata* was the most abundant species in FAD sets (279765 individuals) and *Carcharhinus falciformis* (1147 individuals) in Free School sets.

Furthermore, the application of the different species abundance models to rank abundance curves in both fishing modes showed that by-catch communities in FAD sets followed a Log-normal distribution, and the by-catch communities in Free School sets a Zipf-Mandelbrot distribution (Figure 46) based on the lowest AIC values (see S3. Table 2 in Supplementary material-Chapter 3).

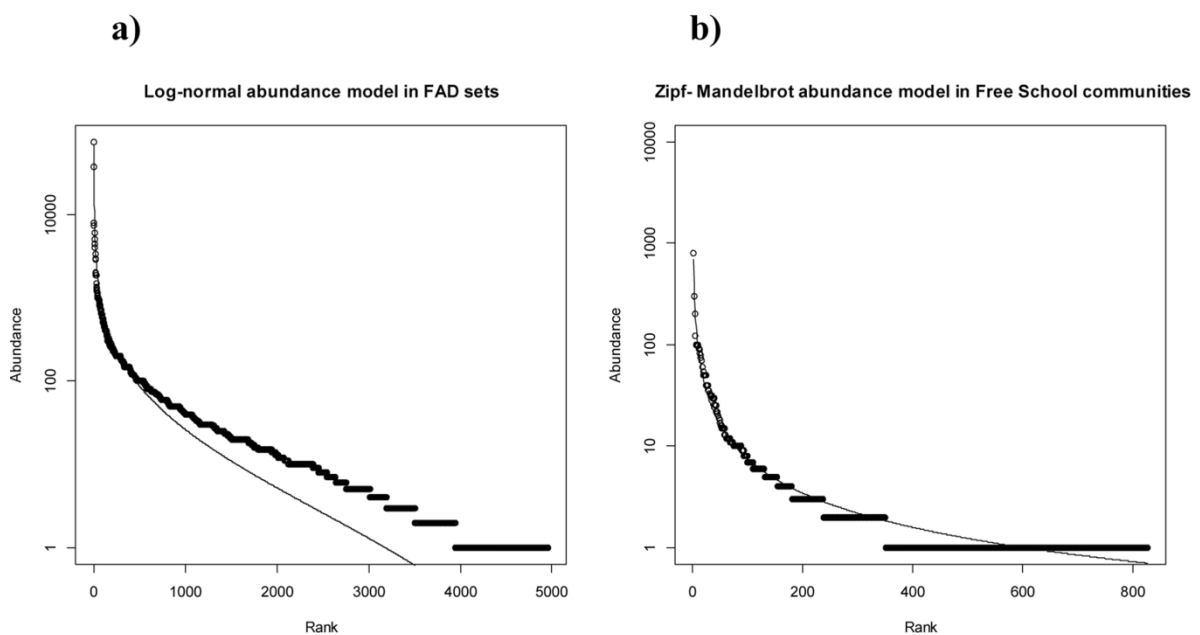


Figure 46. Models selected to fit log-rank abundance curves in Fish Aggregating Device (FAD) (a) and (b) Free School sets.

Table 12. Distribution of sets (N), observed species richness, Chao2 non-parametric estimator, mean Richness, mean Evenness and mean Shannon diversity index by areas in Fish Aggregating Devices (FADs) and Free School sets.

ET areas	N	FAD					Free School					
		Observed Richness	Chao2	Mean Richness	Mean Evenness	Mean Shannon	N	Observed Richness	Chao2	Mean Richness	Mean Evenness	Mean Shannon
Cape Lopez	195	44	57	3.57	0.54	0.64	166	40	104	1.51	0.50	0.22
Coastal	16	21	32	4.88	0.48	0.85	12	10	42	1.08	0.93	0.06
Equator NE	191	39	53	5.17	0.52	0.99	49	23	28	1.47	0.70	0.23
Piccolo	189	35	55	5.12	0.51	0.94	69	26	33	1.32	0.41	0.10
Piccolo NW	239	47	57	5.37	0.27	0.95	137	33	57	1.56	0.65	0.27
Senegal	24	23	27	5.46	0.63	1.07	19	20	34	1.74	0.68	0.36
South Equator	176	36	39	4.62	0.63	0.98	109	29	62	1.40	0.56	0.20
Total	1030	64	84	4.84	0.66	0.91	561	60	72	1.47	0.39	0.21

Table 13. Species abundance in Fish Aggregating Devices (FADs) and Free School sets.

Species	FAD			School sets			
	Rank	Abundance	Proportion	Species	Rank	Abundance	Proportion
<i>Canthidermis maculatus</i>	1	16983197	46.2	<i>Seriola lalandi</i>	1	231807	21.7
<i>Coryphaena hippurus</i>	2	6589668	17.9	<i>Sectator ocyurus</i>	2	173652	16.3
<i>Acanthocybium solandri</i>	3	3885018	10.6	<i>Coryphaena hippurus</i>	3	131939	12.4
<i>Sectator ocyurus</i>	4	3333164	9.1	<i>Caranx sexfasciatus</i>	4	93892	8.8
<i>Elagatis bipinnulata</i>	5	1482598	4	<i>Canthidermis maculatus</i>	5	89783	8.4
<i>Aluterus scriptus</i>	6	1222902	3.3	<i>Carcharhinus falciformis</i>	6	66943	6.3
<i>Coryphaena equiselis</i>	7	990409	2.7	<i>Acanthocybium solandri</i>	7	62226	5.8
<i>Aluterus monoceros</i>	8	881017	2.4	<i>Sphyrna spp.</i>	8	55523	5.2
<i>Carcharhinus falciformis</i>	9	468542	1.3	<i>Elagatis bipinnulata</i>	9	20634	1.9
<i>Seriola lalandi</i>	10	256284	0.7	<i>Mobula thurstoni</i>	10	17602	1.6

Shannon index showed highest diversity in FAD sets around Senegal, Equator NE and South Equator, while Cape Lopez was the area with lowest diversity values (Table 12 and Figure 47c). According to these results, the main coastal upwelling areas showed lower diversity values than the equatorial areas in FAD sets. On the other hand, the Shannon index showed the highest diversity in Senegal and Piccolo NW ET areas and lowest values around the Coast ET area in Free School sets (Figure 47d).

The Kruskal-Wallis test showed significant differences in diversity between areas in FAD sets ($p < 0.05$) (Table 14), whereas no significant differences were observed in Free School sets ($p > 0.05$). Specifically, the area of Cape Lopez showed differences ($p < 0.05$) in diversity (0.00) with all areas except with the Coastal area (1.00) in FAD sets.

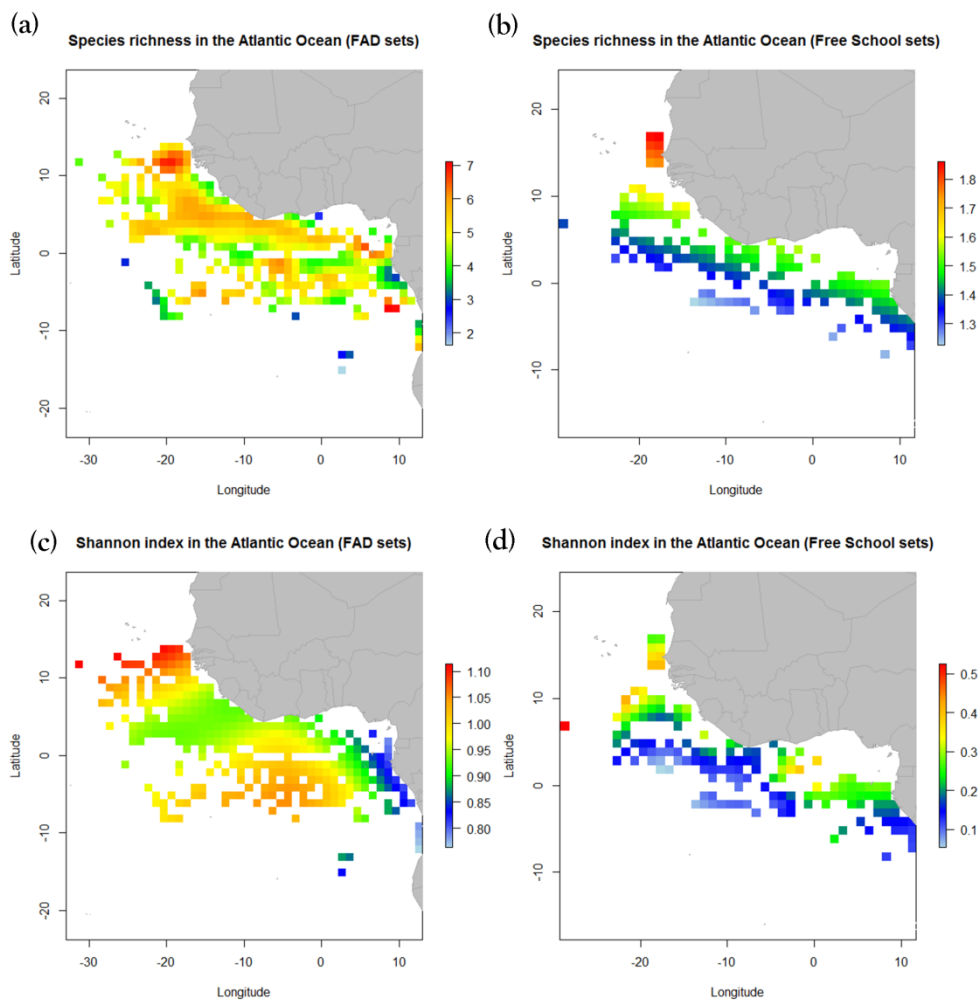


Figure 47. Richness index between 2003 and 2011 in (a) Fish Aggregating Device (FAD) sets and (b) Free School sets. Shannon index between 2003 and 2011 in (c) Fish Aggregating Device (FAD) sets and (d) Free School sets.

Table 14. Kruskal-Wallis test and Wilcoxon rank sum test in Fish Aggregating Devices (FADs) and Free School sets for comparing Shannon diversity index (SH) between areas.

FAD			Free School		
SH Kruskal-Wallis			SH Kruskal-Wallis		
Chi-squared	df	p-value	Chi-squared	df	p-value
68.0474	6	1.03e ⁻¹²⁷	15.5873	6	0.01
SH_Wilcoxon			SH_Wilcoxon		
Cape Lopez	Coastal	1.00	Cape Lopez	Coastal	0.93
Cape Lopez	Other areas	0.00*	Cape Lopez	Other areas	1.00

*significant p-value (p<0.05)

4.2. Beta diversity

Coastal upwelling areas (Senegal ET area) and equatorial areas in the north hemisphere (Piccolo and Equator NE areas) showed similar species composition in FAD sets in comparison with the south hemisphere (Figure 48a). On the other hand, the some coastal upwelling areas (represented Coastal and Cape Lopez ET areas) showed similar species composition in Free School sets (Figure 48b).

In general, higher dissimilarity values in species composition were found between ET areas in Free School (higher value of 0.60) sets than in FADs sets (higher value of 0.27).

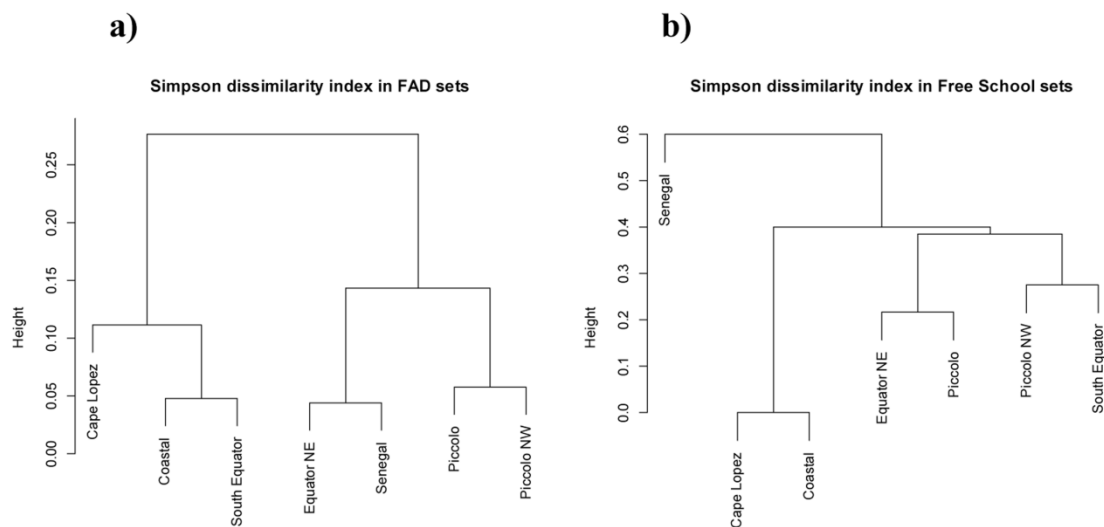


Figure 48. Simpson dissimilarity index in Fish Aggregating Device (FAD) (a) and (b) Free School sets.

The results of Mantel test showed that there is a correlation between species similarity and environmental factor (0.17) and geographical distance (0.16) for FAD communities (based on significance of p-values). Free School communities, on the other hand, only showed correlation with geographical factors (0.10) (Table 15).

Table 15. Mantel correlation test between species similarity and environmental variables and geographical distance in Fish Aggregating Device (FAD) and Free School communities.

FAD communities		Mantel r	p-value	Environmental variables selected
Bray x distance	0.1613	0.001	latitude, longitude	
Bray x environment	0.1792	0.001	SST, SLA, Cl, Cl.18, Therm.Prof, Therm.Grad, Sal20, WT	
Free School communities		Mantel r	p-value	Environmental variables selected
Bray x distance	0.1026	0.001	latitude, longitude	
Bray x environment	0.0168	0.181	SST, SLA, Cl, Cl.18, Therm.Prof, Therm.Grad, Sal20, WT	

* The p-value of the significance test was obtained by computing 999 permutations.

4.3. Geographical and habitat preferences of by-catch communities

In the case of FAD sets and based on the backward stepwise procedure, the final model included species richness as a response variable, area as a geographical variable (as a factor) and month, sea surface temperature, chlorophyll 18 days before, geostrophic current speed and gradient of the thermocline as temporal/environmental variables. The estimated parameters for species richness data and p-values are listed in Table 16 and Figure 49. The model explained 29.6 % of the variance with a R² of 0.25 with 632 samples. The results showed that the highest numbers of species were observed in the area of Angola and Senegal, during Spring-Autumn (April-September). Furthermore, highest richness values were found in areas with low chlorophyll concentration (<5 mg/m³), low speed of the geostrophic current (<0.3 knots), high gradient of the thermocline and high sea surface temperatures (>27°C).

With regard to Free School sets, richness diversity pattern was explained in the final model, which includes area (as a factor), and month, chlorophyll, salinity and gradient of the thermocline as temporal and environmental variables. Results showed that the model explained 19.1% of the variance with a R² of 0.12 with 413 samples (Table 16, Figure 50). Highest richness values were found in May and November around Senegal with high concentration of chlorophyll (>10 mg/m³), low salinity values (<34.0 psu) and low gradient of the thermocline.

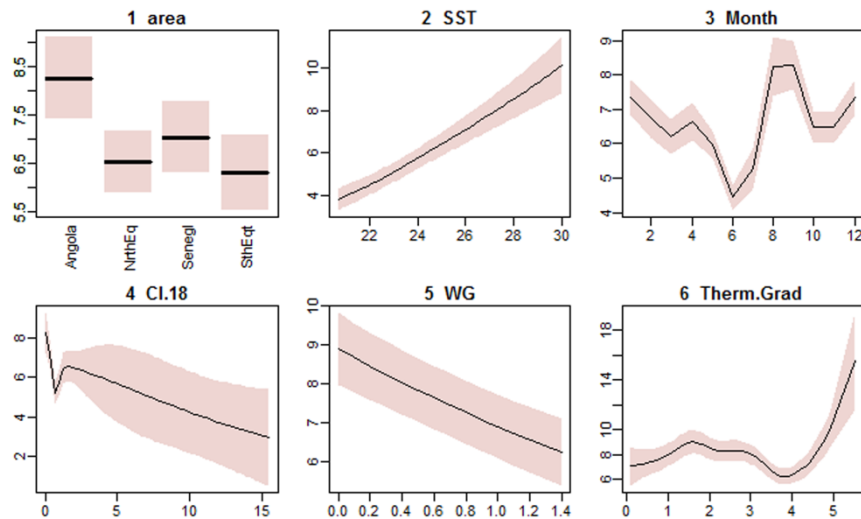


Figure 49. Smoothed fits of covariates modelling the species richness index: 1) Area, 2) SST (Sea surface temperature), 3) Month, 4) Cl.18 (Chlorophyll 18 days before), 5) WG (Speed of the current) and 6) Therm.Grad (Gradient of the thermocline) variables in Fish Aggregating Device (FAD) fishing mode. The y-axis represents the spline function. Dashed lines indicate approximate 95% confidence bounds.

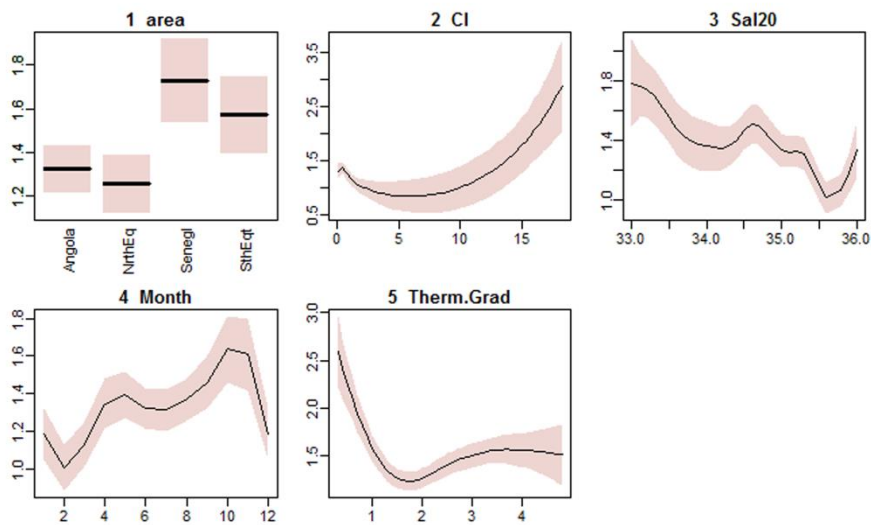


Figure 50. Smoothed fits of covariates modelling the Shannon diversity index: 1) Area, 2) Month, 3) SST (Sea surface temperature), 4) Cl (Chlorophyll) and 5) Therm.Grad (Gradient of the thermocline) variables in Free School fishing mode. The y-axis represents the spline function. Dashed lines indicate approximate 95% confidence bounds.

Table 16. Summary results for the optimal Generalized Additive Models (GAMs) selected for species richness index and Shannon diversity index in Fish Aggregating Devices (FADs) and Free School sets. Variables: SST (Sea surface temperature), SLA (Sea Level Anomaly), CL (Chlorophyll), Cl.18 (Chlorophyll 18 days before), Therm. Prof (Depth of the thermocline), Therm. Grad (Gradient of the thermocline), Sal20 (Salinity at 20 m depth), WG (Geostrophic current speed) and WT (Total surface current speed).

	FAD				Free School			
	Richness index		Shannon index		Richness index		Shannon index	
Family	Quasipoisson		Gaussian		Quasipoisson		Gaussian	
Link function	Log		Identity		Log		Identity	
Adjusted R ²	0.25		0.23		0.12		0.11	
Deviance explained	29.60%		26.60%		19.10%		14.90%	
	Estimate	p-value	Estimate	p-value	Estimate	p-value	Estimate	p-value
Latitude · Longitude	-	-	-	-	-	-	-	-
Area	1.653	<2e ⁻¹⁶	0.968	<2e ⁻¹⁶	0.313	3.80e ⁻⁰⁷	0.202	4.40e ⁻⁰⁶
Month	6.827	1.40e ⁻⁰⁷	6.696	2.70e ⁻⁰⁸	5.493	0.007	2.878	0.03
SST	2.197	2.30e ⁻⁰⁵	5.464	0.025	-	-	3.252	0.057
SLA	-	-	-	-	-	-	-	-
CL	-	-	-	-	3.711	0.023	3.253	0.039
Cl.18	5.161	0.004	4.997	0.021	-	-	-	-
Therm.Prof	-	-	-	-	-	-	-	-
Therm.Grad	6.44	0.008	7.082	0.001	4.111	3.20e ⁻⁰⁵	3.906	9.70e ⁻⁰⁵
Sal20	-	-	-	-	7.144	0.013	-	-
WG	1	0.021	1	0.002	-	-	-	-
WT	-	-	-	-	-	-	-	-

The final GAM for FAD sets included Shannon diversity index as response variable, area as geographical variable (as factor), month as temporal variable and sea surface temperature, chlorophyll 18 days before, speed of the geostrophic current and thermocline gradient as environmental variables. Gaussian model for Shannon diversity index explained 26.6% of the variance with a R² of 0.23 with 632 samples (Table 16). As the results showed similar diversity patterns (see S3. Figure 2 in Supplementary material-Chapter 3) to those obtained with richness index in FAD fishing mode, only the model with richness index was showed due to its high percentage of deviance explained.

Finally, for Free School sets, the final model (Gaussian model)-based on the backward stepwise procedure - was constructed with area as geographical variable (as factor), month as temporal variable and sea surface temperature, chlorophyll and gradient of the thermocline as environmental variables. Results showed that the model explained 14.9% of the variance with a

R² of 0.11 with 413 samples (Table 16, Figure 51). High diversity was found in May and November around Senegal with high concentration of chlorophyll (>10mg/m³), high sea surface temperatures (>27°C) and low gradient of the thermocline.

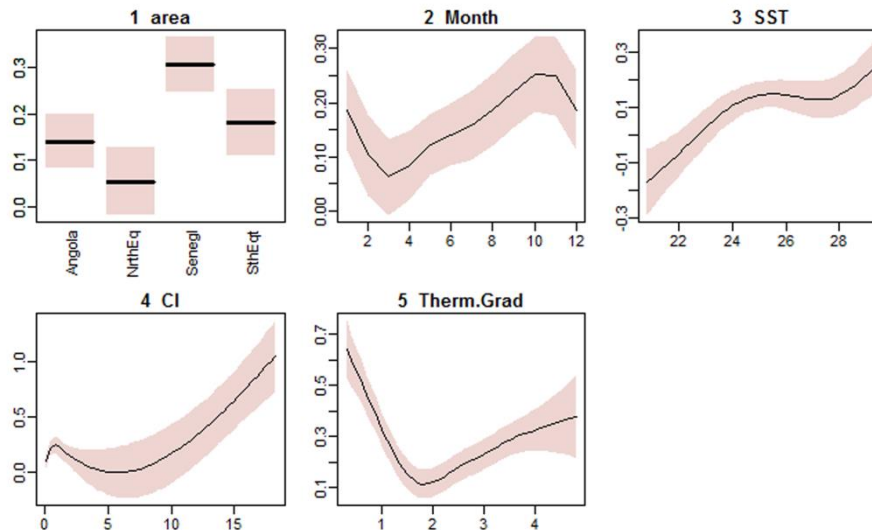


Figure 51. Estimated smoothing curves obtained by the Generalized Additive Model (GAM) applied to Shannon diversity index for 1) Area, 2) Month, 3) SST (Sea surface temperature), 4) Cl (Chlorophyll) and 5) Therm.Grad (Gradient of the thermocline) variables in Free School fishing mode.

5. DISCUSSION

Fishing overexploitation and marine habitat loss caused by human impact has been the origin for changes in the marine ecosystem (Coll et al. 2014). The need to maintain marine biodiversity has become one of the main concerns in recent years. Therefore, it is necessary a better understanding of the ecosystem processes and the species that inhabit them, in order to achieve a sustainable management of the ecosystem.

In this study we show that by-catch data collected by observer programs on tropical tuna purse seine fisheries in the Atlantic Ocean between 2003 and 2011 can be useful to measure different levels of diversity such as Alpha and Beta diversity. Furthermore, these diversity measures can be modeled with different environmental variables, enabling us to better understand geographical and habitat preferences of the by-catch communities. However, some difficulties and limits were observed in the data, which could influence the results. In general, there is a need to increase the sampling effort to obtain more accurate results and higher percentage of deviance explained by the models. Despite these inconveniences, our findings provide new information to understand

the structure and patterns of diversity of the by-catch communities of the two fishing modes employed by tuna purse-seiners in the tropical Atlantic Ocean.

5.1. Alpha and Beta diversity

Biodiversity metrics can provide information to interpret ecosystem processes and spatial distribution of species to be used in future conservation plans (Iknayan et al. 2014). In general, these measures have different characteristics and some of them may be more sensitive to concrete attributes than others, so it is difficult to choose one as a measure of ecosystem overfishing (Murawski 2000). Hortal et al. (2006) for example, proved that incidence-based estimator such as Chao2 estimator is accurate and less sensitive to fishing effort distribution and intensity in comparison to sampling effort. Our results suggest that Chao2 estimator, as used in the work of Torres-Irineo et al. (2014) and Lezama-Ochoa et al. (2015) was a good option for estimating the total species richness in both fishing modes despite the low sample size for some areas. In addition, the calculation of the mean of each index resolved the problem of obtaining results influenced by the sample size.

The first step to develop any biodiversity study is to obtain a good and complete inventory of the population. In that sense, observer programs provide the necessary information for that purpose; but with limitations and differences between countries and oceans. Our results are in concordance with the work performed by Torres-Irineo et al. (2014) and Lezama-Ochoa et al. (2015) focused on the species richness estimation of the by-catch communities in the Western Indian and Atlantic Oceans, respectively. More sample size is necessary to obtain an accurate estimation of the total number by-catch species in both fishing modes. The shape of the accumulation curves that can't reach the asymptote lead us to suggest that not all species appeared in both fishing modes and therefore, the results about diversity patterns and distribution must be interpreted with caution. This problem seems to be associated with the low coverage rate of the observer programs which is around 10%. In contrast, in the Eastern Pacific Ocean, where the coverage rate reaches 100%, a better estimation of the total number of by-catch species was obtained (Lezama-Ochoa et al. 2015, submitted). In this case, the complete information allowed defining the diversity areas and modeling the habitat preferences with precision. These results let us to infer that coverage rate and the sample size may play an important role on the estimation of biodiversity of the by-catch species for each fishing mode.

Another important result obtained in this work is that a much larger sample size is required in FAD fishing mode to obtain the same number of species than in Free School fishing mode; as in the Indian and Pacific Ocean (Lezama-Ochoa et al. 2015; Lezama-Ochoa et al. 2015, submitted). Each set is characterized by higher number of species in FAD fishing mode compared with Free School (Amandè et al. 2010). Nevertheless, the species aggregated under the FAD and which are caught in each set are normally the same and comprise about 80-90% of the total by-catch (Amandè et al. 2008a). Thus, it seems reasonable to assume that the sample size necessary to find higher variability of different species may be higher in FAD sets than in Free School sets; since FAD sets are widely distributed and in a more extended area in the pelagic ecosystem compared with Free School sets, which are patchily aggregated in smaller areas. Thus, both types of fishing must be considered to develop biodiversity studies since the integration of both fishing modes provide more complete and variable information that separately.

One of the applications of the log-abundance curves in ecology is to describe which are the most common and rarest species; in this case, the by-catch species from the tropical tuna purse-seine fishery on the pelagic ecosystem. In this work, rough triggerfish, *Canthidermis maculata*, was the by-catch species mostly caught in FAD sets and silky shark, *Carcharhinus falciformis*, in Free School sets. Rough triggerfish, usually caught in FAD sets, is abundant but it is normally discarded. Although silky shark (listed as near-threatened species by IUCN) is mainly associated with FADs (Torres-Irineo et al. 2014), it was found as the most abundant by-catch species 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). Therefore, technological improvements for mitigating incidental catch of vulnerable species such as silky shark are necessary to achieve an effective fishery management and reduce their mortalities. For example, in recent years, their survival rate has been increased with some new methods developed for mitigating the captures of sharks and other vulnerable species (Gilman 2011; Poisson et al. 2014).

In addition to providing information about the most common/rare by-catch species, the log-abundance curves also allow knowing the structure of the by-catch communities using species distribution models. Thus, similar species distribution models for each fishing mode explain the structure of these communities in the Pacific, Atlantic and Indian Oceans (Lezama-Ochoa et al. 2015; Lezama-Ochoa et al. 2015, submitted). By-catch communities in FAD sets are formed by permanent species (species which are aggregated under FADs for hours or days) in the same habitat and normally distributed (Magurran 2004), in large and natural areas (Log-normal model). On the contrary, by-catch species in Free School sets are formed by different and rare species that

move across oceans with migratory species such as tunas for reproductive or feeding activities (Zipf or Mandelbrot model) (Lezama-Ochoa et al. 2015). This leads to suggest that the structure of the pelagic communities is explained by similar species distribution models depending on the fishing mode in the three oceans. The by-catch species in each ocean represent different communities depending of the fishing mode, and therefore, the environment conditions and the areas where the species are found are also different.

The species composition of a given area is usually related to oceanographic characteristics. Thus, as demonstrated by Lezama-Ochoa et al. (2015) in the Western Indian Ocean and Lezama-Ochoa et al. (2015, submitted) in the Eastern Pacific Ocean, the species composition of the by-catch communities for each fishing mode may be related with the surface currents, upwelling regions and monsoon systems. Thus, not only the environment, but also the fishing types determine differences and similarities in species composition between areas. In this case, a clear pattern to explain the differences in species composition between areas and modes of fishing was not found, probably due to low observation coverage. However, in FAD sets, different species composition between the north and south of the study area seems to be related with the north and south equatorial surface currents. In the case of the Free School sets, it seems that the Senegal, Cape Lopez and Coast ET areas could have similar species composition related to coastal upwelling systems; however, any concrete conclusion cannot be drawn yet.

5.2. Geographical and habitat preferences of by-catch communities

Studies of oceanic biogeography have consistently shown that the distributions of pelagic communities match the distribution of water masses (Angel 1993), but determination of the dominant factors influencing the distributions of these communities is not an easy task. In that sense, the GAM approach can contribute to understand the geographical and habitat preferences of these communities. The percentage of deviance explained by the models presented some similitudes with the work from (López 2015) about the distribution of the by-catch species in the Atlantic Ocean using similar environmental variables; however, the results and conclusions should be taken with caution, due to the low number of samples and coverage rate.

Our results clearly show that temporal factors have larger influence on diversity patterns of by-catch species than environmental factors in Free School sets. In contrast, sea surface temperature, chlorophyll concentration or thermocline gradient seem to explain some important patterns in FAD sets (see S3. Table 3 in Supplementary material-Chapter 3).

Thus, sea surface temperature was one of the most important environment variables influencing diversity patterns of the by-catch communities in FAD sets. The sea surface temperature, associated with equatorial upwelling divergences and frontal systems (Lezama-Ochoa et al. 2015, submitted), determines the distribution of these species, which tend to be aggregated in the warm side of the systems and to move to the cold one to feed.

The second most important variable was the chlorophyll content (18 days before). Fonteneau et al. (2008) found interesting relationships between chlorophyll-a peak levels 18 days before and free swimming tuna abundance in the Indian Ocean; however, these relationships have not been found yet in the Atlantic Ocean for tuna and non-tuna species (López 2015). In contrast, in this study we observed that diversity increase in water contents between 0 and 0, 5 mg/m³. However, for higher values, this effect become negative on diversity, suggesting that by-catch species in FAD sets prefers intermediate productivity waters (equatorial waters) than very productive waters (coastal upwelling waters).

Diversity may be explained by equatorial upwelling which is present to the east of 20° W between July and September and the presence of the northern and southern surface equatorial currents (Tomczak and Godfrey 2003). The north equatorial countercurrent (NECC) moves towards the west and towards the north, reaching its maximum width around the month of September (Fonteneau and Marcille 1993). The most diverse areas may be explained by the drifting of the FADs towards the west with surface currents and equatorial upwelling; this may result in the expansion of fishing grounds across the Gulf of Guinea. This is quite coherent with results obtained by Ariz et al. (1993) and Sarralde et al. (2005), who studied the distribution of FAD sets in the tropical Atlantic. They found that tuna catches on artificial objects occur to the north and to the south of the equator.

There is a correspondence between catches and rainy seasons during the third and fourth quarters, when the fishing peaks occur. Furthermore, the Guinea dome, where the thermocline is shallower, may explain diversity during summer in FAD sets. During March-April, diversity may be explained by the presence of the Angola dome that is associated with the termination of the south sub-superficial counter current (Tomczak and Godfrey 2003). The thermocline within the domes is located above the Oxygen Minimum Zones (OMZs) (Karstensen et al. 2008). The low concentration of oxygen at these rather shallow depths may induce the catch of the top predators and by-catch species around this area. A similar example occurs in the Mexican area, where dolphins and tuna are associated and where there is also OMZs below a shallow thermocline. All these common dynamic processes are important to the nutrient enrichment of the tropical Atlantic Ocean.

Concerning the results obtained in Free School sets, diversity of the by-catch species was related with the fishing strategy based on seasonal sampling (Month was the variable with the highest % of deviance explained). In accordance with the work published by Sarralde et al. (2005) and Delgado de Molina et al. (2010) about the distribution of the tuna catches in Free School sets, this work found similar distribution patterns of by-catch species with respect to diversity. High diversity was found in relation to the seasonal coastal upwelling of Senegal during November (5-10°N/10-15°W).

In addition, high diversity found at low thermocline gradients and high chlorophyll concentrations suggests that these species were mainly observed near the coast around very productive upwelling systems. This result is in agreement with the work of Ingham (1970), who observed that the thermocline is much thinner in the eastern Atlantic than in the western Atlantic affecting the distribution and abundance of regional fisheries. Grodsky et al. (2008) also found that the highest chlorophyll concentrations (> 0.6 mg/m³) in the tropical Atlantic occur in coastal and adjacent areas as a result of river discharge and coastal upwelling. This may explain the high diversity found at high concentrations of chlorophyll, in Free School sets compared with FAD sets.

Diversity patterns between both fishing modes were different. Whereas, by-catch species in Free School sets seem to be aggregated around seasonal coastal upwelling areas, in the case of the FAD sets, diversity was found around intermediate productivity waters in stable systems. This finding may be explained under the “ecological trap” theory (Marsac et al. 2000) as this hypothesis suggests that the use of FADs may alter the movements of tuna and by-catch species from coastal high productivity areas (where Free School sets are often deployed), towards less productive areas. However, in this case, as FADs follow the surface currents, the drift could benefit the aggregation of species around equatorial areas which are more stable (less undisturbed) and diverse (Lezama-Ochoa et al. 2015, submitted) than coastal upwelling areas and where FADs are deployed and accumulated throughout the year (such along the equatorial area and towards the west). As such, whereas the chlorophyll is an important environmental factor for by-catch species in Free School sets in relation with upwelling systems, it seems that surface currents determine the patterns of diversity of by-catch species in FAD sets.

In summary, bycatch species are associated with surface equatorial currents and domes in FAD sets and with seasonal upwelling's around the coast in Free School sets. However, low diversity was found in one of the most important permanent upwelling systems such as the Benguela coastal upwelling system (around Cape Lopez ET area). It's an unstable system characterized by high productivity rates but low diversity of species (Barnes and Hughes 2009). Similar results were

obtained in Lezama-Ochoa et al. (2015, submitted) about the California and Peru permanent coastal upwelling systems. Despite the weak performance of the models, our results suggest that diversity patterns of by-catch communities between both fishing modes are explained according to the specific oceanographic characteristics of the tropical Atlantic. However, other indexes or even parameters such as dissolved oxygen should be proposed and introduced in the models to integrate the effect of key limiting factors on the distribution of by-catch species and to improve the results.

5.3. Implications for fisheries management

By-catch may be contributing to biological overfishing and altering the structure of marine ecosystems (Alverson 1994). For that reason, responsible fisheries management is of increasing interest to all interested parties; from scientific and conservation or environmental groups to policy makers.

ICCAT has established a number of recommendations to reduce the by-catch amounts (www.iccat.es). However, some actions performed, such as the establishment of time-area closures has not been effective as do not account for fishermen's behavior at sea (Torres-Irineo et al. 2011). As such, all possible factors, both technical and environmental, could be integrated for a correct management of the fishery. The change from the management of a single species to the integration of all part of the ecosystem would be desirable. Single species management approaches will never be able to provide information about changes in ecosystem structure and functioning, biodiversity or impacts on habitat. In contrast, the application of EAFM allows for including all these factors (Link 2010).

However, to integrate all those factors in a EAFM is quite costly since the amount of information necessary increased moving from single species assessment to an application of ecosystem assessment (Link 2010). In that sense, the use of routine observer programs could be seen as an alternative tool providing information of by-catch data with the aim to investigate the diversity of marine communities.

The number and abundance of the by-catch species may vary in relation to catch composition (fishing mode), seasons or fishing areas. Despite that trends in biodiversity can vary enormously between areas or habitats, observer programs should be designed to take account of this spatial variation (Buckland et al. 2005).

Although these programs are time-consuming, costly and require well trained observer for a correct identification of the species (Lewison et al. 2004), are indispensable for estimation of by-catch. For that reason, an appropriate level of observer coverage is needed for future biodiversity studies to reduce the bias associated with fishing effort.

Due to other observers programs (REC ICCAT 14-01, ISSF commitments, etc.) implemented together with the EU scientific observer program, 2013 onwards this observer coverage increased gradually and reached 100% in 2015. This trend is expected to continue with 100% coverage and therefore, future studies could face this problem and to satisfy the management objectives of the EAFM.

6. CONCLUSION

This work has improved our understanding of structure and diversity of the by-catch communities in the eastern Atlantic Ocean. Indeed, it has revealed different spatial and habitat preferences of the by-catch species depending of the type of fishing. All the analysis led us to infer that FAD sets can aggregate higher number of by-catch species and more diversity than Free School sets, in agreement with previous studies by Romanov (2002), Amandè et al. (2010), Torres-Irineo et al. (2014) and Lezama-Ochoa et al. (2015). However, diversity varies by areas and seasons in both fishing modes; suggesting that it is necessary to integrate data from both fishing modes for a better knowledge of the distribution of these species communities. The GAM analysis gives new insight on different diversity preferences of the by-catch communities. The selection of new areas for develops these models based on the diversity and oceanography of the area and not in the catches was essential for explaining these patterns. These biodiversity studies are necessary for providing a better understanding of the ecosystem processes and the species that inhabit, and to achieve the objectives of the EAFM. This study contributed to the understanding and integration of different components and diversity measures to help to implement an ecosystem-based fishery management.

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CHAPTER 4

Present and future potential habitat distribution of *Carcharhinus falciformis* and *Canthidermis maculata* by-catch species in the tropical tuna purse-seine fishery under Climate Change

Nerea Lezama-Ochoa¹ • Hilario Murua¹ • Guillem Chust¹ • Emiel Van Loon² • Jon Ruiz¹ • Martin Hall³ • Pierre Chavance⁴ • Alicia Delgado de Molina⁵ • Ernesto Villarino¹

¹Azti-Tecnalia. Herrera kaia, portualdea z/g, 20110, Pasaia, Spain

²Institute for Biodiversity and Ecosystems Dynamics, University of Amsterdam, Netherlands

³ Inter-American Tropical Tuna Commission, 8901 La Jolla Shores Drive, CA 92037, USA

⁴Institut de Recherche pour le Développement (IRD), Sète, France

⁵Instituto Español de Oceanografía (IEO), Tenerife-Canary Island, Spain

ABSTRACT

By-catch species from tropical tuna purse seine fishery have been affected by fishery pressures since the last century; however, the habitat distribution and the climate change impacts on these species are poorly known. With the objective of predicting the potential suitable habitat for a shark (*Carcharhinus falciformis*) and a teleost (*Canthidermis maculata*) in the Indian, Atlantic and Eastern Pacific Oceans, a MaxEnt species distribution model (SDM) was developed using data collected by observers in tuna purse seiners. The relative percentage of contribution of some environmental variables (depth, sea surface temperature, salinity and primary production) and the potential impact of climate change on species habitat by the end of the century under the A2

scenario (scenario with average concentrations of carbon dioxide of 856 ppm by 2100) were also evaluated. Results showed that by-catch species can be correctly modelled using observed occurrence records and few environmental variables with SDM. Results from projected maps showed that the equatorial band and some coastal upwelling regions were the most suitable areas for both by-catch species in the three oceans in concordance with the main fishing grounds. Sea surface temperature was the most important environmental variable which contributed to explain the habitat distribution of the two species in the three oceans in general. Under climate change scenarios, the largest change in present habitat suitability is observed in the Atlantic Ocean (around 16% of the present habitat suitability area of *Carcharhinus falciformis* and *Canthidermis maculata*, respectively) whereas the change is less in the Pacific (around 10% and 8%) and Indian Oceans (around 3% and 2%). In some regions such as Somalia, the Atlantic equatorial band or Peru's coastal upwelling areas, these species could lose potential habitat whereas in the south of the equator in the Indian Ocean, the Benguela System and in the Pacific coast of Central America, they could gain suitable habitat as consequence of global warming. This work presents new information about the present and future habitat distribution under climate change of both by-catch species which can contribute to the development of ecosystem-based fishery management and spatially driven management measures.

Key-words: By-catch·MaxEnt·Silky shark·Rough triggerfish·Habitat suitability·Climate change·Tropical purse seiners·Ecosystem Approach to Fishery Management

1. INTRODUCTION

Anthropogenic pressures such as exploitation, pollution, introduction of non-native species and habitat destruction are currently affecting the marine biodiversity and driving changes in species composition and distribution (Jones et al. 2013; Worm et al. 2006). The marine ecosystem is also being impacted by climate change in some habitats and species (e.g. (Hoegh-Guldberg and Bruno 2010). Thus, global warming may change the oceanographic conditions of the oceans forcing to the pelagic species adapt to them by shifting their distributions (Komoroske and Lewison 2015). However, the complex interactions between climate change and fishing on the species are difficult to assess (Jones et al. 2013). Commercial fisheries can alter marine ecosystems by removing species with low reproductive rates, altering size spectra and reducing habitat quality (Dayton et al. 1995). The tropical tuna purse seine fishery, one of the most important fisheries of the world in terms of

economic and ecological significance, captures by-catch or the “part of the capture formed by non-target species, which are accidentally caught” (Hall and Roman 2013). The by-catch in the purse seine fishery is normally discarded dead by their low economic value. However, they can be also retained on board as by-product or be landed and sold in local markets (Amandè et al. 2010). In any case, by-catch has negative connotation because it is a wasteful use of resources (if they are not retained or sold) and due to conservation, economic and ethical concerns (Kelleher 2005).

By-catch is comprised of a large variety of species. In particular, some of these species, such as sharks are vulnerable to fishing due to its large body sizes, slow growth rates and late maturation (“k” strategy species) which make them especially sensitive to overexploitation (Froese and Pauly 2014; Poisson 2007).

Even though most of pelagic sharks are caught by longliners or other fishing gears (Gilman 2011), there is a need to reduce the incidental catches of sharks made by purse seiners. Concretely, the silky shark (*Carcharhinus falciformis*) represents high % of all sharks (around 85%) caught by the purse seine fishery (Amandè et al. 2008a; Hall and Roman 2013) and reduce their mortality is one of the major objectives of Ecosystem Approach to Fishery Management (EAFM). Silky sharks play an important role as tope predators in the ecosystem, with the capacity to influence community structure and essential to the maintenance and stability of food webs (Duffy et al. 2015; Olson et al. 2010; Olson et al. 2014; Scott et al. 2012).

In contrast, other by-catch fish species, such as rough triggerfish (*Canthidermis maculata*) are more abundant, have higher reproductive rates (“r” strategy species) and their populations are not overexploited. However, little is known about the biology, ecology and role of this important species of the ecosystem.

Because the issue of by-catch is a recognized cause of biodiversity loss, improving our knowledge about the changes in both common and vulnerable by-catch species and their habitats is necessary to support conservation plans and to account for the impact of climate change on their populations (Cheung et al. 2012; Nguyen 2012) .

Thus, species distributions models (SDM), also called “habitat” models, are useful tools to determine species habitat, manage threatened species, and identifying special areas of interest for biodiversity (Franklin and Miller 2009). Such models predict the probability of occurrence of species in an area where no biological information is currently available. Some authors believe that for any successful application of the Ecosystem Approach to Fishery Management (EAFM), impact of climate change in species distribution range should be considered (Cheung et al. 2012; Nguyen 2012). Thus, modeling species distribution under different climate change scenarios

provide also useful ways to project species distribution changes anticipating consequences of global warming on marine ecosystems (Chust et al. 2014; Khanum et al. 2013; Villarino et al. 2015).

Although SDM have been applied to fisheries research (e.g. (Chust et al. 2014), and its use is increasing, it is still scarcely applied in comparison with terrestrial systems (Kumar and Stohlgren 2009; Muthoni 2010; Thuiller et al. 2005). In the case of tropical tuna purse seine fisheries, some studies have described the distribution of the megafauna associated to the tuna schools and taken by purse seiners (Peavey 2010; Sequeira et al. 2012). However, they have not yet been applied to compare the potential habitat of vulnerable and more common by-catch species and the changes of their distribution as consequence of the climate change impact. The use of SMD in by-catch species is an emergent issue of global interest which could provide relevant information about the ecology and distribution of these pelagic species which can contribute to adopt spatially structure management measures. Therefore, the application of these models in by-catch species will help to move towards the correct implementation of the Ecosystem Approach to Fishery Management (EAFM) in the tropical tuna purse seine fisheries.

The main objectives of this work are to: 1) predict the suitable habitat for *Carcharhinus falciformis* and *Canthidermis maculata* in the Indian, Atlantic and Eastern Pacific Oceans on the basis of by-catch observations from the tropical tuna purse seine fishery, 2) identify the relative percentage of contribution of each environmental variable considered to describe the species distributions in each ocean, and 3) evaluate the potential impact of climate change on their species habitats under the A2 scenario (average concentrations of carbon dioxide of 856 ppm by 2100) (Kumar and Stohlgren 2009; Muthoni 2010; Thuiller et al. 2005) by the end of the century. We hypothesize that the potential suitable areas for the two species could vary as climate and ocean conditions change according to the specific oceanographic characteristics of each ocean.

2. MATERIAL

2.1. Study area

Our study area comprises the Western Indian (20° N/30° S and 30° E/80° E), Eastern Atlantic (30° N/15° S and 40° W/15° E) and Eastern Pacific Ocean (30° N/20° S and 70° W/150° W) (see S4. Figure 1 in Supplementary material-Chapter 4). The three oceans are considered

separately in this study because they differ greatly among them with respect to climate, oceanographic characteristics, current dynamics and upwelling systems (Tomczak and Godfrey 2003).

2.2. Data collection

Occurrences of *Carcharhinus falciformis* and *Canthidermis maculata* for the Atlantic and Indian Ocean were obtained from the European Union observer programs in support to its Common Fishery Policy under the EU Data Collection Regulations (EC-DCR) No 1639/2001 and 665/2008. French (Institut de Recherche pour le Développement (IRD)) and Spanish scientific institutes (Instituto Español de Oceanografía (IEO) and AZTI) were responsible for collecting by-catch data in the Atlantic and Indian Oceans with a coverage rate of around 10% of the fleet trips from 2003 to 2010/11 (Amandè et al. 2010). By-catch data from the tropical tuna purse seine fisheries in the Eastern Pacific Ocean from 1993 to 2011 was collected by the Inter-American Tropical Tuna Commission (IATTC) observer program, with 100% coverage of the purse seine vessels of carrying capacity greater than 363 metric tons. Those observer programs record all the captures in each set, in numbers when possible and in weights otherwise. The objective of those programs is to estimate the amount of by-catch species in order to increase their knowledge which will allow developing measures to reduce their incidental mortality. Thus, the objective of the observer program is directly related with the collection of information on those species and thus, the occurrence of those species is well collected (by trained observers using fish/shark guides and photographs).

Up to date, the information available on by-catch species from the observer programs is one of the most important in terms of fishery dependent data. It has allowed publishing diverse studies which provide useful information on the ecology, conservation and habitat distribution of these pelagic species (Amandè et al. 2008a; Amandè et al. 2008b; Amandè et al. 2010; Gaertner et al. 2002; Gerrodette et al. 2012; Hall and Roman 2013; Lezama-Ochoa et al. 2015; Martínez Rincón 2012; Minami et al. 2007; Torres-Irineo et al. 2014; Watson 2007). This is why we consider it valid to the meet the aforementioned objectives.

The data recorded by observers in this study included information about the position of the set and the by-catch level of *Carcharhinus falciformis* and *Canthidermis maculata*.

In this study, both by-catch species were selected to contrast a vulnerable with a common species. These species are frequently caught in tuna purse seine gear (Hall and Roman 2013). Moreover,

they also have scientific interest, economic and social importance and adequate information available for the Indian, Atlantic and Pacific Oceans. For that reason, we selected both by-catch species based on their ecological importance, but also on the availability of the most complete data to develop the SDM correctly. The silky shark, *Carcharhinus falciformis* (Müller and Henle, 1839), is a pelagic species vulnerable to fishing and listed on the IUCN (Commission 2000) (www.iucn.org) as Near Threatened. Rough triggerfish or spotted oceanic triggerfish, *Canthidermis maculata* (Bloch, 1786), is an epipelagic species which inhabits temperate and tropical waters (46°N - 18°S) and usually discarded dead. Despite the fact that the two by-catch species have many ecological differences, they both are tropical species and is expected that their potential range distribution be similar. Although these species usually appear in FAD sets of the fishery, they can be also found in Free School sets.

A total of 1013 occurrences (59 in Free School sets and 954 in FAD sets) were observed in the Indian Ocean, 370 (79 in Free School sets and 291 in FAD sets) in the Atlantic Ocean and 28866 occurrences (1887 in Free School sets and 26979 in FAD sets) in the Eastern Pacific Ocean for *Carcharhinus falciformis*; whereas 656 (21 in Free School sets and 976 in FAD sets), 997 (12 in Free School sets and 644 in FAD sets) and 29874 (247 in Free School sets and 29627 in FAD sets) occurrences were observed for *Canthidermis maculata* in the Indian, Atlantic and Pacific Ocean, respectively. In the Pacific Ocean 1000 subsamples were randomly selected to compare similar number of sets between oceans.

With the aim of obtaining the potential habitat for these two species, the main types of sets (FAD and Free School) were combined for the analyses. We combine information from both fishing modes to show the entire range distribution of the species, as sampling sites of both types of fishing provide useful information to map the occurrence of both species in relation to local environmental conditions. In the case of FAD sets, we justified its inclusion in the study as both by-catch species can appear in the same areas for each fishing mode (Lezama-Ochoa et al. 2015) (see S4. Figure 2 in Supplementary material-Chapter 4). Therefore, on the scale of the area modeled (with reference to the movement of the FAD) not matter as the tropical area does not show high oceanographic variability (Longhurst and Pauly 1987). In addition, the by-catch species can be aggregated to a FAD and thus, be attached to the movement of the FAD for a while (Castro et al. 2002; Fréon and Dagorn 2000; Girard et al. 2004). However, as they are not always associated to the FAD, these species can leave the FAD when environmental conditions are not optimal (López 2015).

2.3. Environmental variables

Environmental data were extracted from the AquaMaps database (Kaschner et al. 2013) at 0.5° resolution and stored as sets of cell attributes in a Half-degree Cell Authority File (HCAF) along with their associated Land Ocean Interactions in the Coastal Zone (LOICZ) (<http://www.loicz.org>) and C-squares ID numbers (<https://www.marine.csiro.au/csquares>). The HCAF contains such environmental attributes for a grid of 164520 half-degree cells over oceanic waters. We considered 4 environmental variables as potential predictors of *Carcharhinus falciformis* and *Canthidermis maculata* habitat distribution: depth, sea surface temperature (SST), salinity and primary production (Prim. Prod). These environmental variables were selected by their general relevance for (epi) pelagic species and their relation to the specific oceanographic conditions in each ocean (Arrizabalaga et al. 2015; Ballance et al. 2006; Martínez Rincón 2012). Depth was selected because it may mark the difference between the coast, the open ocean or other geological features such as seamounts, marine trenches or ridges. Cell bathymetry was derived from ETOPO 2 min negative bathymetry elevation. Sea surface temperature was selected because it has a strong impact on the spatial distribution of marine fish. Concretely, it is important in areas where some phenomenon such as “El Niño” could alter the normal oceanographic conditions and fishery production (Fiedler 2002). Salinity is important for the fish’s osmoregulation (Lenoir et al. 2011) and primary production determines important fishing habitats in relation with the chlorophyll concentration in equatorial and coastal upwelling areas. Temperature, salinity and primary production were modelled by their annual mean and projected to the future by the IPSL model. All variables (see S4. Figure 3 in Supplementary material-Chapter 4) were converted to raster files with the “raster” package” in R (Hijmans and van Etten 2012). The environmental variables used and their values and characteristics are summarized and explained in Table 17 and Table 18.

3. METHODS

3.1. Habitat modelling

MaxEnt (Phillips et al. 2006) is one of the most used species distribution modeling method that estimates the probability of species distribution based on continuous or categorical environmental data layers (Franklin and Miller 2009). The model implements a sequential-update algorithm to find an optimum relation between environmental variables and species occurrence based on the maximum entropy principle (Elith et al. 2011). The MaxEnt logistic output was used as a

suitability index (ranging from not suitable (0) to suitable (1)), which is interpreted as a probability of occurrence, conditional on the environmental variables used to construct the model.

Table 17. Environmental data used to generate the species distribution models (Present) and to project the data (Future) from AquaMaps database.

Variable	Characteristics	Present	Future	Units
Mean sea depth	Cell bathymetry derived from ETOPO 2 min negative bathymetry elevation	-	-	meters
Sea surface temperature	Modeled current and 2100. Mean annual sea surface temperature (IPSL model A2 scenario)	2001-2010	2090-2099	Annual average degrees
Salinity	Modeled current and 2100. Mean annual salinity (IPSL model A2 scenario)	2001-2011	2090-2100	Practical Salinity Units (PSU)
Primary production	Proportion of annual primary production (IPSL model A2 scenario) in a cell	Present	2100	MgC·m ⁻³

Table 18. Mean of environmental variables in the three oceans considered in this study. See Table 1 for the explanation of the variables and data sources, and the maps in the supplementary material (Figure 2) for the spatial distribution of the variables.

Variables	Measure	Indian Ocean		Atlantic Ocean		Eastern Pacific Ocean	
		Present	A2 (2100)	Present	A2 (2100)	Present	A2 (2100)
Depth	mean	3493.8	3493.8	4342.6	4342.6	3722.2	3722.2
SST	mean	26.9	28.9	25.1	27.0	26.0	27.8
Salinity	mean	36.0	36.0	36.0	36.2	35.6	35.7
Prim. Prod	mean	58.3	46.6	63.7	53.9	116.7	91.7

Response curves were generated to analyze the species response to a given environmental gradient. Although MaxEnt can fit complex relationships to environmental variables, we chose to only fit linear and quadratic relationships due to the difficult interpretation of more complex relationships (Louzao et al. 2012). MaxEnt species distribution model was chosen in this work because it is considered one of the best modeling techniques (P Anderson et al. 2006) which shows higher predictive accuracy than GLMs, GAMs, BIOCLIM or GARP distribution models (Franklin and Miller 2009).

In addition, this type of model is useful to obtain an overall perspective of their habitat with different number of samples and few predictors. Thus, MaxEnt is useful for modeling pelagic species with only-occurrences data and in environments where is difficult to obtain this

information because of the complexity of the marine ecosystem and the low variability of its oceanography.

Prior to modelling, strongly ‘correlated’ (correlation (r) >0.6) environmental predictors were identified by estimating all pair-wise Spearman rank correlation coefficients. This step is necessary to find any collinearity between explanatory variables (Louzao et al. 2012). In addition, we evaluated percentage of contribution of the environmental variables to the MaxEnt model based on a jackknife procedure, which provides the explanatory power of each variable when used in isolation.

Suitability maps for *Carcharhinus falciformis* and *Canthidermis maculata* were constructed using the MaxEnt algorithm with “dismo” package in R software (Hijmans et al. 2013).

3.2. Pseudo-absence data generation

The occurrences for silky shark and rough triggerfish were obtained from the same dataset in each ocean. All the sampled occurrences were selected in the Indian Ocean and Atlantic Ocean dataset. In contrast, in the Pacific Ocean 1000 subsamples were randomly selected to compare similar number of occurrences between oceans. The total fishing effort is showed for each ocean in S4. Figure 4 in Supplementary Material-Chapter 4).

The absence of species in a set may be explained by three reasons: 1) the species was not present, 2) the species was present but escaped from the net and it was not captured or recorded, 3) the species was captured but it was not recorded by the observer. The species absence in a specific set could be reconstructed from the general species list but introduces a risk of creating erroneous data. In this work, shark and triggerfish data was considered presence-only, as true absences were unknown. Where absence data are unavailable to use in habitat models, an alternative approach is to generate pseudo-absences that should, ideally, also account for any spatial bias in the sampling effort (Phillips et al. 2009). For that reason, we have generated pseudo-absences for model evaluation purposes. We generated the pseudo-absences following the next method: pseudo-absence points were selected randomly from across the sampled area in each ocean. Furthermore, an equal number of pseudo-absence points as presences points were used for the random selection method (Senay et al. 2013). We generated each set of pseudo-absences excluding the presence points using the randomPoints function from the “dismo” package in R (see S4. Figure 5 in Supplementary material-Chapter 4).

3.3. Model validation

A validation step is necessary to assess the predictive performance of the model using an independent data set. The most common approach used is to split randomly the data into two portions: one set used to fit the model (e.g. 80% of data), called the training data, and the other used to validate the predictions with the presences and pseudo-absences occurrences (e.g. 20% of data), called the testing data (Kumar and Stohlgren 2009; Muthoni 2010; Thuiller et al. 2005). Cross-validation is a straightforward and useful method for resampling data for training and testing models. In *k*-fold cross validation the data are divided into a small number (*k*, usually five or ten) of mutually exclusive subsets (Kohavi 1995). Model performance is assessed by successively removing each subset, re-estimating the model on the retained data, and predicting the omitted data (Elith and Leathwick 2009). In this study, a *k*-fold partitioning method (with *k*=5) was used to construct the testing (20%) and training data (80%) from occurrence records. Finally, we ran MaxEnt 5 times for the *k*-fold partitioning method. We calculated the mean of the 5 MaxEnt predictions to obtain an average prediction and coefficient of variation of predictions.

3.4. Model evaluation

The accuracy of the model and the five replicate model cross-validations were evaluated using the area under the receiver operating characteristic curve (AUC) (Fielding and Bell 1997). Given the defined threshold value, a confusion matrix or error matrix (Pearson et al. 2007), which represents a cross-tabulation of the modelled occurrence (presence/pseudo-absence) against the observations dataset, was also calculated based on the following indexes (Pearson et al. 2007): sensitivity (proportion of observed occurrences correctly predicted), specificity (proportion of pseudo-absences correctly predicted), accuracy (proportion of the presence and pseudo-absence records correctly assigned) and omission error (proportion of observed occurrences incorrectly predicted). The modelled probability of species presence was converted to either presence or absence using probability thresholds obtained using two criteria: sensitivity is equal to specificity, and maximization of sensitivity plus specificity, following (Jiménez-Valverde and Lobo 2007). Thus, the cases above this threshold are assigned to presences, and below to absences.

AUC values and accuracy values from the confusion matrix range in both cases between 0.5 (random sorting) and 1 (perfect discrimination). The comparison between the accuracy of the model with all observations and the accuracy of the cross-validated model permits the detection of model overfitting (Chust et al. 2014; Khanum et al. 2013; Villarino et al. 2015).

3.5. Projections for the 21th century

Habitat suitability of *Carcharhinus falciformis* and *Canthidermis maculata* was modelled at present (2001-2010/11) and future (2090-2099/2100) conditions under the A2 climate change scenario (Kumar and Stohlgren 2009; Muthoni 2010; Thuiller et al. 2005). The A2 scenario (concentrations of carbon dioxide of 856 ppm by 2100) (Kumar and Stohlgren 2009; Muthoni 2010; Rombouts et al. 2012; Thuiller et al. 2005), which was used in this study describes a very heterogeneous world with high population growth, slow economic development primarily regionally oriented and slow technological change.

The same environmental variables used for the present conditions were also obtained from the Aquamaps database for the future climate under the A2 scenario (Kaschner et al. 2013).

Once the habitat models were built on the basis of present environmental data and occurrence observations, they were projected to future climate conditions to assess the habitat distribution response to climate change. Changes on species suitable habitat distribution were assessed by spatial overlap between suitable areas predicted under present and future scenarios. Percentages of gain and loss of suitable habitat from present to future modelled conditions were calculated for the two species. The percentage of suitable habitat which remains suitable in the future is defined as the percent of grid cells suitable for the species both at present and future. From the current suitable habitat, the grid cells predicted to become unsuitable represented the percentage of habitat loss. The percentage of new suitable or gained habitat (habitat unsuitable at the present but suitable at the future) is calculated as the ratio between the number of new grids cells and the habitat size not currently suitable (i.e. grid cells not suitable at the present) (Kumar and Stohlgren 2009; Muthoni 2010; Thuiller et al. 2005).

4. RESULTS

4.1. Habitat suitability models

The resulting predicted habitat suitability maps for *Carcharhinus falciformis* and *Canthidermis maculata* are depicted in Figure 52 and Figure 53.

The MaxEnt model predicted current potential suitable habitat for silky shark: a) along the equatorial band (10°N-10°S/50°-90°E) in the Indian Ocean, b) around Cap Lopez (5°S-10°E) and the north equatorial band (0°-10°N) in the Eastern Atlantic Ocean and c) along both sides of

Equator, especially in the northern hemisphere (0-10°N) and near the coast in the Eastern Pacific Ocean.

The most suitable habitats for rough triggerfish were predicted: a) around the equatorial band (10°N-10°S/50°-90°E) in the Indian Ocean, b) along the Equator in the northern hemisphere (0-10°N/10-25°W) and to a lesser extent, around Cap Lopez (5°S-10°E) in the Atlantic Ocean and c) along the Equator (10°N-10°S/80-110°W) and close to the coast of Central and South America (10°N-10°S; 80°-90°W) in the Eastern Pacific Ocean. In general, model predictions showed that both by-catch species were found with higher probability (the lower the CV, the lower the uncertainty) in the Indian and the Pacific Ocean (represented by light blue color in the maps). Rough triggerfish showed better values (lower coefficient of variation along all the study area) in general than silky shark. In contrast, CVs were found for both species in the Atlantic Ocean, but out of their potential habitat distribution. All those areas were consistently identified as important due to the low coefficient of variation in predictions (see S4. Figure 6 in Supplementary material-Chapter 4).

The percent contribution of each environmental variable for both species in each ocean is shown in Table 19. Results from Jackknife procedure are showed in S4. Figure 7 in Supplementary material-Chapter 4. Low correlations were found among environment variables ($r < 0.6$) in each ocean and in general (see S4. Table 1 in Supplementary material-Chapter 4). Therefore, they all were included in the analysis.

Sea surface temperature and depth were respectively the most important predictors for silky shark (86.3% and 13.9%) and rough triggerfish (81% and 17.8%) in the habitat models in the Indian Ocean. Sea surface temperature and salinity were the variables that most contributed to the model for silky shark (85.5 and 11.5%) and rough triggerfish (91.1% and 4.1%) in the Eastern Atlantic Ocean. Finally, in the Eastern Pacific Ocean, sea surface temperature was the most important variable for silky shark with 66.3% contribution and primary production for rough triggerfish (56.6%). In general, sea surface temperature was the variable that most contributed to explain the habitat distribution for the two species in each ocean (Table 19).

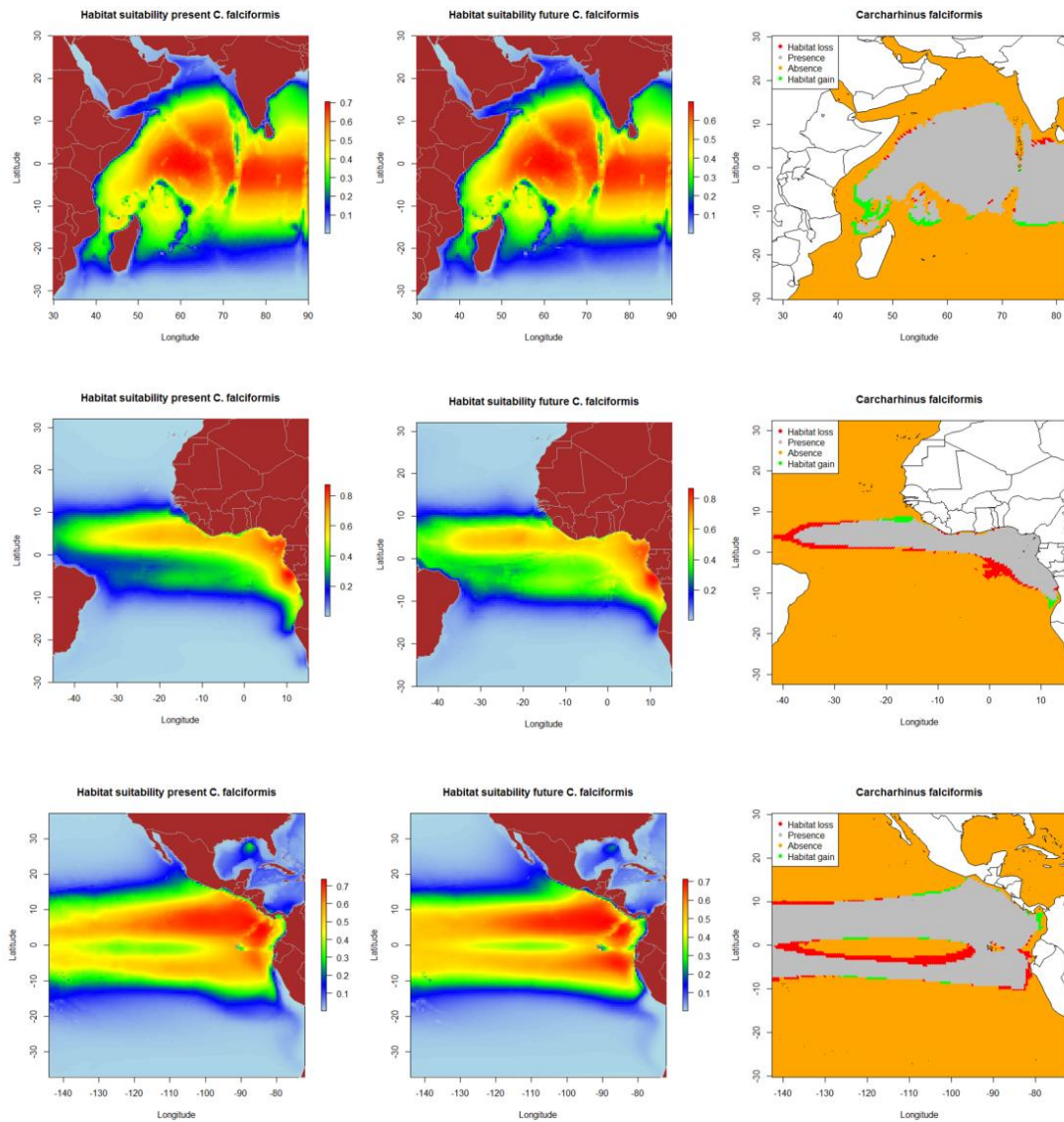


Figure 52. Predicted current conditions (first column), future conditions (second column) and differences between future and present conditions (third column) for habitat suitability areas for *Carcharhinus falciformis* in the Indian, Atlantic and Eastern Pacific Ocean. The maps (first and second columns) show the probability of occurrence of each species from lowest (blue) to highest value (red).

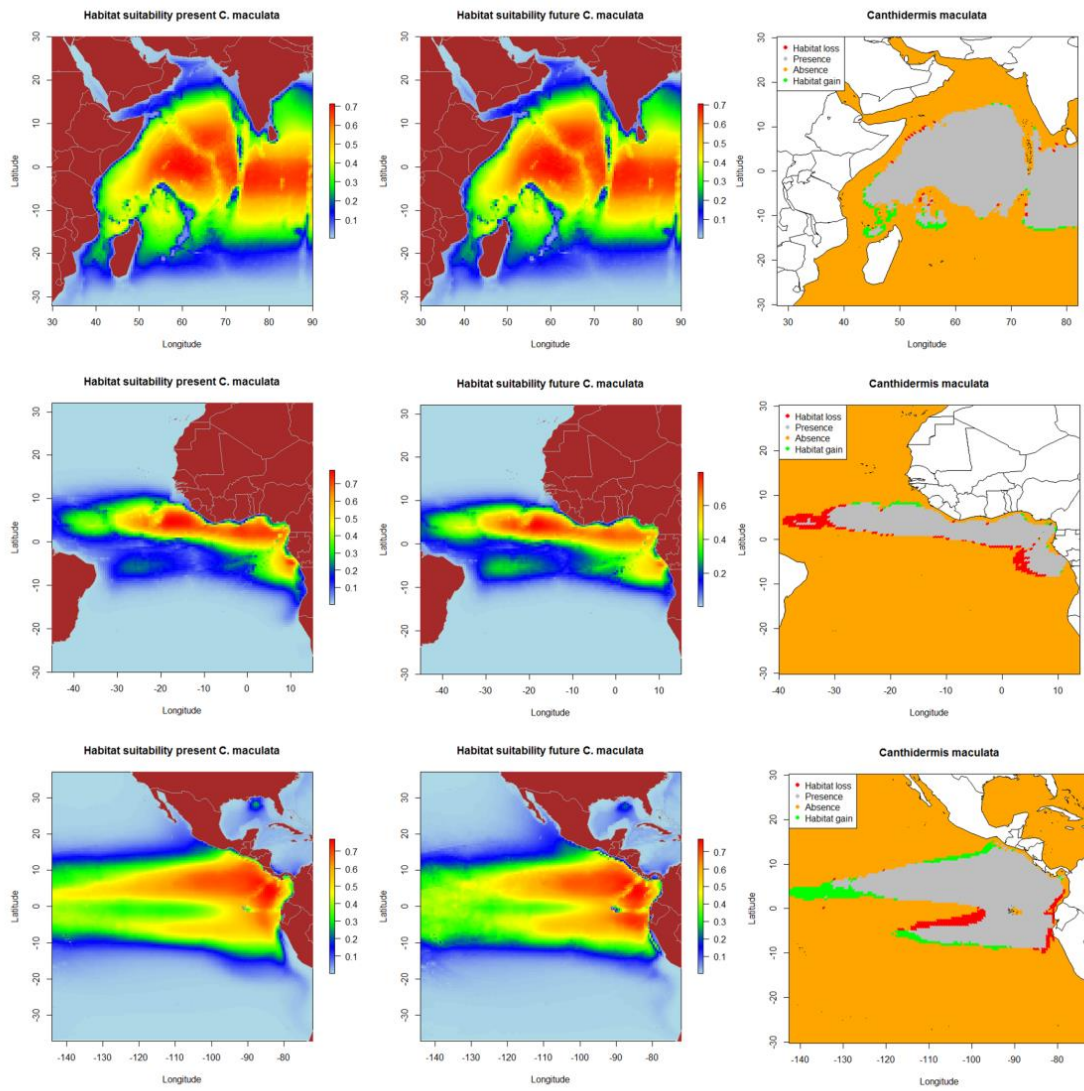


Figure 53. Predicted current conditions (first column), future conditions (second column) and differences between future and present conditions (third column) for habitat suitability areas for *Canthidermis maculata* in the Indian, Atlantic and Eastern Pacific Ocean. The maps (first and second columns) show the probability of occurrence of each species from lowest (blue) to highest value (red).

Table 19. Logistitc model output values: percentage of importance of each environmental variable with all observations (t) and cross-validated (k) for *Carcharhinus falciformis* and *Canthidermis maculata* in the Indian (IO), Atlantic (AO) and Eastern Pacific Ocean (EPO).

Ocean	By-catch species	SST (t/k)	Salinity (t/k)	Depth (t/k)	Prim.Prod (t/k)
IO	<i>Carcharhinus falciformis</i>	65.5/86.3	0/1.5	13.5/13.9	21.1/20.9
	<i>Canthidermis maculata</i>	71.5/81	0.2/0.7	14.2/17.8	14/10.6
AO	<i>Carcharhinus falciformis</i>	61.8/85.5	16.7/11.5	15.1/11.3	6.3/1.6
	<i>Canthidermis maculata</i>	90.7/91.1	2.5/4.1	3.3/3.2	3.5/1.5
EPO	<i>Carcharhinus falciformis</i>	64.6/66.3	1.5/0.1	2.4/2.0	31.5/31.6
	<i>Canthidermis maculata</i>	37.9/41	0.1/0.2	5/2.1	57/56.6

The relationships between presence probability and environmental variables for each ocean are illustrated in Figure 54 and Figure 55. Silky shark and rough triggerfish presence probability increased with sea surface temperature and decreased linearly with salinity, whereas non-linear relationships were found in some cases for depth and primary production. Concretely, maximum presence probability was found at high temperatures (26-30°) and low salinities (20-30 psu) for both by-catch species in all oceans. Both by-catch species showed preference by deep ocean regions (5000-6000 meters) in the Indian Ocean and by intermediate deep regions (3000-4000 meters) in the Atlantic and Pacific Ocean (with the exception of silky shark in the Atlantic; its presence probability decreased with depth). Furthermore, probability of presence for both species was found to be higher at low primary production concentrations (50-100 mg·m⁻³) in the Indian Ocean, intermediate concentrations (100-150 mg·m⁻³) in the Atlantic Ocean and at high concentrations (200-300 mg·m⁻³) in the Pacific Ocean.

4.2. Model evaluation

AUC values and accuracy indexes for all-observations (t) and cross-validated (k) models are shown in Table 20. MaxEnt models for both species in all oceans showed good agreement between AUC values (0.60 to 0.80) and accuracy values for cross-validated models (0.50 to 0.75). The intermediate-high accuracy values for cross-validated models, compared with the models using all observations, indicate that the models were not over-fitted. Sensitivity and specificity values for all observations and cross-validated models showed slightly high values for both species, with the exception of the Indian Ocean (around 0.55), where these values were lower (Table 20). The omission error was low in general (0.05-0.08), indicating that the model performed well.

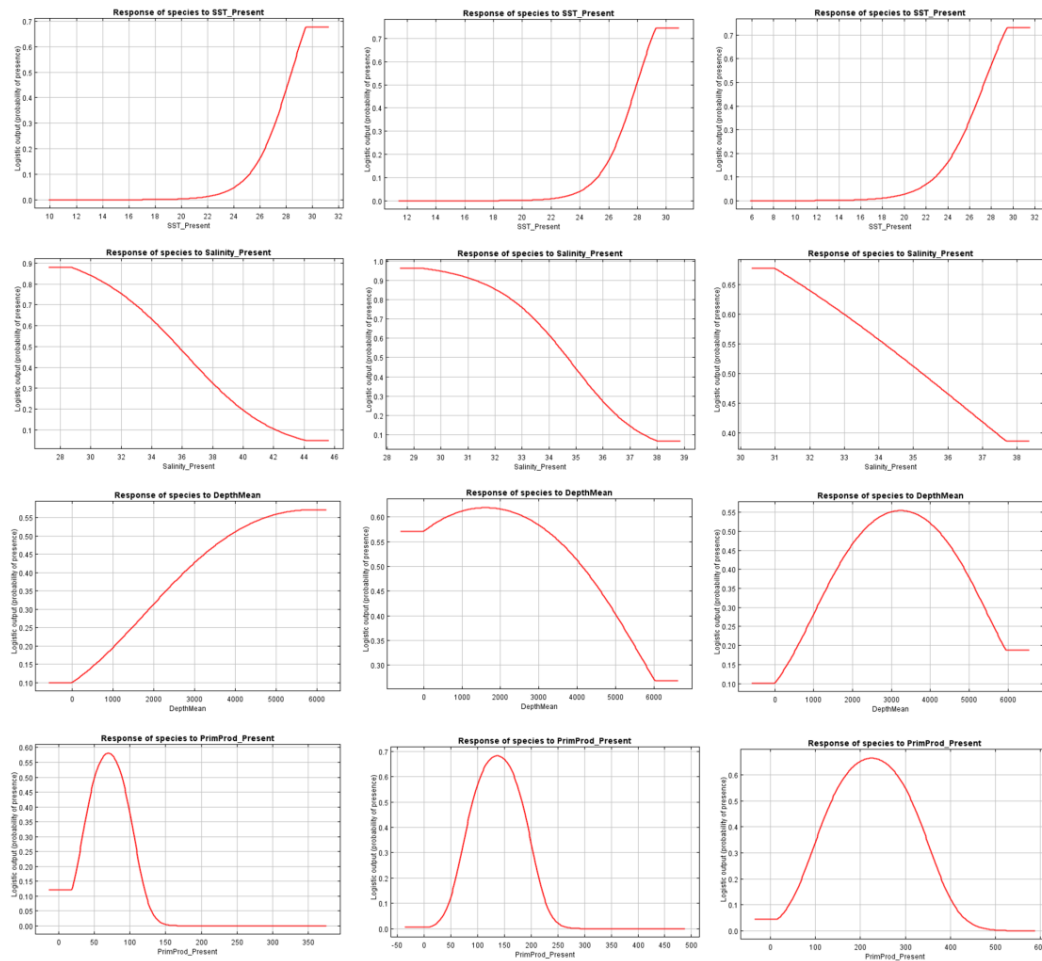


Figure 54. Present response curves (sea surface temperature, salinity, depth and primary production) for *Carcharhinus falciformis* in the Indian (first column), Atlantic (second column) and Eastern Pacific Ocean (third column).

Finally, low-intermediate threshold values were obtained in all cases (around 0.45), showing good proportion of predicted area suitability (Pearson et al. 2007).

In general, distribution models for both by-catch species showed reasonable model performance, although rough triggerfish showed better accuracy values (between 0.60 and 0.80) than silky shark (around 0.60-0.70) in each ocean. At the same time, the Indian Ocean had the worst performance values (around 0.50-0.60) for both by-catch species in comparison with the Atlantic (0.7/0.8) and Pacific Oceans (0.65/0.75). Finally, to verify that the occurrences randomly taken in the Pacific Ocean were a good representation of the species distribution, the model it was run several times with different sets of 1000 occurrences. In all cases, the results showed high accuracy values.

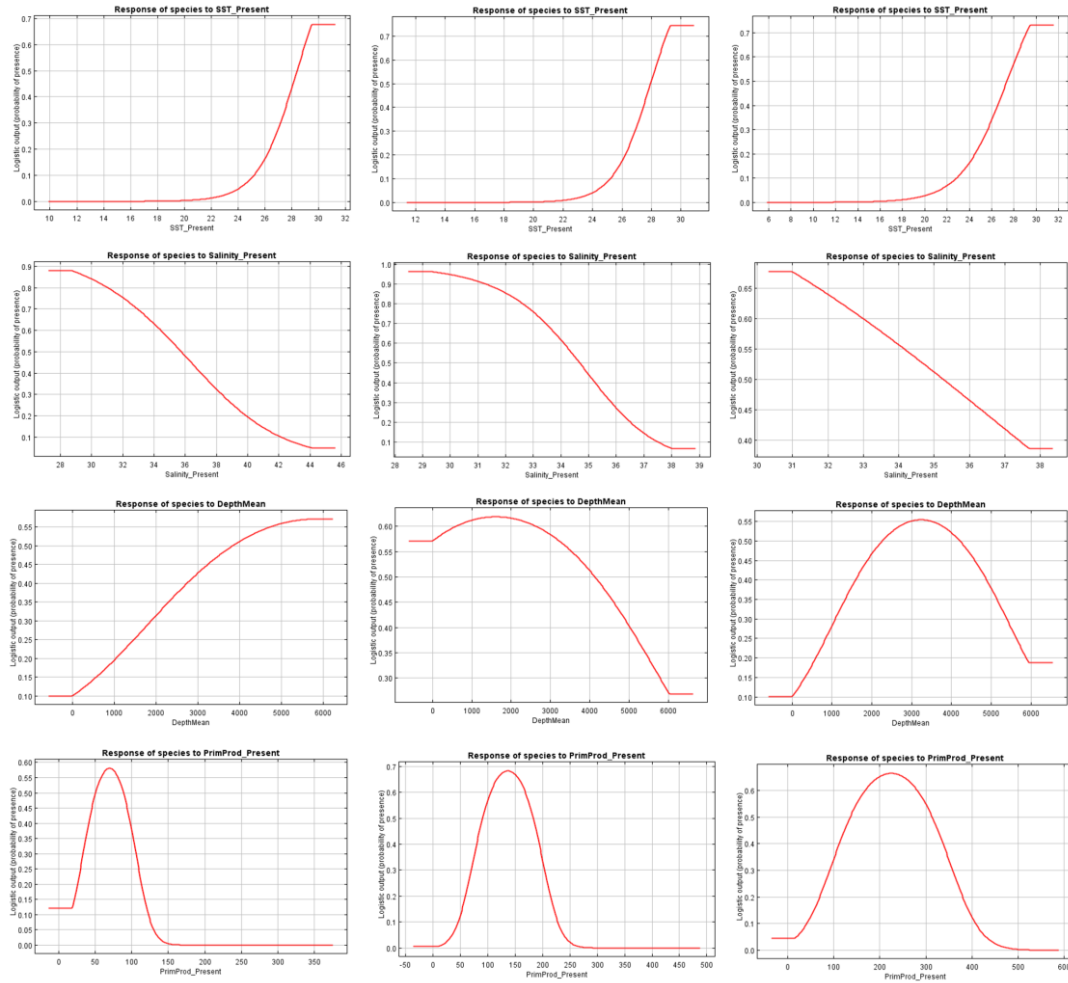


Figure 55. Present response curves (sea surface temperature, salinity, depth and primary production) for *Canthidermis maculata* in the Indian (first column), Atlantic (second column) and Eastern Pacific Ocean (third column).

Table 20. Model evaluations with all observations (t) and cross-validated (k) for *Carcharhinus falciformis* and *Canthidermis maculata* in the Indian (IO), Atlantic (AO) and Eastern Pacific Ocean (EPO). Threshold values obtained from maximization of sensitivity plus specificity.

Ocean	By-catch species	AUC	Sensitivity	Specificity	Accuracy	Omission	Threshold
		(t/k)	(t/k)	(t/k)	(t/k)	(t/k)	
IO	<i>Carcharhinus falciformis</i>	0.63/0.62	0.68/0.86	0.56/0.41	0.63/0.50	0.42/0.08	0.41
	<i>Canthidermis maculata</i>	0.64/0.62	0.70/0.84	0.56/0.44	0.64/0.52	0.39/0.08	0.46
AO	<i>Carcharhinus falciformis</i>	0.76/0.77	0.80/0.84	0.64/0.63	0.72/0.66	0.24/0.05	0.5
	<i>Canthidermis maculata</i>	0.82/0.83	0.74/0.78	0.79/0.77	0.77/0.77	0.29/0.05	0.4
EPO	<i>Carcharhinus falciformis</i>	0.67/0.67	0.68/0.67	0.60/0.60	0.64/0.61	0.35/0.01	0.49
	<i>Canthidermis maculata</i>	0.76/0.75	0.72/0.77	0.69/0.65	0.71/0.67	0.28/0.07	0.45

4.3. Projected habitat suitability differences

The projected habitat suitability maps for *Carcharhinus falciformis* and *Canthidermis maculata* under A2 future scenario of climate change and differences between future and present conditions (binary maps) for each ocean are depicted in Figure 52 and Figure 53, respectively. The percentages of suitable and loss/gain habitat suitability for silky shark and rough triggerfish in the Indian, Atlantic and Pacific Oceans are shown in Table 21.

Under the A2 scenario for 2100, 3.1% of the present habitat for silky shark was predicted to change in the future in the Indian Ocean (Table 21 and Figure 52). The gained areas were mostly located in the south (mostly around 12°S) while the lost areas were located near the Somali coast, the central part of the study area and the south of India. In the Eastern Atlantic Ocean, under climate change impacts, the model predicts that silky shark could gain some habitat north of the equator and in the Cap Lopez area and would loss habitat around the equatorial band between 0°-10°S (Table 21, Figure 52), with a total change of the present habitat of 15.9%. In the Eastern Pacific Ocean, under the A2 scenario of climate change, 10.4% of the present habitat was predicted to change in the future. Habitat is predicted to be lost near the coastal upwelling area of Peru, and in the equatorial band (10°N and 10°S), while the gains would occur north and south of the Equator (10°N and 10°S) and along the coast of Central America (Nicaragua, Costa Rica, Panamá, Colombia) in an area called “Panama Bight” (Forsbergh, 1969).

On the other hand, because of changes in oceanographic conditions, 2.4% of the present habitat was predicted to change in the future for rough triggerfish in the Indian Ocean. The gained and lost areas were detected in similar areas as for silky sharks. In the Eastern Atlantic Ocean, under the climate change scenario used, 15.7% of the present habitat was predicted to change in the future. The climatic model for 2100 projected a potential gain for rough triggerfish of habitat in the Cap Lopez area and the north of the Equator and loss of habitat in the north (0-10°N/20-40°W) and south (0-10°S/0-10°E) of the Equator. Finally, under the A2 scenario of climate change, 8.7% % of the present habitat in the Pacific was predicted to change in the future; with an increase in suitable habitat in the north and south of Equator (around 90-110°W and 125-140°W). The model predicted loss of habitat at south of Equator (around 100-110°W) and in the coastal upwelling area of Peru (Table 21, Figure 53).

Table 21. Predicted changes in habitat suitability areas by the year 2100 for the A2 scenario of climate change for both by-catch species. Loss is the area that would no longer be suitable for the species. Gain is the area that would become suitable habitat due to the change. Suitable present-future is the area which will remain suitable in the future. Total change is the area which will change in the future as consequence of gain and loss of habitat.

Oceans	Species	Loss (%)	Gain (%)	Suitable present-future (%)	Total change (% loss + % gain)
Indian Ocean	<i>Carcharhinus falciformis</i>	1.4	1.8	98.8	3.1
Indian Ocean	<i>Canthidermis maculata</i>	1.0	1.4	99.0	2.4
Atlantic Ocean	<i>Carcharhinus falciformis</i>	15.5	0.3	84.4	15.9
Atlantic Ocean	<i>Canthidermis maculata</i>	15.4	0.2	84.5	15.7
Pacific Ocean	<i>Carcharhinus falciformis</i>	9.9	0.4	90.1	10.4
Pacific Ocean	<i>Canthidermis maculata</i>	7.0	1.7	92.9	8.7

5. DISCUSSION

The influence of fishing pressure and climate change on marine ecosystems and more particularly on species distribution has become a general concern (Jones et al. 2013). In this study, we show that species distribution habitats for common and threatened by-catch species can be modeled using MaxEnt species distribution model, even with a limited set of environmental variables. The application of SDM on by-catch species opens a new range of possibilities to study more pelagic species in different areas and fisheries. Potential habitat of species fished in different fisheries could provide important information about species distribution range in the open sea and useful for spatially structured management plans.

We obtained reasonable accurate values using MaxEnt species distribution model, as Peavey (2010) and Sequeira et al. (2012) did. Moderately high AUC and overall prediction accuracy around 0.70 were found for both by-catch species in different oceans. Our distribution models were able to predict habitat suitability for silky shark and rough triggerfish over a more extensive area than that covered only by the observer data (occurrences). The observer dataset we used contained only silky shark and rough triggerfish presences. We addressed this drawback by randomly generating pseudo-absences (Senay et al. 2013) and running 5 times the prediction to account for the robustness of the models. However, the correct selection of pseudo-absence data directly affects the accuracy of model prediction. For that reason, the accurate identification of the area (in this case, the sampled area and not areas out of the sampled area) for the creation of pseudo-absences was essential for the correct model performance.

5.1. Habitat suitability areas

The analysis and modelling of by-catch data collected by observer programs has provided predictions of the pelagic distribution of two wide-ranging species. Thus, the predictive maps produced by our models revealed that the regions close to equatorial and upwelling regions were the most suitable habitats for these species in the Atlantic, Indian and Pacific Ocean in correspondence to the main fishing grounds. These areas are the most important in the tropical tuna purse seine fisheries (Hall and Roman 2013) because they are characterized by warm waters, strong surface currents, upwelling systems and different wind patterns supporting a great variety of organisms and in consequence, high marine biodiversity. Lezama-Ochoa et al. (2015) and Torres-Irineo et al. (2014) showed that higher numbers of species were found close to coastal upwelling areas in the Indian Ocean associated to the monsoon system and with the equatorial counter-current in the Atlantic Ocean. In the Pacific Ocean, the higher numbers of species were found at north of the Equator (10°N) in an area of marked frontal systems and near the coast of Central America (mainly Costa Rica and Panama) (Lezama-Ochoa et al., 2015b (submitted)). Our results suggest that the distributions of these two species coincide with the areas where the highest biodiversity was found.

It is important to note that the use of this type of data is valid since the information provided by the models reveals interesting findings. Results showed some areas which can be suitable for these species independent of the area of fishing effort. That means these models provide new information (for example, at south (20°S-80°E) and close to the Indian Continent in the Western Indian Ocean, or the coast of Nigeria and Cameroon in the Atlantic Ocean) of areas which can be suitable despite not being fished. In contrast, other areas (for example, north and south (15°N-20°S) in the Atlantic Ocean) which are located inside the fishing effort area are not suitable for these species. It means that both target and non-target species may have different habitat distributions and preferences.

This study was compared with the results from Froese and Pauly (2014) from AquaMaps (Kaschner et al. 2013). Both works showed similar habitat preferences of *Carcharhinus falciformis* around coastal and oceanic upwelling waters. However, Froese and Pauly (2014) did not show any climatic projection for the future. In the case of *Canthidermis maculata*, the habitat distribution published by Froese and Pauly (2014) only frames the coastal areas, which results in different distribution ranges and future projections compared with our work. The differences were based on the different sources of information used (museum collections, different databases, literature references) compared to our work which contains a large number of offshore observations since it is based on observer programs covering the wide distribution of the tropical tuna fisheries. In that

sense, the presence data of our sampling provides new information about the distribution of the two species. This new information may be a result of the expansion of the FAD fisheries.

The habitat models derived in this study suggest that *Carcharhinus falciformis* and *Canthidermis maculata* responded mainly to variation in SST in the three oceans. These by-catch species are often distributed in warm waters and aggregated around floating objects (e.g. logs, Fish Aggregating Devices) in productive areas (Dagorn et al. 2013).

In the Western Indian Ocean, the monsoon system determines the wind and current patterns of the area, with coastal upwelling systems close to Somalia in summer and Mozambique in winter. These systems are associated with changes in the surface temperatures and therefore, affect the habitat and distribution of the by-catch species. In addition, the depth of the ocean basins seems to play an important role in the habitat distribution of both by-catch species. The continental shelf in the Indian Ocean is narrower than in the other oceans and therefore, the distribution of the species in open ocean is close to the coast (Tomczak and Godfrey 2003).

In the Atlantic Ocean, the SST is also the most important environmental variable followed by low salinity and high primary production concentrations as a consequence of the Benguela upwelling system (Tomczak and Godfrey 2003).

In the Eastern Pacific Ocean, the SST plays an important role in relation with ENSO conditions in equatorial and coastal upwelling areas of the Pacific. Thus, determines tuna, other teleost species and shark distributions around the “warm pool” area close to the Gulf of Tehuantepec and Central America (Martínez Arroyo et al. 2011). In addition, the primary production is also important in the Eastern Pacific Ocean. The equatorial and Peru eastern boundary currents are associated with highly productive upwelling systems, which form some of the most important fishing areas of the world (Fiedler et al. 1992; Pennington et al. 2006). Thus, these environmental variables had important implications on the biogeographic patterns of both species abundance and distribution in each Ocean.

5.2. Projected habitat suitability

The Intergovernmental Panel on Climate Change (IPCC) estimates ocean warming in the top one hundred meters between 0.6°C and 2.0°C by the end of the 21st century (Collins et al. 2013). Species may respond to climate change by shifting their geographical or bathymetric distributions (horizontal or vertical distributions) depending on the extent of the species geographical ranges,

dispersal mechanism, life-history strategies, genetic adaptations and biotic interactions or extinction factors (Thuiller 2004).

Our results suggest that climate change will affect the distribution of these species depending on the oceanographic conditions of each ocean. In this study, changes in species distribution as a consequence of climate change were predominant around the equatorial band and in some cases, around upwelling systems (Panama in the Eastern Pacific Ocean, Benguela in the Atlantic Ocean (in a lesser extent)) where fisheries are quite significant. This is not in agreement with the general expectations of migration to deeper waters and poleward shifting of marine fishes in response to sea warming (Cheung et al. 2013; Walther et al. 2002). Moreover, climate change can impact the strength, direction and behavior of the world's main currents and therefore, affecting also in this way the species geographical distributions (Hoegh-Guldberg and Bruno 2010).

5.3. Habitat loss

The percentage of habitat suitability that could disappear, or persist for each species is a good way to assess the potential impact of climate change at a regional scale (Thuiller 2004).

If we focus on the habitats in each ocean, the Atlantic Ocean temperatures are projected to increase due to the much larger warming associated with increases of greenhouse gases in this region (Change 2007); and therefore, a greater and faster loss of habitat in this area is expected. In the case of the Western Indian Ocean, the area around the Somali coastal upwelling system could be unsuitable for the two species as a response to temperature warming, affecting one of the most diverse areas for these by-catch species (Amandè et al. 2011a; Lezama-Ochoa et al. 2015).

With regard to the Eastern Pacific Ocean, the A2 climate change scenario projected habitat losses around 8-10% for both by-catch species around the coast of Peru and north and south of the Equator (10°N-10°S). In that sense, some authors suggested a reduction of primary production around these areas as consequence of global warming (Blanchard et al. 2012; Gregg et al. 2003; Hoegh-Guldberg and Bruno 2010). The results obtained in this work lead us to suggest that these zones could be not suitable for studied by-catch species by 2100 if the primary production is reduced; since these species depend on high nutrient levels and the preys associated to those conditions.

5.4. Habitat gain

Climate change induced some positive effects with gain of habitat for both species in each Ocean. According to Bindoff et al. (2007), the Indian Ocean has been warming in the last years except for an area located at the latitude 12°S along the South Equatorial Current. Therefore, it is believed that this trend will continue in the future. In that sense, our model projects a slight potential colonization for the two by-catch species along this area (12°S) as a consequence of the positive effect of the ocean warming.

Carcharhinus falciformis and *Canthidermis maculata* could gain new habitat in the Atlantic Ocean near the Angola and Namibia coasts. Global warming could increase the evaporation and, therefore, the rainfall with a consequent increase in the flow of the rivers, providing nutrients to feed plankton in the coastal areas (Justic et al. 1998). Thus, the area located near the mouth of the Congo River could increase its productivity and, hence, the habitat suitability for by-catch species. Other possible explanation for the increase in primary production in the western coast of Africa could be that suggested by De Young et al. (2012) who showed that an increase in upwelling-favorable winds in the Benguela system could increase primary production. This could benefit the habitat suitability for some species around this area due to an increase of nutrients supplies.

In the Eastern Pacific Ocean, a significant gain of habitat suitability for both by-catch species as a consequence of the increase in primary productivity around Central America is expected by the end of the century. In this region, the temperature increase in the continent as a consequence of global warming will be higher than in the open ocean, which could increase wind intensity favoring upwelling in the coast of Central America where three “wind corridors” play a major role in coastal production (Martínez Arroyo et al. 2011).

In general, there were not significant differences between the percentages of habitat loss and habitat gain for each by-catch species. High percentage of change of habitat was found in the Atlantic Ocean, and a lesser extent, in the Pacific Ocean. In contrast, the Indian Ocean didn't show any relevant change on their distributions. The global warming could impact more the equatorial areas from the Pacific and Atlantic Oceans, which share similar oceanographic features (Tomczak and Godfrey 2003). The environmental processes in the tropical Indian Ocean, in contrast, seem to play a different role in the diversity (Lezama-Ochoa et al. 2015) and the habitat of the by-catch communities as consequence of the strongest monsoon on Earth. For that reason, the results were expected to be also different. The lack of the permanent equatorial upwelling in the Indian Ocean (as consequence of the steady equatorial easterlies) and the position of the land

mass in the north area, seems to influence in the oceanography and environment of this area (Tomczak and Godfrey 2003).

In an environmental or fisheries management context the question is not necessarily how the climate or ocean abiotic conditions will change, but how the species of the ecosystem might respond to these changes (Payne et al. 2015). We obtained that both by-catch species respond in similar way to the future climate changes. However, with respect to their populations, the silky shark could be largely affected in the Atlantic and the Pacific Ocean if no management measure is taken to reduce its mortality. Silky shark population should be considered more cautiously since this is a vulnerable species less resilient to climate change than small body-size organisms (Lefort et al. 2015). The use of good practices onboard (Gilman 2011) to increase the post-release survivorship is the best option to reduce their mortality. In addition, understanding its spatio-temporal distribution will help to develop spatially structured mitigation or management measures”.

In contrast, although a similar percentage of habitat loss occurred in triggerfish, their population seems to be stable due to its “r” life-strategy. Even so, it must take into account these species in the future management plans.

5.5. Limitation of the work

Accurately describing and understanding the processes that determine the diversity and distribution of organisms is a fundamental problem in ecology and always inevitably associated with a degree of uncertainty (Payne et al. 2015). This uncertainty is multifaceted and can be decomposed into several elements. Identifying these different factors helps to better address them for obtaining a better model performance. Two of the most important uncertainties in species distribution models (considered as empirical models, see Payne et al. (2015)) are structural and scenario uncertainties. Thus, the quality of model outputs can depend on the variables (biological data and environmental data) and the space-time scale considered (Payne et al. 2015) (Phillips et al. 2009). There is not best model, and the choice should be driven by the question and the objective of the study.

In this work, the MaxEnt habitat modelling method allowed in an easy way to obtain essential information with few environmental variables about pelagic species. However, the gained experience leads us to discuss several aspects which must be considered and improved applying future habitat models. The selection of the occurrence by-catch data from the fishery not targeting

those species can lead to assume that the data quality is not enough. However, we demonstrated that observer data is been used in multiple ecological and habitat studies similar to the one described here. Nevertheless, further increase of the coverage rates (in the case of the Atlantic and Indian Ocean) and the sample size is essential for doing comparisons between years and periods.

The selection of the environmental variables was based in the main oceanographic characteristics of each ocean, and thus, as showed by the results, the response curves explained correctly the high mobility character of the species and their relationship with the upwelling and surface current systems. However, the selection of other environmental variables related with the ecology of the species (nutrients, oxygen, etc...) could also improve the results. The habitat model performed better at large spatial scales (in the Atlantic and the Pacific Ocean) than at small scales (Indian Ocean). The complex oceanographic processes in the Indian Ocean compared with the Atlantic and Pacific Ocean, which share some oceanographic features, could difficult the selection of specific factors which explain the distribution of the two by-catch species. Thus, a better selection of the environmental data and the application of the other habitat models to compare predictions in this Ocean would be further recommended.

Secondly, the lack of absence data was the most important factor discussed and considered in this study. As we know that the model with presences and absences performs better than the only-presence models, we decided to generated and include the pseudo-absences to evaluate the models. Within the numerous ways of addressing the problem of generate pseudo-absences (Barbet-Massin et al. 2012; Fourcade et al. 2014; Sequeira et al. 2012), here it was solved with the generation of the same number of pseudo-absences (randomly) as presences in places where presences were not observed within the sampled area. However, in future works, it would be worth to compare among different ways to generate pseudo-absences.

5.6. The applicability of habitat models on fisheries management plans

By-catch is a significant issue for the fishing industry, scientists and managers, and it needs to be managed and mitigated. Invasions and extinctions of by-catch species in an area can affect not only their species distribution range, but also the marine biodiversity, community structure, size spectra, and ecosystem functions (Sala and Knowlton 2006). In this context, by-catch monitoring programs with observers onboard can be expensive and sometimes difficult to implement. However, they are an important source of data to identify suitable habitats to be used in conservation biology field (Franklin and Miller 2009).

Thus, there is still a need to develop SDM for other by-catch species and/or habitats of interest for these species (e.g. upwelling areas, seamounts, coastal areas) to investigate their spatial distributions and to assess the effects that fishing and climate change may have on those populations. Concretely, it would be interesting to apply this habitat model in other tuna target-species to describe their potential habitat distribution and identify any possible overlap with the by-catch species. Thus, the future gain areas by the by-catch species, provided that target species distribution remains the same, could be act as a refuge for by-catch species. Similarly, those losses areas could be considered to be protected in future management plans. Moreover, other habitat suitability distribution approaches (such as ensembles of different algorithms) and other more sophisticated and descriptive environmental predictors, as well as new climate change scenarios may help to improve habitat distribution projections.

Monitoring and understanding changes in by-catch species distributions, in addition to those of the harvested species (tunas), are necessary for a better understanding of the pelagic ecosystem and towards a correct implementation of the EAFM.

6. CONCLUSION

Our model predicts that potential habitat distribution areas for *Carcharhinus falciformis* and *Canthidermis maculata* in the Atlantic, Indian and Pacific Oceans are close to equatorial and coastal upwelling areas, and mainly associated with sea surface temperature. These habitat distribution models, based on the information collected by observer programs from the tropical tuna purse seine fisheries in the three oceans, provide a good estimation of the pelagic distribution of these wide-ranging by-catch species. The global ocean warming could impact some of these unstable and vulnerable ecosystems (mainly in the Atlantic and the Pacific Ocean) affecting the distribution of these species in accordance with the particular oceanographic conditions of each ocean. Under climate change scenarios, the largest change in present habitat suitability was observed in the Atlantic Ocean (around 16% of the present habitat suitability area of *Carcharhinus falciformis* and *Canthidermis maculata*) whereas the change was less in the Pacific Ocean (around 10% and 8%) and any significant change was observed in the Indian Ocean (around 3% and 2%).

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DISCUSSION

As consequence of the direct human pressures and global environmental changes, the loss and changes on species diversity has become a great concern and of major interest in theoretical and applied studies (Granger et al. 2015). In this context, biodiversity studies are vital tools to study spatio-temporal variations in natural communities, to identify priority areas of protection and to support effective conservation planning (Granger et al. 2015).

The work developed in this PhD Thesis is mainly focused on biodiversity and habitat modelling of the by-catch species from the tuna purse-seine fishery in the tropical area oceanwide. This dissertation concludes that diversity of the by-catch communities of this fishery are highly variable in space and time (Chapter 1, 2 and 3) and that certain species show different preferences to oceanographic processes and environmental variables which can be considerable affected by climate change (Chapter 4).

Based on the combination of existing knowledge and on the gained experience of the author, this general discussion follows the logical structure of the current PhD Thesis and tries to integrate, discuss, compare and synthesize the most important results found about the by-catch communities of the tropical tuna purse seiner fisheries and their relationship with the environment. Moreover, the results of the PhD Thesis are discussed in light of their implications for fisheries management as well as on limitations encountered and the future work perspectives.

Biodiversity of the purse seiner by-catch communities in the tropical area

Knowing the number of existing marine species is of primary important because it provides a metric to better understand the ecosystem and life in the ocean (Appeltans et al. 2012). Moreover, the changes in the number of species and their abundance describe the impacts and consequences of the human practices and environmental processes. There is increasing evidence that the tropical tuna purse-seine fishery has effects on species level diversity in a temporal (seasonal and annual) and spatial scale (geographically); with differences in abundances and species composition depending on the environmental characteristics of each ocean basin. However, methodological features, like the sampling size and coverage rate, and fishing mode (FAD vs. free) also affects the diversity patterns.

Up to date, many ecological indicators have been considered to detect and describe the effects of fishing on marine ecosystems; however, few have been evaluated formally (Fulton et al. 2005). The most widely used metric of biodiversity is species richness, and much has been written about how many species may exist on land and in the sea (Appeltans et al. 2012). Whereas richness may be more interesting ecologically, species evenness or the relative abundance of each species is more meaningful for conservation and management (Van Dyke 2008). High species evenness may improve compositional stability within assemblages and reduce the risk of local extinction and invasion (Cusson et al. 2014). In Chapters 1, 2 and 3 of this Thesis we worked with these biodiversity measures, which were definitely essential to consolidate and support some previous findings and to provide new information about these pelagic by-catch communities.

In general, using species richness, evenness and Shannon diversity measures, by-catch communities in FAD sets are more diverse (higher number of species evenly distributed) than in Free School sets as it was observed in the Indian (Chapter1), the Pacific (Chapter 2) and the Atlantic Ocean (Chapter 3). According to the present work, FADs tend to aggregate more species, both in number and abundance, as it was published in previous works (Amandè et al. 2010; Romanov 2002; Torres-Irineo et al. 2014).

Nevertheless, this PhD also showed that the sample size and coverage rate play an important role in the final estimation of by-catch diversity (Chapter 2). Thus, for the correct implementation of conservation measures, biodiversity studies must have sufficient and adequate quality data. The first three chapters of this Thesis represent different scenarios for studying biodiversity based on the information available about by-catch communities (see S5. Figure 1 in Supplementary material-Discussion). The Atlantic Ocean (Chapter3) represents the most difficult scenario because not only had the lower sample size and coverage rate, but the complex seasonal environmental processes in the Gulf of Guinea also make difficult to find any clear diversity spatio-temporal pattern related to environmental-distribution factors. Moreover, it is difficult to clearly identify areas where the species composition is correlated with the geographical position and/or the environment variables (based on the Mantel test). Therefore, for the Atlantic model results and diversity indices should be taken with caution before implementing any conservation measure.

On the contrary, the Western Indian Ocean (Chapter1) represents an intermediate scenario for studying biodiversity of the by-catch communities. Despite the low coverage rate and sample size, Alpha and Beta diversity patterns were clearly described in both fishing modes in relation to the environmental seasonal patterns marked by the monsoon system. In the case of the by-catch communities in FAD sets, increasing diversity was positively related with upwelling off the coast of Somalia (Summer Monsoon) and eddy circulation in the Mozambique Channel (Winter

Monsoon). On the other hand, diversity was found to be higher around Somalia (North and South) for Free School sets. Finally, the Eastern Pacific Ocean represents the best scenario to conduct biodiversity studies on by-catch communities due to the extended sampling reaching 100% observer coverage. As showed in Chapter 2, the total number of possible species that could be found in the tropical area is directly dependent on both the sample size and coverage rate. This relevant result reflects the importance of having a good observer coverage to sample the pelagic ecosystem.

The tropical area covers a significant extension of the world's oceans where the by-catch species can be aggregated around FADs or dispersed following the movement of the tropical tunas. Despite the number of species and their abundance is higher in FAD sets compared to Free School sets worldwide (Chapter 1, 2 and 3), results from the EPO (Chapter 2, good coverage rate) suggested that the total number of species caught by the two fishing modes may not differ significantly, being the information obtained from each of them a very useful tool to adequately estimate the diversity of the pelagic ecosystem. The overall view of the communities is widely used by ecologists and proven to be essential to improve faunal inventories prior to carry out any biodiversity study (Colwell 2009; Gotelli and Colwell 2001). Knowing the exact number of species living in the habitat improves the capacity of better understanding and managing correctly habitat changes and losses. As the low sampling coverage could, in some extent, affect the generalization of the results obtained, we believe that there is an urgent need to further increase the sample size and coverage rate of observer data, which would lead to improve final estimates of by-catch diversity studies.

Research carried out in Chapter 1, Chapter 2 and Chapter 3 suggest that the sample size to find the same number of species in both fishing modes needs to be higher in FAD sets. This is probably due to the fact that FADs tend usually to aggregate the same species around them (Amandè et al. 2008a) and thus, the probability of finding new or rare species at one point, is more difficult than in Free School sets. In addition, FAD sets are distributed over a much larger area than Free school sets, which appear in a few well-defined spots and, therefore, the effort needed to find the maximum number of species could be higher in the first case. This last point is ecologically relevant because FADs tend to be concentrated in areas of high biodiversity or "hotspots", such as front systems (Chapter 2) or productive surface currents (Chapter 1 and 2). However, they don't entirely represent the habitat distribution of the by-catch species in the tropical pelagic ecosystem. For that reason, information collected from observer programs in the purse seiner fishery, both in FAD and Free School sets, should be used as tools for studying the

biodiversity, the habitat and the behavior of the by-catch communities for a better fishery management.

This dissertation showed that the by-catch species composition of the tropical tuna purse-seine fishery evidences high degree of similarity between all the oceans. Whereas the by-catch species composition in Free School sets presents a high variability between sets, it is more stable in the case of the FAD sets. It was shown that more than 330 species belonging to 96 families are associated with FADs (Castro et al. 2002), despite not all them present a strong association tendency. Taking into consideration different degrees of the associative behavior, Fréon and Dagorn (2000) revised the work of Parin and Fedoryako (1992) and proposed three spatial groups for fish associated with FADs: i) intranant species (up to 2m away from the FAD, formed by juvenile and demersal-pelagic species such as *Lobotes* or *Coryphaena*), ii) extranant species (2m to 10-50 m from FADs, with species such as *Caranx* or *Aluterus*) and iii) circumnatanant species (50 m to several nautical miles from the FAD, with predators such as rainbow runner, tropical tunas, triggerfish, carangids or sharks). This means that the diversity at FADs is not only high in terms of species but also in life strategies, ecology and behavior of the species.

This Thesis found species belonging to the three types of spatial groups, with both “r” (such as *Canthidermis maculata* or *Elagatis bipinnulata*) and “k” (such as *Carcharhinus falciformis* or *Sphyræna barracuda*) life strategies associated with FADs in the three oceans. Furthermore, the analogous species composition found between areas with similar habitat characteristics, such as the Somali and Mozambique Channel upwelling systems (Chapter 1), California and Peru coastal upwelling systems (Chapter 2) and the Pacific and Atlantic seasonal equatorial upwelling systems (Chapter 2 and 3) led us to conclude that the species composition may be directly related with certain environmental conditions and the fishing mode. In addition, an increase in sample size makes this relation more clear (with differences of similarity between the equatorial and permanent coastal upwelling areas in the Eastern Pacific Ocean) (Chapter 2) compared to the Atlantic Ocean (Chapter 3). Again, this highlights the importance of obtaining and working with adequate data quantity and quality.

In the Indian Ocean (Chapter 1), the monsoon system determines the similarity between species composition in FAD sets. In fact, the productivity conditions driven by the monsoon dynamics make Somalia and Mozambique areas to behave similarly in different periods of the year, where FADs show higher diversity values. Despite the differences observed between oceans, it's clear that by-catch communities follow surface currents associated with FADs in intermediate productive waters; however, the reason driving this associative behavior is still unknown. Some experts hypothesized the possibility of tunas being trapped in a non-favourable area by FADs, a

phenomenon known as ecological trap for tunas on FADs (Hallier and Gaertner 2008; Marsac et al. 2000). The idea behind is that the association of tunas to FADs could compromise their original behavior, movement and health condition drifting them to “unfavorable” conditions. Similar concerns could be extended to by-catch species. Although there are no reasons to explain why fish associate with FADs, studies like the current work are of primary importance to better assess the effect of FADs in the pelagic ecosystem.

Nevertheless, and as it was described in the introduction of this Thesis, several hypotheses have been proposed to explain the associative behavior of tunas with floating objects (Castro et al. 2002; Fréon and Dagorn 2000) but only two of them (i.e, meeting point and indicator log-hypothesis) are currently the most broadly accepted by the scientific community. Thus, this Thesis supports the complementarity of both hypotheses, considering the use of floating objects for the constitution of bigger schools for the survival of the species (Fréon and Dagorn 2000) and as indicators of the quality of the environment (Hall et al. 1992). As it was demonstrated in the Chapter 1, 2 and Chapter 3, highest diversity of by-catch communities in FAD sets occurs commonly in relation with front systems, domes, river discharges and oceanic convergences; that is, in relation to productive waters. Thus, the environment of the pelagic ecosystem is directly correlated with the number and abundance of the species, indicating that by-catch aggregated to floating objects to increase their encounter rate and diversity, limiting the distribution of their habitat to the most productive waters along the tropical area.

Habitat preferences of the by-catch communities at global, basin and local scale

The number of species in an area and their abundance depends on habitat characteristics (MacArthur 1965). Thus, knowing the stability, concentration of nutrients, or environmental processes of a particular habitat is a key requirement for understanding the diversity in that area.

This PhD Thesis also aimed to study the habitat preferences of the by-catch communities in the tropical area. After identifying the spatial-temporal dynamics of by-catch biodiversity (i.e., most diverse areas and trimesters), we explored the effects of the environmental variables that could explain positive and negative patterns of by-catch diversity. For that purpose, Generalized Additive Models (GAMs) were developed in Chapters 1, 2 and 3 where results showed both significant differences and similarities between oceans and fishing modes.

It is important to note that most aspects of the marine environment are highly dynamic. When evaluating the ecological or biological significance of an area based on a particular criterion (as in our case, diversity), the spatial and temporal variability of an environmental feature (e.g. sea surface temperature, sea level anomaly, etc) on an organism's behaviour must be taken into account (Gray 1997). In this specific case, diversity of the by-catch communities in the tropical areas seems to be explained by environmental features at global, basin and local scale. Thus, in this Thesis, diversity was found to be directly related with the habitat in which the species live.

Results of the present work revealed that there is a global latitudinal and longitudinal diversity gradient around tropical areas. By-catch communities' diversity showed at global scale a general pattern, indicating peaks of diversity at low latitudes (0 to 10°N or S) and lower diversity toward intermediate latitudes. In the specific cases of the Pacific and Atlantic Oceans, trade winds blow from the Northeast and Southeast and converge along the equator. This results in seasonal divergence events in the equator, with denser, nutrient-rich water being upwelled from the bottom (Chapter 2 and Chapter 3) (Picaut et al. 1984). Diversity also appeared to be higher at FADs located in western regions of the Pacific (Chapter 2) and the Atlantic Oceans (Chapter 3) compared to eastern regions. According to Briggs (2007), on the western sides of the Pacific and Atlantic oceans, the North and South Equatorial currents transport warm water to higher latitudes whereas on the eastern sides, the major currents transport cool water towards the tropics. This allows the tropical seas to occupy a broad latitudinal area in the west but only a relatively narrow in the east (Briggs 2007). Thus, a positive relationship between species diversity and geographical area can be expected, where more diversity on the western regions is found (Chapter 2 and 3) compared to the eastern parts. On the other hand, the diversity of the Western Indian Ocean (Chapter 1) is regulated by the monsoon system, with different environmental processes in each area, and therefore, different habitat distribution of the marine species.

Interestingly, and in accordance with the work of Briggs (2007), all the distribution models highlighted the significance of geographical locations as one of the main explanatory factors of diversity pattern. Indeed, high diversity geographical locations differed by fishing mode and Ocean. This reveals that the heterogeneous distribution of diversity in the by-catch communities in the tropical pelagic ecosystem may be determined by different environmental parameters and an active selection of preferred habitat.

A priori, one can think that these results could be related somehow with the fishing strategy of fleet. However, in this fishery, although highly seasonal, fisher are permanently looking for both Free School and FAD sets, with preferences in Free School sets if there is availability. In addition, results obtained with good coverage data also support the idea of a spatial differentiation between

FAD and FS communities, which could support the assumption that effort could not significantly affect final results of this study.

At basin scale, oceanographic processes play an essential role in the distribution of diversity for the by-catch communities in the tropical area. The main oceanographic characteristics explaining high or low diversities in FAD and Free School sets at basin scale are surface currents and seasonal or permanent upwelling systems (Figure 54).

As stated by Longhurst and Pauly (1987), the permanent coastal upwelling systems are the most important features supporting the fisheries of the tropics. Situated in the eastern parts of the tropical Atlantic and Pacific oceans basins (Benguella, California and Peru upwellings), these systems are among the most biologically active regions of the world oceans. In these regions the thermocline is shallow and is affected by strong vertical movement of water with high concentrations of nutrients (Picaut et al. 1984). Although there is a tendency to assume that those systems of high productivity supports also high diversity, we found that (Chapter 2 and Chapter 3) the high productivity permanent coastal upwellings of California, Peru and Benguela are also high instable systems resulting of low-diversity ecosystems.

It is important to note that upwelling features in the tropics are not only confined to coastal permanent upwellings systems (such as Peru, California and Benguela where the upwelling occurs persistently throughout the year) associated to the cold eastern boundary currents. Equatorial and coastal divergences driven by wind forces and Ekman transport also occur in many other tropical locations resulting in seasonal upwellings (where they occur in particular locations around the world at specific times of the year) and upwellings events could also be associated with eddies (Robinson 2010). In this case, those systems support high diversity of by-catch species. Some examples of this are the upwelling of the Gulfs of Tehuantepec and Panama (Chapter 2), the upwelling of Gulf of Guinea (Chapter 3), the upwelling on the Somali coast (Chapter 1) and the equatorial upwellings in the Pacific (Chapter 2) and the Atlantic Ocean (Chapter 3) (in the case of the equatorial upwellings they are associated with the Intertropical Convergence Zone (ITCZ) , which support highest diversity at FADs and Free School sets (Figure 56)). For a long time, ecologists have suggested that more diverse communities are located in more stable ecosystems (Cusson et al. 2014). This means that the stability of the ecosystem determine not only the diversity of the area, but also the composition of species, something necessary to take into account for a sustainable management of the fishery. Results obtained in this work suggest that these stable areas are ideal habitats for marine species.

In general, diversity in equatorial divergences may directly be associated with the North Equatorial Countercurrent (intermediate-high speed of the current), intermediate concentrations of chlorophyll, high sea level anomalies and high depths of the thermocline for the by-catch species caught in FAD sets in the Atlantic and Pacific Oceans during Summer season (Chapter 2 and 3). In contrast, the Western Indian Ocean (Chapter 1) diversity seems to be positively related with the Somali Current during the Summer Monsoon.

Environmental limits with regard to factors such as temperature, chlorophyll or salinity tend to explain the distribution and movements of pelagic species (Arrizabalaga et al. 2015; Ballance et al. 2006; Martínez Rincón 2012). Results of this work revealed that sea surface temperature and chlorophyll (proxies of productivity) could be identified as main factors in terms of habitat preferences, with direct relation to upwelling's and warm regions. In the upwelling areas, temperatures are lower and chlorophyll concentrations determine the nutrients and the stability of the ecosystem. Indeed, productivity has always been relevant for the distribution of marine species, especially for large predators (Longhurst and Pauly 1987). In that sense, chlorophyll plays a key role in marine ecosystems as it is the source of the energy circulating through the trophic levels and, thus, it can be seen as a proxy of prey enrichment (Marsac 2013). SST clearly emerged as the strongest predictor of diversity, showing a positive relationship with warm regions in the Pacific (Chapter 2) and Indian Oceans (Chapter 1). Furthermore, SST is also a key parameters of the diversity differences between the Pacific, which has a marked annual sea surface temperature variability, and the Atlantic Ocean, marked by seasonal temperature variations (Picaut et al. 1984).

As it was showed in Chapter 2 and 3, the Pacific and Atlantic Ocean share similar oceanographic features. The environmental processes in the tropical Indian Ocean, in contrast, seem to play an important and different role in the diversity and the habitat of the by-catch communities as consequence of the strongest monsoon system on Earth. This area forms the major part of the largest warm pool on Earth, and its interaction with the atmosphere plays an important role in shaping climate on both regional and global scales (Schott et al. 2009). In addition, the lack of the equatorial upwelling (as consequence of the steady equatorial easterlies) and the position of the land mass in the north area, influence the oceanography and environment of this area (Tomczak and Godfrey 2003) and, therefore, diversity in the Indian Ocean is very seasonal in terms of time and space (Chapter 1).

On the other hand, studies performed on a regional scale indicated that predator species may aggregate in areas of high species diversity- usually called "hotspots"- which may represent important oceanic habitats and provide particular value for biodiversity conservation (Worm et al.

2005). Thus, at local scale, by-catch diversity revealed relationships with mesoscale features, such as fronts (Chapter 2), eddies (Chapter 1) and domes (Chapter 2 and 3) as it was described in this Thesis (Figure 56). The innate attraction of species to objects, which tend to drift and to accumulate within these structures, drives the species to distribute in those zones and increase the diversity of the area (Bakun 2010). These processes provide information about the most diverse areas exploited by tropical fisheries, and therefore, may help to define conservation strategies, such as the delimitation of essential fish habitats and marine protected areas in the open sea (Tew-Kai and Marsac 2009).

The upper zone of the pelagic environment (i.e., above the thermocline) in which many tuna and by-catch species live is considered to be relatively unproductive (Sund et al. 1981). The environment processes which increase productivity and therefore, aggregate preys will be the key factor determining the diversity and distribution of the predators (Sund et al. 1981). Such phenomena, called fronts (Chapter 2), usually are a mix of cold waters and warm waters, recognizable by strong gradients of temperature and or salinity, which produce the increase of productivity, attracting preys to these areas (Worm et al. 2005). Thus, prey can maintain their position in the front and, therefore, the increase of secondary producers attracts higher trophic level predators such as seabirds, tuna, turtles, billfish or whales; assembling a complete pelagic food web. In accordance with Polovina et al. (2001), who studied the travel of albacore tuna along a front across the North Pacific as migratory pattern, we suggest that by-catch species may use fronts in the Eastern Pacific Ocean (Chapter 2) to migrate. These regions are areas where they may gain energy by following currents (Olson and Backus 1985) or increasing their diversity. In addition, the front may acts as a barrier that prohibits movement of by-catch communities to less productive waters (Mugo et al. 2014).

Besides the fronts, the domes are mesoscale structures which concentrate high productivity for the animal habitat. They are characterized by upward displacement of isotherms in the thermocline layers down to depths of more than 300 m (Siedler et al. 1992). As discussed in this dissertation, the high diversity of the by-catch communities in FAD sets were explained by the Guinea Dome in the tropical North Atlantic (Chapter 3), the Angola Dome in the South Atlantic (Chapter 3) and the Costa Rica Dome (Chapter 3) in the North Pacific (Voituriez and Herbland 1982). These domes are caused by the interaction of the Pacific and Atlantic Equatorial Counter Currents and the coastline. The rotation of currents incites a cyclonic circulation which creates under the thermocline a permanent subsurface thermal domes (Voituriez 1981). When the wind and pressure conditions are favorable to rise the under currents to the surface, these deep

domes emerge at the level of the thermocline dome with high nutrients concentrations (Voituriez and Herbland 1982).

Organisms are not evenly distributed in the ocean; they are associated with specific habitats which can change along their life-history. Mesoscale features (and more specifically mesoscale eddies) are essential for a number of processes influencing dynamics of pelagic communities, from plankton to top predators (Tew-Kai and Marsac 2009). Cyclonic eddies have an upward circulation in their center that increases nutrient input in the euphotic zone and enhances primary production. As result, these structures not only play a role in supporting tuna and by-catch concentration, they also favor biodiversity hotspots (Tew-Kai and Marsac 2009).

Several authors observed the potential role of mesoscale eddies on the aggregation of top predators as seals, birds, and turtles (Tew-Kai and Marsac 2009). As discussed in Chapter 1, Mozambique Channel is known as an area of high eddies circulation which increases the diversity of the by-catch communities during the Winter Monsoon. The frontal structures that develop between eddies of opposite signs in this area are meeting points for a variety of communities, from preys which inhabit continental shelf to pelagic species living offshore (Tew-Kai and Marsac 2009). Thus, negative and positive sea level anomalies (SLA) found in Chapter 1 may be associated to larger and lower concentrations of chlorophyll as consequence of eddies circulation around this area (Kahru et al. 2007).

In the case of the Eastern Pacific Ocean (Chapter 2), the diversity of the by-catch communities in Free School sets seems to be related with the generation of oceanic eddies in the Gulfs of Tehuantepec, Papagayo and Panama as consequence of the wind jets which blow through mountain gaps of southern Mexico and Central America (this area is called "Panama Bight"). These eddies could transport nutrients from the continental margin, and thus, increasing diversity during March.

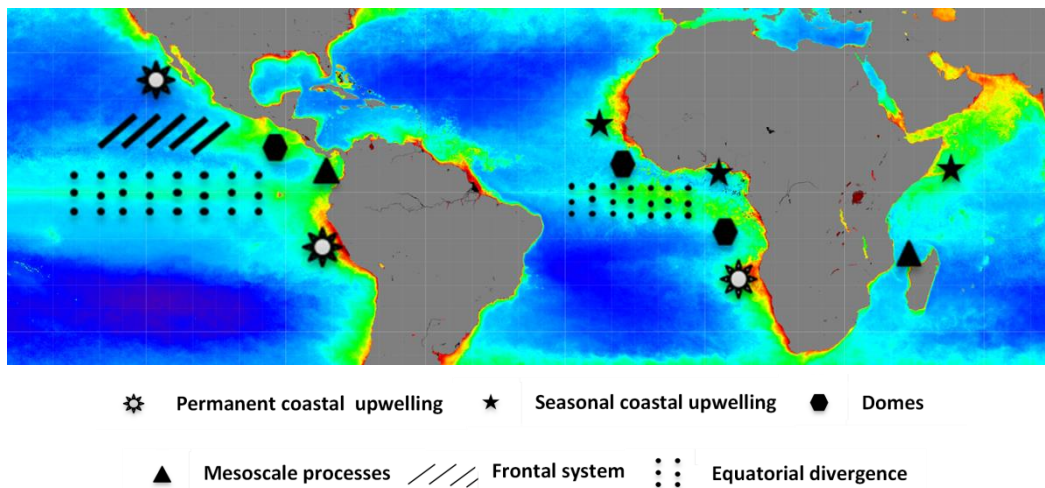


Figure 56. Main oceanographic processes involved in this study of diversity of the by-catch communities (in FAD and Free School sets) in the tropical tuna purse-seine fishery in the Western Indian, Eastern Atlantic and Eastern Pacific Ocean.

Habitat distribution models in by-catch communities in the tropical area

The four chapter of this PhD Thesis was focused on the applicability of the MaxEnt habitat suitability model for by-catch species at present and under the future climate change scenario, which will contribute to conservation of by-catch species. This model enabled us to gain knowledge on the habitat and distribution of two of the most caught by-catch species in the purse seine fishery with very different life strategies: silky shark (*Carcharhinus falciformis*), a vulnerable shark species (“k” strategy species) compared with rough triggerfish (*Canthidermis maculata*), a common by-catch species which have high reproductive rates (“r” strategy species). Our findings showed the role of temperature in the distribution of both species, and indicated that changes in ocean temperature, in conjunction with human impacts, will ultimately determine the global distribution of by-catch species.

It is not possible to manage a fishery if the habitat in which the species live and distribute is not well known. Therefore, the conservation measures should combine and integrate the species distribution considering their biological characteristics, but also the environment in which are embedded, for these measures to be more effective. According to the MaxEnt habitat distribution model developed in the Chapter 4 of this Thesis, the most suitable habitats for silky shark and rough triggerfish are the equatorial areas and some coastal upwelling areas such as Cape Lopez in the Atlantic, the Central America in the Pacific and the coast of Somalia in the Indian Ocean. These areas are related with the main fishing grounds as well as the most diverse areas which were found in the other three chapters of this dissertation.

The climate change impacts on marine biodiversity are likely to intensify in the future (Cheung et al. 2012). The intensity of these changes will vary geographically according to the conditions of each ocean and the sensitivity of the species as was observed in this Thesis. The Atlantic Ocean is the Ocean in which the climate change could affect the habitat distribution of both species to a greater degree (see S5. Figure 1 in Supplementary material-Discussion); therefore a greater effort is necessary to study the effects of the global warming on these species in this Ocean.

Climate change may impact the biological and environmental functioning of the marine ecosystem or food webs reducing the goods and services which humans obtain from the sea (Hoegh-Guldberg and Bruno 2010). Furthermore, it may also affect threatened species by influencing or reducing the efficacy of measures designed to protect them, such as marine protected areas (Jones et al. 2013). Thus, there is necessary to understand the effect of global warning in the marine environment to increase the efficiency of these measures to protect those species and their habitat for fishery effects under climate change. Although it is estimated that both species studied in the Chapter 4 will lose similar percentage of habitat in each ocean, silky shark with a lower reproductive potential could be less resilient to climate change than small body-size organisms (Lefort et al. 2015) and, therefore, it deserves more consideration for management. The PhD Thesis shows that this type of models can successfully applied to tropical tuna purse-seiner by-catch pelagic species and, therefore, it is recommended to also apply to other pelagic by-catch species such as manta rays or marine turtles. This in turn will contribute to broaden the fishery management framework including the potential impact of climate change on the most vulnerable species. The use of good practices onboard (Gilman 2011; Poisson et al. 2014) for increasing the probability of survival at release or the knowledge of the distribution and habitat of vulnerable species to avoid the interaction with them are among the best option to reduce their mortality.

We concluded that sea surface temperature is the limiting factor explaining the distribution of both by-catch species in each ocean similar to other studies which found that marine species distribution is directly correlated with their thermal tolerance limits (Sunday et al. 2012). Despite that these species live in a wide range of temperatures, they have preferences for the tropical waters and, therefore, the climate change could affect their natural distribution. Although this work obtained interesting results, other environmental variables, such as dissolved oxygen or variables associated with eddies and fronts, habitat models (presence/absence GAMs habitat models) as well as other climate change scenarios (A1B or B1) should also be investigated to better understand the habitat suitability of by-catch species for conservation purposes.

The use of habitat modelling to project future changes in species distribution is associated with an inevitable degree of uncertainty (Wenger et al. 2013). It should always be used with caution in an ecosystem management context: they must be interpreted as indications of possible future changes. However, despite this high level of uncertainty, habitat suitability models can be considered among best available tools to forecast the possible fishery effects under climate change on species distribution patterns and, hence, will contribute towards a practical application of ecosystem-based fishery management.

Limitations of the work

Accurately describing and understanding the processes that determine the diversity and distribution of organisms is a fundamental problem in ecology and depends on the objectives of the analysis and the spatial and temporal scale of available biological and environmental data.

Uncertainty may be produced by limitations in biological data, such as those derived from insufficient data or by spatial and temporal bias (Phillips et al. 2009). The metrics and models (diversity measures and GAMS) developed within the context of this PhD Thesis were in some extent subjected to limitations in sample data (such Chapter 1 and Chapter 3). In general, as some diversity indices are sensible to sample size, the application of mean diversity instead of the observed diversity helped us to standardize the sample and account for the different sample sizes between areas/Oceans. In the case of Generalized Additive Models, they didn't fit equally well (showed clear patterns) (Chapter 1 and Chapter 3) when compared with those models undertaken on a large dataset (Chapter 2). In addition, the low percentage of deviance explained in all the models could be explained by the following: 1) there are not enough sample data, 2) some other environment variables were not considered, 3) the interaction between some environment variables were not considered, 4) tuna vessels only fishing in determined areas.

As observer programs provide high amount of data, they can be useful tools for constructing habitat models. However, as showed in this PhD Thesis and increase coverage rate is necessary in the Indian and Atlantic Ocean to obtain more robust results (over all years and sampling seasons) as in the case of the Pacific Ocean. In any case, based on the similar results obtained about the species distribution models (the Log-normal model explained the structure of by-catch communities in FAD sets and the Zipf Mandelbrot in Free School) and GAMs (with respect to percentage of deviance explained), we can conclude that the structure and diversity of the pelagic communities in the tropical area is explained by similar variables (environmental variables such as

sea surface temperature or chlorophyll and temporal component) but by different oceanographic processes (upwellings, front systems, domes, etc...) depending on the ocean and type of fishing.

Other interesting point is the identification of the species by observers. Although individuals not identified to species level were successfully relocated among other groups, the improvement of the species identification through training courses and experience of observers decreases the percentage of unidentified taxa (called taxonomic uncertainty) along the studied period (i.e. species identification was more accurate in recent years). This in turn could have affected in some extent the results obtained (see S5. Figure 2 in Supplementary material-Discussion); however we are confident that it is not the case as similar species richness has been observed in the period studies and because we have pooled the information of all years in the study. Nevertheless, for the future it is recommended that routine observer training courses as well as identification guides are frequently updated to avoid taxonomic uncertainty and improve the accuracy of this type of studies.

As pointed out in the discussion of Chapter 1, 2 and 3, the inclusion of other oceanographic variables could have increased the variance explained by the models in relation to the diversity patterns of the by-catch communities. For example, the oxygen minimum concentration could be an interesting variable to include in future models because the areas with minimum oxygen concentrations (called OMZ) may limit the vertical distribution of the tuna and by-catch species (Karstensen et al. 2008). In our case, this information was not included in the GAMs because we did not have access to adequate fine-scale OMZ data for our study period and location. Marine species distribution and habitat models, therefore, must be flexible enough to incorporate a wide range of model structures and types of habitat/environmental variables if they are used to explain or predict species distributions (Redfern et al. 2006). Moreover, it should be take into account that in some cases the typical areas of fishing, and hence observed sampling are, were not always representative of the diversity patterns at ocean scale. For example, in the Pacific and Atlantic Oceans, different areas were selected to develop the GAMs based on the oceanography of the Ocean and, therefore, future works on biodiversity should be consider main oceanographic processes .

The habitat modelling method (Chapter 4) allowed in an easy way to obtain essential information with few environmental variables about pelagic species. However, the gained experience leads us to discuss several aspects which must be considered before applying future habitat modelling using this dataset. For example, the limitation and the selection of the appropriate environmental data could difficult the achievement of reasonable and realistic response curves as well as to explain the species distributions based on these variables. The complexity of marine ecosystem,

together with the incomplete knowledge about the processes driving the species response to environmental factors may present important limitations to predictive modelling. However, in our case the selection of the environmental variables in Chapter 4 was based in the main oceanographic characteristics of each ocean and the response curves of species distribution explained correctly the high mobility character of the species and their relationship with the upwelling and surface current systems. Secondly, the lack of “real” absence data was the most important factor discussed and considered in Chapter 4. As it is recognized that habitat models with presence and absence data performs better than the only-presence habitat models, we decided to generate and include pseudo-absences data to evaluate the models. Within the numerous ways of addressing the problem of generate pseudo-absences (Barbet-Massin et al. 2012; Fourcade et al. 2014; Sequeira et al. 2012), we solved this with the generation of the same number of pseudo-absences (randomly) as presences in places where presences were not observed over the sampled area. This allowed solving the sampling bias related to the lack of real absences and, thus, the models were constructed and evaluated in a more robust way.

Management of by-catch diversity

Human exploitation of living marine resources definitely produces a deep impact on marine species, communities, and ecosystems. The spatial management of human activities in the marine environment with the creation of marine protected areas or temporal closures has been applied as an ecosystem management tool to control human threats (Kaplan et al. 2010).

The potential benefits of using spatial approaches for the management of pelagic ecosystems and the fisheries that depend on them have received significant attention recently. In that sense, offshore closures differ greatly from coastal closures, where most of the marine spatial management efforts have been focused. The problem is that pelagic ecosystems are generally characterized by larger spatial scales, greater mobility of the species and a limited knowledge of ecosystem functioning and diversity (Cullis-Suzuki and Pauly 2010). However, as by-catch occurs in all marine environments and has gained particular importance in pelagic fisheries (Lewison and Crowder 2007), the spatial management of these species and their habitat has become of public interest.

This Thesis applied diversity measures (Chapter 1, 2 and 3) and habitat modelling (Chapter 4) as a research method to better understand the marine ecosystem and related human impacts, and based on the results, explores the possibility of consider the areas with higher diversity as areas of special interest for future planning of fisheries management.

The time-area closures (the closure of a specific fishing ground, or part of it, for a specific period of time) are widely used in fisheries management to avoid overfishing and marine biodiversity loss. Closing an area to fishing allows increasing the habitat structure, and therefore, the productivity, size and community composition of fishes (Link 2010). It can also be used to reduce by-catch or protect vulnerable species (Dunn et al. 2011). When a closure is being implemented with the objective to mitigate the by-catch, the spatial overlap between the by-catch and target species and the relation of the by-catch with a specific oceanographic variable need to be considered (Dunn et al. 2011). These fishery closures may be dynamic (i.e. generated by an event), seasonal or permanent. However, some closures could be less effective when established in areas where there is no clear seasonal pattern or may have the contrary effect when increasing effort in adjacent areas open to fishing (Bromhead et al. 2003).

FAD fishing are relatively homogeneous over space compared with those for free-swimming school fishing and therefore, the majority of measures have been applied in this fishing mode. The closures applied on FADs-based purse seine fisheries have been considered by the international tuna commissions the most effective option for reducing by-catch and have been widely adopted in the Indian, Atlantic and Eastern Pacific Oceans (Bromhead et al. 2003). These management planning's require the presence of observers on board all fishing vessels to ensure that purse seine vessels set only on free schools and not on FADs (Bromhead et al. 2003).

Marine protected areas (MPA), on the other hand, could be also considered as a key tool for the successful application of an Ecosystem Approach To Fishery Management (EAFM) and an essential element on sustainable fisheries policy; which tries to preserve biodiversity and maximize fishery yields (Abbott and Haynie 2012). The location and size of MPA are crucial for avoiding the impact on by-catch as consequence of the reallocation of fishing effort outside the protected area or for evaluating the MPA effectiveness facing oceanographic variability across space (Torres-Irineo et al. 2011). Although it has been postulated that marine reserves should protect more than 20% of the habitat to enhance fisheries (Sala et al. 2002), there is not still agreement about how much habitat should be protected to ensure biodiversity (Sala et al. 2002). In any case, MPAs, as temporal-closures, should be selected on the basis of biological, oceanographic, physiographic, socio-cultural, political and economic criteria (Dunn 2014; Zacharias et al. 2006).

The spatio-temporal associations between fishing effort, by-catch species and oceanographic features are essential to identify critical pelagic areas that can be delimited and managed using static or dynamic fishery management tools (e.g. closures) (Dunn 2014). Temporal-closures or marine protected areas should have into account the environment and high diversity areas for by-catch communities in the tropical area. In this Thesis, the most diverse areas explained above (in

the section about the habitat preferences) could be considered as potential biodiversity hotspots to manage by-catch communities in the tropical area. Concretely, and based on the results from the Chapter 4, some vulnerable species, such as silky shark, could be protected in areas of high habitat suitability and in relation with the main oceanographic characteristics which affects their distribution. For example, the Somali area in the Indian Ocean (Chapter 1 and 4) and the area situated between 0°N and 10°N in the Eastern Pacific Ocean (Chapter 2), within the boundaries of the North Equatorial Counter Current, could be areas of high ecological interest in accordance with previous works (Amandè et al. 2011b; Watson 2007).

The integration of areas of high diversity with areas of species ecological interest (for example, nursery grounds, reproduction, etc) is key for the conservation of not only the species, but also their habitat. In addition, the habitat models (Chapter 4) can be used to regulate fishing based on the probability of occurrence in an area in which the by-catch species is commonly found, and thus, help to design and develop marine conservation strategies and monitoring programmes towards the most sensitive regions and species to account for the impact of climate change (Cheung et al. 2012). As the relationships of habitat with the oceanographic features of each ocean have rarely been integrated into actual management planning (Dunn et al. 2011), this Thesis propose the incorporation of this type of models, which allows to increase the knowledge of the habitat of these species, in future management plans of those species.

As demonstrated in Chapter 1, 2 and 3, the structure and composition of by-catch species along the tropical area seem to be explained by the same factors. However, the diversity and habitat preferences depend on the environment characteristics specific of each ocean, and therefore, the management measures should be also be different, depending on the seasonal or annual variations, the environmental conditions, the most vulnerable species of each ocean and the fishing strategy. In summary, it is clear that the application of a single management option alone will not solve the problems in any region, and therefore, the combination of different management measures will be more appropriate to assure the sustainability of marine resources in different regions (Bromhead et al. 2003).

Finally, we consider necessary to continue studying the variability induced by climate change and other global processes, such as the ENSO phenomenon. These processes can affect the oceanographic conditions, and thereby species distribution ranges, migration patterns, and resource availability (Gray 1997); making the effect of fishing or any other human activity more pronounced.

Future perspectives

Achieve sustainable fisheries is only possible when yield of target species is maximized at the same level that mortality of vulnerable and non-target species is minimized.

Thus, the monitoring programs which collect by-catch information must continue and improve to provide information of enough quality which will contribute to integrate all the components of the ecosystem in the analysis towards the common objective of a sustainable Ecosystem Approach for Fishery Management.

Thus, we believe that increasing the coverage on purse seine fleets oceanwide as well as of other fleets (for the European PS the 100% of coverage is already in place since 2014) will improve the quality of data and the analyses. Moreover, we recommend performing similar studies, as done with a lower coverage, with 100% coverage to compare the results obtained with different level of coverage. This will allow validating the results and the methodologies applied in this PdD Thesis but also it will allow identifying the differences and biases caused due to sample size and coverage rate.

It is also important to coordinate the different observer programs between different organizations on issues such as harmonization of data or data sharing to compare studies among regions/oceans and to gain general patterns across oceans/regions/fisheries. Moreover, the implementation and success of any measures to reduce the by-catch will be more easily obtained if all stakeholders, from the scientists, industry, managers and the society, are involved in the discussion and decision taken process (e.g. co-management). Moreover, we promote the use of new technologies such as the electronic monitoring because it could contribute to complement the work of the observer helping the correct identification of species. It also allows obtaining a larger set of data in fleets (longling, gillnets) that cannot carry out human observer.

The ideal for biodiversity studies would have to get 100% of sampling coverage which will allow developing temporal indices and models, which in turn would be contribute to evaluate, compare and predict changes by year, season and/Ocean. Moreover, it would be interesting to use fishery dependent and independent data on future biodiversity studies and to include other levels of biodiversity, such as genetic and functional diversity. This future work will complement current approaches and knowledge about by-catch communities and pelagic diversity providing a more comprehensive understanding of the this issue for the application of Ecosystem Approach to Fishery Management.

CONCLUSIONS

- Diversity of the the by-catch communities from the tropical tuna purse-seine fishery depends directly on the habitat, area, time of year and fishing mode.
- Diversity of the by-catch communities in FAD sets is higher than in Free School sets in the Indian, the Pacific and the Atlantic Oceans, based on species richness, evenness and Shannon diversity indices. However, both types of fishing must be considered as good indicators for describing the variability of diversity in space and time and to identify priority areas for conservation since the integration of both fishing modes provides more complete and variable information than separately.
- The total number of possible by-catch species caught in purse-seine fisheries in the tropical area is directly related with the sample size and coverage rate, which is determinant for obtain a good inventory of the population prior to any accurate biodiversity study.
- The Pacific, Indian and Atlantic Oceans represent three different cases for studying the biodiversity of the bycatch communities: the Pacific Ocean represents the best scenario to carry out biodiversity studies due to 100% of observer coverage rate. The Indian Ocean represents an intermediate scenario with lower sample size and coverage rate but with well defined biodiversity patterns as consequence of the monsoon system. Finally, the Atlantic Ocean is the most difficult scenario due to the low coverage rate and the complexity of the oceanographic processes of this area.
- The fishing mode and the environment influence the species composition of the by-catch communities. Beta diversity showed similarity in species composition of the by-catch communities among upwelling systems in FAD sets within a particular Ocean. Concretely, similar species composition was found between equatorial areas in the Pacific and the Atlantic Oceans, and between the Somali upwelling and the circulation of the Mozambique Channel in the Indian Ocean. In the case of the Free School sets, species composition showed variability among oceans and areas.
- Diversity of the by-catch communities from the tropical tuna purse seine fishery is directly related with the habitat in which the species live. At a global scale, by-catch communities are primarily associated with surface currents dynamics and upwelling systems. Diversity in equatorial

divergences in the Pacific and Atlantic Oceans is directly associated with the North Equatorial Countercurrent. Furthermore, the upwelling of the Gulfs of Tehuantepec and Panama, the upwelling of Gulf of Guinea, the upwelling on the Somali coast and the equatorial upwellings in the Pacific and the Atlantic Ocean support highest diversity of by-catch communities in FAD and Free School sets. These stable areas seems to be the ideal habitat for pelagic species.

- At a local scale, by-catch communities may aggregate at distinct diversity hotspots in relation with front systems, convergence zones, domes and eddies in the Indian, Pacific and Atlantic Oceans. These dynamic ocean processes promote biological productivity and structure marine ecosystems by aggregating and dispersing nutrients and organisms. For pelagic species, interactions of differing water masses generally support higher biological diversity than individual water masses.
- Diversity of the by-catch communities in the equatorial area in the Eastern Pacific Ocean is directly related with ENSO phenomenon in FAD sets. The most important events of El Niño and La Niña matched perfectly to the highest and lowest values of by-catch diversity.
- The MaxEnt habitat distribution model provides a good estimation of the pelagic distribution of by-catch species. The potential habitat distribution for *Carcharhinus falciformis* and *Canthidermis maculata* in the Atlantic, Indian and Pacific Ocean is located close to equatorial and coastal upwelling areas, and mainly associated with sea surface temperature.
- Climate change impacts the distribution of *Carcharhinus falciformis* and *Canthidermis maculata* in accordance with the particular oceanographic conditions of each ocean. In some regions such as Somalia, the south Atlantic equatorial band or Peru's coastal upwelling areas, these species could lose potential habitat whereas in Benguela and Central America upwelling regions they could gain suitable habitat as consequence of global warming.
- Under the A2 climate change scenario, the largest change in habitat suitability between present and future is observed in the Atlantic Ocean (around 16% of habitat suitability change of *Carcharhinus falciformis* and *Canthidermis maculata*) whereas the change was less in the Pacific (around 10% and 8%) and Indian Oceans (around 3% and 2 %).
- This work has improved our understanding of structure, diversity and the habitat preferences of the by-catch communities from the tropical tuna purse-seine fishery in the Indian, Pacific and Atlantic Oceans. These results could be considered as a step for the future implementation of the

EAFM to manage the pelagic ecosystem in a holistic manner, leaving behind the idea of the management of by-catch single species and towards the integration of biodiversity with the ecosystem.

THESIS

Research on the structure, diversity and the habitat preferences of the by-catch communities from the tropical tuna purse-seine fishery in the Indian, Pacific and Atlantic Oceans has contributed to increase the knowledge of the pelagic ecosystem towards the application of an ecosystem approach to fishery management, and to understand the key aspects involved on the change of habitat distribution of some by-catch species as response to climate change.

SUPPLEMENTARY MATERIAL

S1. Table 1 List of species included in the study.

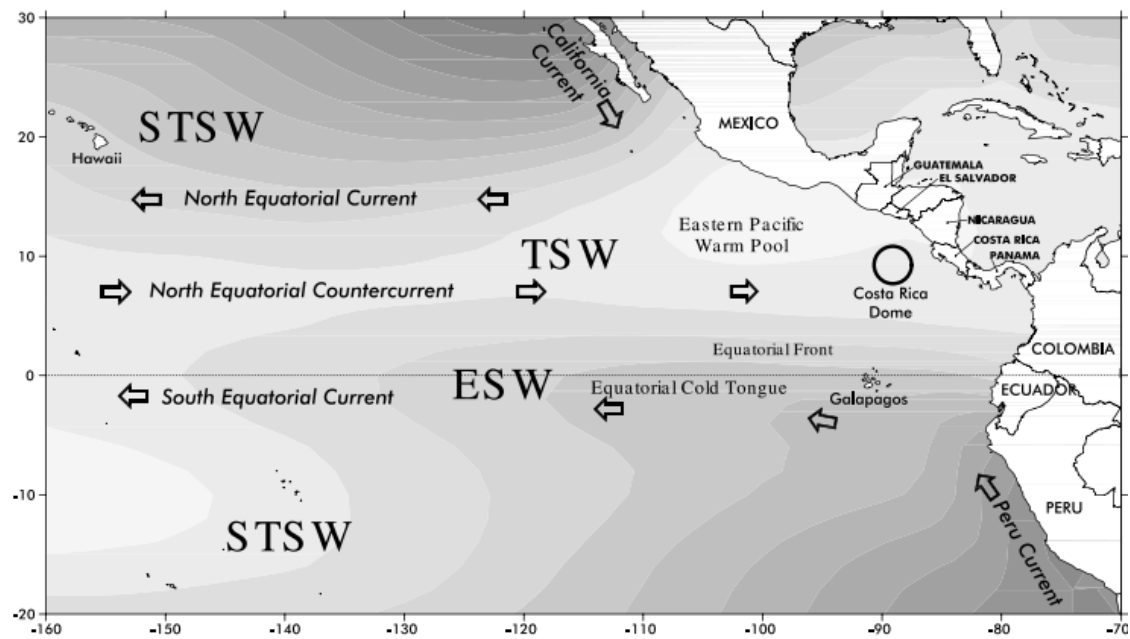
Species	Genus	Family	Order
<i>Abalistes stellatus</i>	Abalistes	Balistidae	Tetraodontiformes
<i>Ablennes hians</i>	Ablennes	Belonidae	Beloniformes
<i>Abudefduf vaigiensis</i>	Abudefduf	Pomacentridae	Perciformes
<i>Acanthocybium solandri</i>	Acanthocybium	Scombridae	Perciformes
<i>Alopias vulpinus</i>	Alopias	Alopiidae	Lamniformes
<i>Aluterus monoceros</i>	Aluterus	Monacanthidae	Tetraodontiformes
<i>Aluterus scriptus</i>	Aluterus	Monacanthidae	Tetraodontiformes
<i>Balaenoptera physalus</i>	Balaenoptera	Balaenopteridae	Cetacea
<i>Balistes carolinensis</i>	Balistes	Balistidae	Tetraodontiformes
<i>Balistes punctatus</i>	Balistes	Balistidae	Tetraodontiformes
<i>Bramidae</i>	-	Bramidae	Perciformes
<i>Canthidermis maculata</i>	Canthidermis	Balistidae	Tetraodontiformes
<i>Carangoides orthogrammus</i>	Carangoides	Carangidae	Perciformes
<i>Caranx sexfasciatus</i>	Caranx	Carangidae	Perciformes
<i>Carcharhinus falciformis</i>	Carcharhinus	Carcharhinidae	Carcharhiniformes
<i>Carcharhinus longimanus</i>	Carcharhinus	Carcharhinidae	Carcharhiniformes
<i>Carcharhinus obscurus</i>	Carcharhinus	Carcharhinidae	Carcharhiniformes
<i>Caretta caretta</i>	Caretta	Cheloniidae	Testudines
<i>Chelonia mydas</i>	Chelonia	Cheloniidae	Testudines
<i>Coryphaena equiselis</i>	Coryphaena	Coryphaenidae	Perciformes
<i>Coryphaena hippurus</i>	Coryphaena	Coryphaenidae	Perciformes
<i>Cubiceps capensis</i>	Cubiceps	Nomeidae	Perciformes
<i>Pteroplatytrygon violacea</i>	Dasyatis	Dasyatidae	Myliobatiformes
<i>Decapterus macarellus</i>	Decapterus	Carangidae	Perciformes
<i>Diodon hystrix</i>	Diodon	Diodontidae	Tetraodontiformes
<i>Elagatis bipinnulata</i>	Elagatis	Carangidae	Perciformes
<i>Eretmochelys imbricata</i>	Eretmochelys	Cheloniidae	Testudines
<i>Etmopterus sp.</i>	Etmopterus	Dalatiidae	Squaliformes
<i>Exocoetidae</i>	-	Exocoetidae	Beloniformes
<i>Galeocerdo cuvier</i>	Galeocerdo	Carcharhinidae	Carcharhiniformes
<i>Istiophorus platypterus</i>	Istiophorus	Istiophoridae	Perciformes
<i>Isurus oxyrinchus</i>	Isurus	Lamnidae	Lamniformes
<i>Kyphosus cinerascens</i>	Kyphosus	Kyphosidae	Perciformes
<i>Kyphosus sectatrix</i>	Kyphosus	Kyphosidae	Perciformes
<i>Kyphosus vaigiensis</i>	Kyphosus	Kyphosidae	Perciformes
<i>Lagocephalus lagocephalus</i>	Lagocephalus	Tetraodontidae	Tetraodontiformes
<i>Lampris guttatus</i>	Lampris	Lampridae	Lampriformes
<i>Lepidochelys kempii</i>	Lepidochelys	Cheloniidae	Testudines
<i>Lepidochelys olivacea</i>	Lepidochelys	Cheloniidae	Testudines

<i>Lobotes surinamensis</i>	Lobotes	Lobotidae	Perciformes
<i>Makaira indica</i>	Makaira	Istiophoridae	Perciformes
<i>Makaira mazara</i>	Makaira	Istiophoridae	Perciformes
<i>Makaira nigricans</i>	Makaira	Istiophoridae	Perciformes
<i>Manta birostris</i>	Manta	Myliobatidae	Myliobatiformes
<i>Masturus lanceolatus</i>	Masturus	Molidae	Tetraodontiformes
<i>Megachasma pelagios</i>	Megachasma	Megachasmidae	Lamniformes
<i>Mobula coilloti</i>	Mobula	Myliobatidae	Myliobatiformes
<i>Mobula japonica (rancureli)</i>	Mobula	Myliobatidae	Myliobatiformes
<i>Mobula mobular</i>	Mobula	Myliobatidae	Myliobatiformes
<i>Mobula tarapacana</i>	Mobula	Myliobatidae	Myliobatiformes
<i>Mola mola</i>	Mola	Molidae	Tetraodontiformes
<i>Myliobatis Aquila</i>	Myliobatis	Myliobatidae	Myliobatiformes
<i>Naucrates ductor</i>	Naucrates	Carangidae	Perciformes
<i>Phtheichthys lineatus</i>	Phtheichthys	Echeneidae	Perciformes
<i>Platax teira</i>	Platax	Ephippidae	Perciformes
<i>Prionace glauca</i>	Prionace	Carcharhinidae	Carcharhiniformes
<i>Pseudorca crassidens</i>	Pseudorca	Delphinidae	Cetacea
<i>Remora australis</i>	Remora	Echeneidae	Perciformes
<i>Remora osteochir</i>	Remora	Echeneidae	Perciformes
<i>Remora remora</i>	Remora	Echeneidae	Perciformes
<i>Remorina albescens</i>	Remorina	Echeneidae	Perciformes
<i>Rhincodon typus</i>	Rhincodon	Rhincodontidae	Orectolobiformes
<i>Ruvettus pretiosus</i>	Ruvettus	Gempylidae	Perciformes
<i>Scomberomorus tritor</i>	Scomberomorus	Scombridae	Perciformes
<i>Seriola rivoliana</i>	Seriola	Carangidae	Perciformes
<i>Serranidae</i>	-	Serranidae	Perciformes
<i>Sphyaena barracuda</i>	Sphyaena	Sphyaenidae	Perciformes
<i>Sphyrna lewini</i>	Sphyrna	Sphyrnidae	Carcharhiniformes
<i>Sphyrna zygaena</i>	Sphyrna	Sphyrnidae	Carcharhiniformes
<i>Tetrapturus angustirostris</i>	Tetrapturus	Istiophoridae	Perciformes
<i>Tetrapturus audax</i>	Tetrapturus	Istiophoridae	Perciformes
<i>Tylosurus crocodilus</i>	Tylosurus	Belonidae	Beloniformes
<i>Uraspis helvola</i>	Uraspis	Carangidae	Perciformes
<i>Uraspis secunda</i>	Uraspis	Carangidae	Perciformes
<i>Uraspis uraspis</i>	Uraspis	Carangidae	Perciformes
<i>Xiphias gladius</i>	Xiphias	Xiphiidae	Perciformes
<i>Zanclus cornutus</i>	Zanclus	Zanclidae	Perciformes

S1. Table 2 AIC results from species abundance models.

Species Distribution Models	FAD	Free School
Null	1326843.5	53490.8
Preemption	90451.8	13910.92
Lognormal	86177.1	1610.78
Zipf	135639.5	1155.44
Mandelbrot	Na	1157.44

S2. Figure 1 Schematic diagram of Surface water masses and currents in the eastern tropical Pacific Ocean (Source: from Fiedler and Talley 2006, with permission of the author).



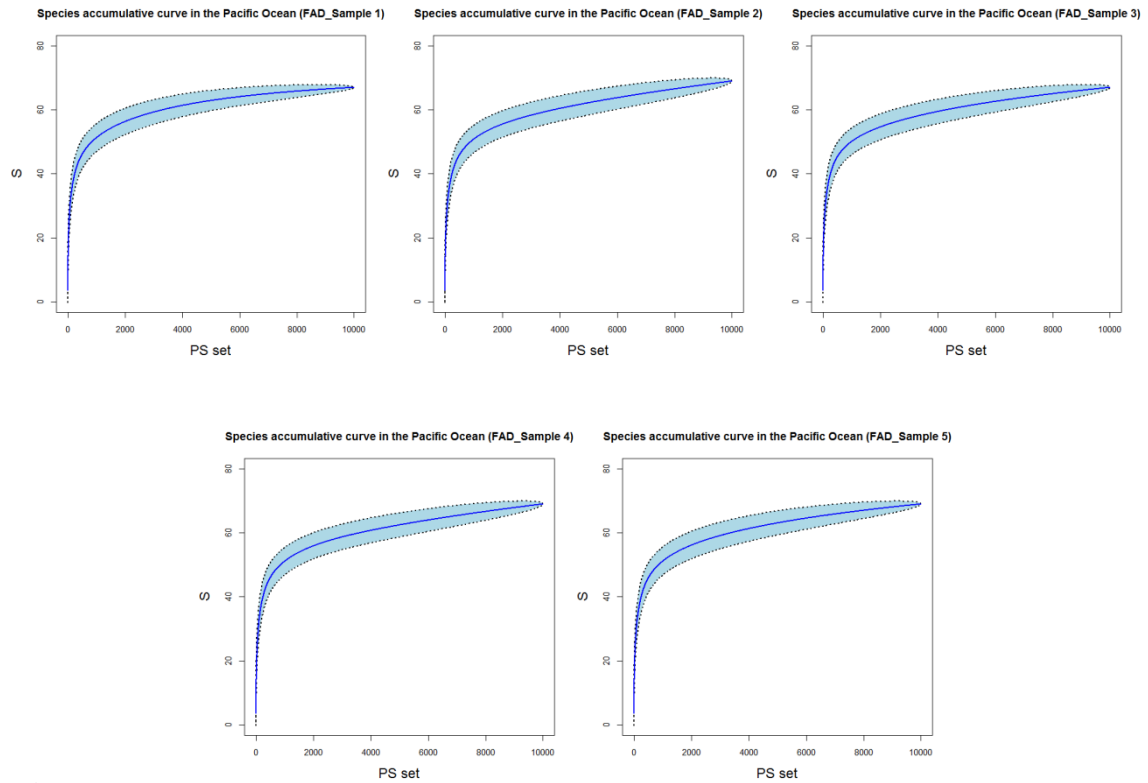
S2. Table 1 List of species included in the study.

Species	Genus	Family	Order
<i>Ablennes hians</i>	Ablennes	Belonidae	Beloniformes
<i>Acanthocybium solandri</i>	Acanthocybium	Scombridae	Perciformes
<i>Alopias pelagicus</i>	Alopias	Alopiidae	Lamniformes
<i>Alopias superciliosus</i>	Alopias	Alopiidae	Lamniformes
<i>Alopias vulpinus</i>	Alopias	Alopiidae	Lamniformes
<i>Aluterus monoceros</i>	Aluterus	Monacanthidae	Tetraodontiformes
<i>Aluterus scriptus</i>	Aluterus	Monacanthidae	Tetraodontiformes
<i>Balistes polylepis</i>	Balistes	Balistidae	Tetraodontiformes
<i>Belonidae</i>	Belonidae	Belonidae	Tetraodontiformes
<i>Canthidermis maculata</i>	Canthidermis	Balistidae	Tetraodontiformes
<i>Carangoides orthogrammus</i>	Carangoides	Carangidae	Perciformes
<i>Caranx caballus</i>	Caranx	Carangidae	Perciformes
<i>Caranx caninus</i>	Caranx	Carangidae	Perciformes
<i>Caranx sexfasciatus</i>	Caranx	Carangidae	Perciformes
<i>Carcharhinus altimus</i>	Carcharhinus	Carcharhinidae	Carcharhiniformes
<i>Carcharhinus brachyurus</i>	Carcharhinus	Carcharhinidae	Carcharhiniformes
<i>Carcharhinus falciformis</i>	Carcharhinus	Carcharhinidae	Carcharhiniformes
<i>Carcharhinus galapagensis</i>	Carcharhinus	Carcharhinidae	Carcharhiniformes
<i>Carcharhinus leucas</i>	Carcharhinus	Carcharhinidae	Carcharhiniformes
<i>Carcharhinus limbatus</i>	Carcharhinus	Carcharhinidae	Carcharhiniformes
<i>Carcharhinus longimanus</i>	Carcharhinus	Carcharhinidae	Carcharhiniformes
<i>Carcharhinus obscurus</i>	Carcharhinus	Carcharhinidae	Carcharhiniformes
<i>Carcharhinus plumbeus</i>	Carcharhinus	Carcharhinidae	Carcharhiniformes
<i>Carcharhinus porosus</i>	Carcharhinus	Carcharhinidae	Carcharhiniformes
<i>Carcharodon carcharias</i>	Carcharodon	Lamnidae	Lamniformes
<i>Caretta caretta</i>	Caretta	Cheloniidae	Testudines
<i>Cetorhinus maximus</i>	Cetorhinus	Cetorhinidae	Lamniformes
<i>Chelonia mydas mydas, C. m. agassizii</i>	Chelonia	Cheloniidae	Testudines
<i>Coryphaena equiselis</i>	Coryphaena	Coryphaenidae	Perciformes
<i>Coryphaena hippurus</i>	Coryphaena	Coryphaenidae	Perciformes
<i>Cubiceps capensis</i>	Cubiceps	Nomeidae	Perciformes
<i>Decapterus macarellus</i>	Decapterus	Carangidae	Perciformes
<i>Dermochelys coriacea</i>	Dermochelys	Dermochelyidae	Testudines
<i>Diodontidae</i>	Diodontidae	Diodontidae	Tetraodontiformes
<i>Elagatis bipinnulata</i>	Elagatis	Carangidae	Perciformes
<i>Eretmochelys imbricata</i>	Eretmochelys	Cheloniidae	Testudines
<i>Exocoetus volitans</i>	Exocoetus	Exocoetidae	Beloniformes
<i>Galeocerdo cuvier</i>	Galeocerdo	Carcharhinidae	Carcharhiniformes
<i>Istiophorus platypterus</i>	Istiophorus	Istiophoridae	Perciformes
<i>Isurus oxyrinchus</i>	Isurus	Lamnidae	Lamniformes
<i>Kajikia audax</i>	Kajikia	Istiophoridae	Perciformes
<i>Kyphosus analogus</i>	Kyphosus	Kyphosidae	Perciformes
<i>Kyphosus elegans</i>	Kyphosus	Kyphosidae	Perciformes

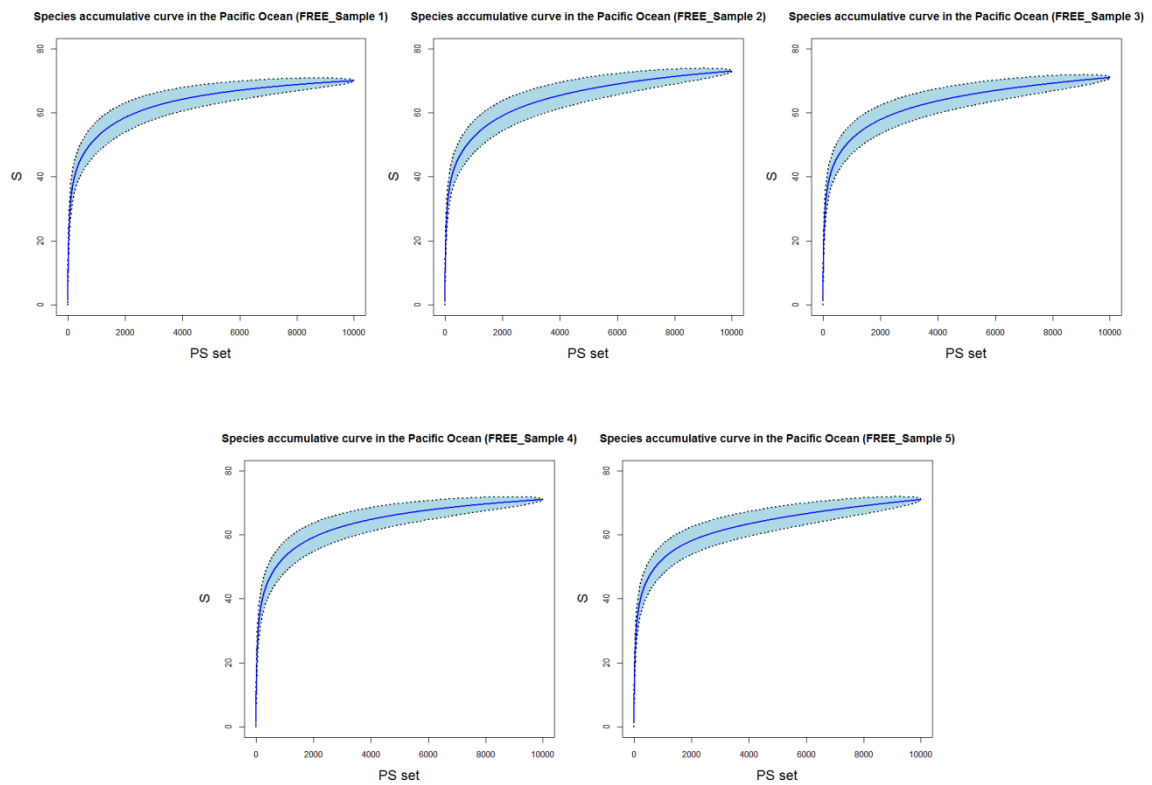
<i>Lepidochelys olivacea</i>	Lepidochelys	Cheloniidae	Testudines
<i>Lobotes surinamensis</i>	Lobotes	Lobotidae	Perciformes
<i>Makaira indica</i>	Makaira	Istiophoridae	Perciformes
<i>Makaira nigricans</i>	Makaira	Istiophoridae	Perciformes
<i>Manta birostris</i>	Manta	Myliobatidae	Myliobatiformes
<i>Masturus lanceolatus</i>	Masturus	Molidae	Tetraodontiformes
<i>Mobula japonica</i>	Mobula	Myliobatidae	Myliobatiformes
<i>Mobula munkiana</i>	Mobula	Myliobatidae	Myliobatiformes
<i>Mobula tarapacana</i>	Mobula	Myliobatidae	Myliobatiformes
<i>Mobula thurstoni</i>	Mobula	Myliobatidae	Myliobatiformes
<i>Mola mola</i>	Mola	Molidae	Tetraodontiformes
Myliobatidae	Myliobatidae	Myliobatidae	Myliobatiformes
<i>Nasolamia velox</i>	Nasolamia	Carcharhinidae	Carcharhiniformes
<i>Naucrates ductor</i>	Naucrates	Carangidae	Perciformes
<i>Negaprion brevirostris</i>	Negaprion	Carcharhinidae	Carcharhiniformes
<i>Prionace glauca</i>	Prionace	Carcharhinidae	Carcharhiniformes
<i>Pteroplatytrygon violacea</i>	Pteroplatytrygon	Dasyatidae	Myliobatiformes
<i>Ranzania laevis</i>	Ranzania	Molidae	Tetraodontiformes
<i>Remora osteochir</i>	Remora	Echeneidae	Perciformes
<i>Remora remora</i>	Remora	Echeneidae	Perciformes
<i>Rhincodon typus</i>	Rhincodon	Rhincodontidae	Orectolobiformes
<i>Rhinoptera steindachneri</i>	Rhinoptera	Myliobatidae	Myliobatiformes
<i>Rhizoprionodon longurio</i>	Rhizoprionodon	Carcharhinidae	Carcharhiniformes
<i>Sectator ocyurus</i>	Sectator	Kyphosidae	Perciformes
<i>Selar crumenophthalmus</i>	Selar	Carangidae	Perciformes
<i>Seriola lalandi</i>	Seriola	Carangidae	Perciformes
<i>Seriola peruana</i>	Seriola	Carangidae	Perciformes
<i>Seriola rivoliana</i>	Seriola	Carangidae	Perciformes
<i>Sphyrna spp.</i>	Sphyrna	Sphyrnidae	Carcharhiniformes
<i>Sphyrna corona</i>	Sphyrna	Sphyrnidae	Carcharhiniformes
<i>Sphyrna lewini</i>	Sphyrna	Sphyrnidae	Carcharhiniformes
<i>Sphyrna media</i>	Sphyrna	Sphyrnidae	Carcharhiniformes
<i>Sphyrna mokarran</i>	Sphyrna	Sphyrnidae	Carcharhiniformes
<i>Sphyrna tiburo</i>	Sphyrna	Sphyrnidae	Carcharhiniformes
<i>Sphyrna zygaena</i>	Sphyrna	Sphyrnidae	Carcharhiniformes
<i>Taractes rubescens</i>	Taractes	Bramidae	Perciformes
<i>Tetrapturus angustirostris</i>	Tetrapturus	Istiophoridae	Perciformes
<i>Trachurus murphyi</i>	Trachurus	Carangidae	Perciformes
<i>Uraspis helwola</i>	Uraspis	Carangidae	Perciformes
<i>Xiphias gladius</i>	Xiphias	Xiphiidae	Perciformes

S2. **Figure 2** Simulation to compare the same number of sets in a) FAD and b) School fishing mode and estimate the total number of species.

a)



b)



S2. Table 2 AIC (Akaike's Information Criterion) for each model to fit log-rank abundance curves in Fish Aggregating Device (FAD) and Free School sets.

Species Distribution Models	FAD	Free School
Null	113610924	6035259
Preemption	81116950	4354447
Lognormal	3685632	250482
Zipf	10608520	166424
Mandelbrot	NA	NA

S2. Table 3 Beta diversity: Bray-Curtis similarity index between areas in FAD and School sets.

FAD				
Areas	1	2	3	4
Area 2	0.51	-		
Area 3	0.63	0.23	-	
Area 4	0.59	0.23	0.13	-
Area 5	0.50	0.23	0.26	0.18
School				
Areas	Area 1	Area 2	Area 3	Area 4
Area 2	0.30	-		
Area 3	0.29	0.22	-	
Area 4	0.31	0.29	0.20	-
Area 5	0.29	0.39	0.37	0.33

S2. Table 4 Percentage deviation explained by the model for each variable in FAD and School sets.

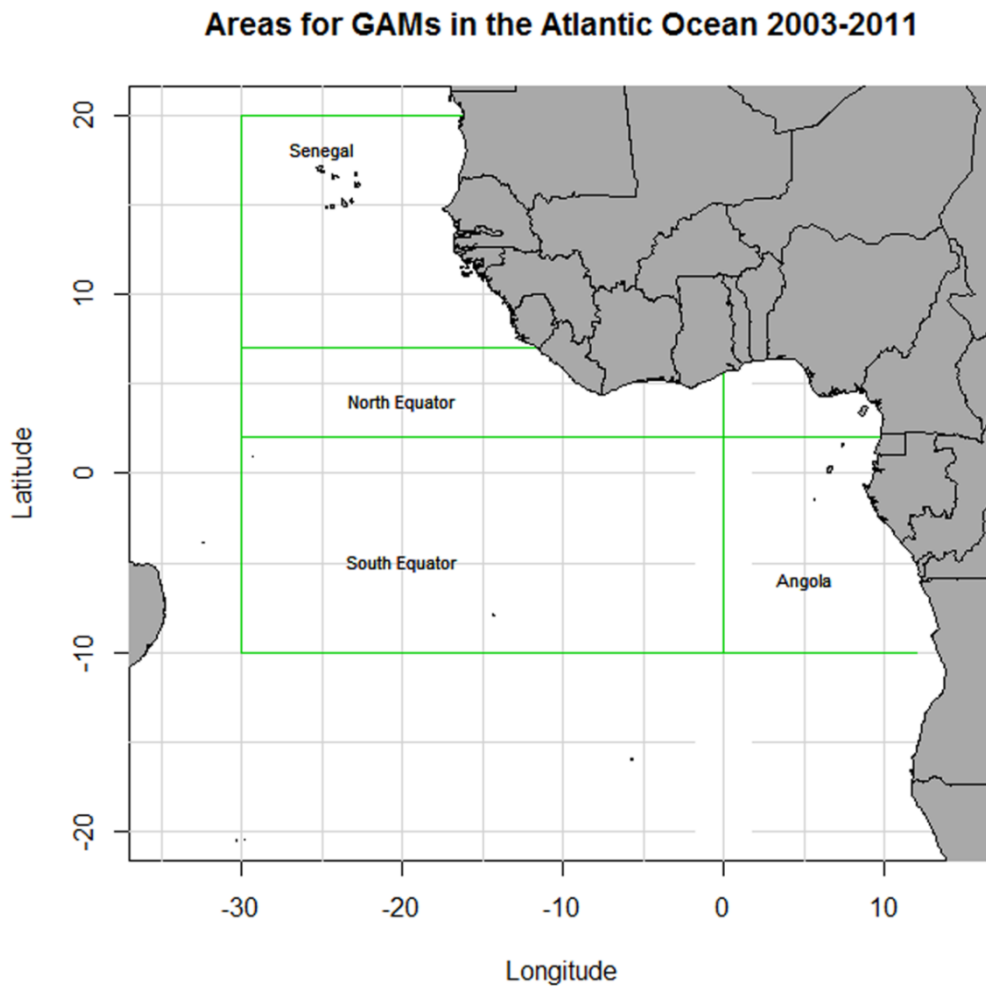
Variables	FAD		School				
	% (Richness)	Variables	% (Shannon)	Variables	% (Richness)	Variables	% (Shannon)
Lat , Long	19.6	Lat, Long	17.8	Lat, Long	11.7	Lat, Long	9.79
Month	6.62	Month	5.33	Month	3.25	Month	3.25
SST	8.08	SST	6.86	SST	1.74	SST	1.87
Cl	3.72	Cl	3.53	Cl	2.44	Cl	2.03
WT	1.63	WT	1.52	WG	0.93	-	-
Sal20	7.11	Sal20	4.55	Therm.Grad	0.88	-	-
Therm.Prof	3.43	Therm.Prof	3.96	-	-	-	-

S3. Table 1 List of species included in the study.

Species	Genus	Family	Order
<i>Ablennes hians</i>	Ablennes	Belonidae	Beloniformes
<i>Acanthocybium solandri</i>	Acanthocybium	Scombridae	Perciformes
<i>Aluterus monoceros</i>	Aluterus	Monacanthidae	Tetraodontiformes
<i>Aluterus scriptus</i>	Aluterus	Monacanthidae	Tetraodontiformes
<i>Balaenoptera edeni</i>	Balaenoptera	Balaenopteridae	Cetacea
<i>Balaenoptera physalus</i>	Balaenoptera	Balaenopteridae	Cetacea
<i>Balistes carolinensis</i>	Balistes	Balistidae	Tetraodontiformes
<i>Balistes punctatus</i>	Balistes	Balistidae	Tetraodontiformes
<i>Bramidae</i>	-	Bramidae	Perciformes
<i>Canthidermis maculata</i>	Canthidermis	Balistidae	Tetraodontiformes
<i>Caranx crysos</i>	Caranx	Carangidae	Perciformes
<i>Carcharhinus falciformis</i>	Carcharhinus	Carcharhinidae	Carcharhiniformes
<i>Carcharhinus longimanus</i>	Carcharhinus	Carcharhinidae	Carcharhiniformes
<i>Carcharodon carcharias</i>	Carcharodon	Lamnidae	Lamniformes
<i>Caretta caretta</i>	Caretta	Cheloniidae	Testudines
<i>Chelonia mydas</i>	Chelonia	Cheloniidae	Testudines
<i>Coryphaena equiselis</i>	Coryphaena	Coryphaenidae	Perciformes
<i>Coryphaena hippurus</i>	Coryphaena	Coryphaenidae	Perciformes
<i>Pteroplatytrygon violacea</i>	Dasyatis	Dasyatidae	Myliobatiformes
<i>Dermochelys coriacea</i>	Dermochelys	Dermochelyidae	Testudines
<i>Diodon eydouxi</i>	Diodon	Diodontidae	Tetraodontiformes
<i>Diodon hystrix</i>	Diodon	Diodontidae	Tetraodontiformes
<i>Elagatis bipinnulata</i>	Elagatis	Carangidae	Perciformes
<i>Eretmochelys imbricata</i>	Eretmochelys	Cheloniidae	Testudines
<i>Exocoetidae</i>	-	Exocoetidae	Beloniformes
<i>Gempylus serpens</i>	Gempylus	Gempylidae	Perciformes
<i>Istiophorus albicans</i>	Istiophorus	Istiophoridae	Perciformes
<i>Isurus oxyrinchus</i>	Isurus	Lamnidae	Lamniformes
<i>Kyphosus sectatrix</i>	Kyphosus	Kyphosidae	Perciformes
<i>Lagocephalus lagocephalus</i>	Lagocephalus	Tetraodontidae	Tetraodontiformes
<i>Lepidochelys kempii</i>	Lepidochelys	Cheloniidae	Testudines
<i>Lepidochelys olivacea</i>	Lepidochelys	Cheloniidae	Testudines
<i>Lobotes surinamensis</i>	Lobotes	Lobotidae	Perciformes
<i>Luvarus imperialis</i>	Luvarus	Luvaridae	Perciformes
<i>Makaira indica</i>	Makaira	Istiophoridae	Perciformes
<i>Makaira nigricans</i>	Makaira	Istiophoridae	Perciformes
<i>Manta birostris</i>	Manta	Myliobatidae	Myliobatiformes
<i>Masturus lanceolatus</i>	Masturus	Molidae	Tetraodontiformes
<i>Megaptera novaeangliae</i>	Megaptera	Balaenopteridae	Cetacea
<i>Mobula coilloti</i>	Mobula	Myliobatidae	Myliobatiformes
<i>Mobula japonica (rancureli)</i>	Mobula	Myliobatidae	Myliobatiformes
<i>Mobula mobular</i>	Mobula	Myliobatidae	Myliobatiformes
<i>Mobula tarapacana</i>	Mobula	Myliobatidae	Myliobatiformes

<i>Mobula thurstoni</i>	Mobula	Myliobatidae	Myliobatiformes
<i>Mola mola</i>	Mola	Molidae	Tetraodontiformes
<i>Naucrates ductor</i>	Naucrates	Carangidae	Perciformes
<i>Odontoceti</i>	-	-	Cetacea
<i>Peponocephala electra</i>	Peponocephala	Delphinidae	Cetacea
<i>Phtheirichthys lineatus</i>	Phtheirichthys	Echeneidae	Perciformes
<i>Prionace glauca</i>	Prionace	Carcharhinidae	Carcharhiniformes
<i>Psenes cyanophrys</i>	Psenes	Nomeidae	Perciformes
<i>Ranzania laevis</i>	Ranzania	Molidae	Tetraodontiformes
<i>Remora brachyptera</i>	Remora	Echeneidae	Perciformes
<i>Remora osteochir</i>	Remora	Echeneidae	Perciformes
<i>Remora remora</i>	Remora	Echeneidae	Perciformes
<i>Remorina albescens</i>	Remorina	Echeneidae	Perciformes
<i>Rhincodon typus</i>	Rhincodon	Rhincodontidae	Orectolobiformes
<i>Ruvettus pretiosus</i>	Ruvettus	Gempylidae	Perciformes
<i>Seriola rivoliana</i>	Seriola	Carangidae	Perciformes
<i>Serranidae</i>	-	Serranidae	Perciformes
<i>Sphyaena barracuda</i>	Sphyaena	Sphyaenidae	Perciformes
<i>Sphyrna lewini</i>	Sphyrna	Sphyrnidae	Carcharhiniformes
<i>Sphyrna mokarran</i>	Sphyrna	Sphyrnidae	Carcharhiniformes
<i>Sphyrna zygaena</i>	Sphyrna	Sphyrnidae	Carcharhiniformes
<i>Squaliformes</i>	-	-	Squaliformes
<i>Tetrapturus albidus</i>	Tetrapturus	Istiophoridae	Perciformes
<i>Tetrapturus angustirostris</i>	Tetrapturus	Istiophoridae	Perciformes
<i>Tetrapturus audax</i>	Tetrapturus	Istiophoridae	Perciformes
<i>Tetrapturus pfluegeri</i>	Tetrapturus	Istiophoridae	Perciformes
<i>Torpedinidae</i>	-	Torpedinidae	Torpediniformes
<i>Uraspis helvola</i>	Uraspis	Carangidae	Perciformes
<i>Uraspis secunda</i>	Uraspis	Carangidae	Perciformes
<i>Uraspis uraspis</i>	Uraspis	Carangidae	Perciformes
<i>Xiphias gladius</i>	Xiphias	Xiphiidae	Perciformes

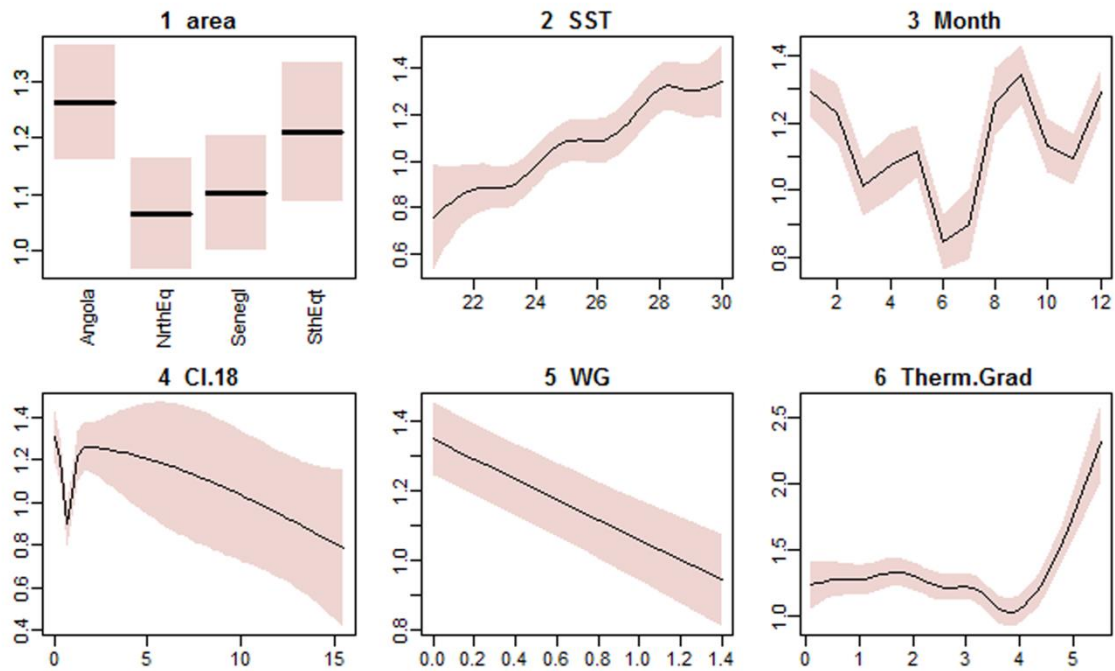
S3. **Figure 1** Selected areas for Generalized Additive Model (GAM) analysis in Fish Aggregating Device (FAD) and Free School sets.



S3. Table 2 AIC (Akaike's Information Criterion) for each model to fit log-rank abundance curves in Fish Aggregating Device (FAD) and Free School sets.

Species Distribution Models	FAD	Free School
Null	1177778.3	4968.14
Preemption	134915	1296.886
Lognormal	31520.7	1061.656
Zipf	56835.3	1637.718
Mandelbrot	46772.5	609.12

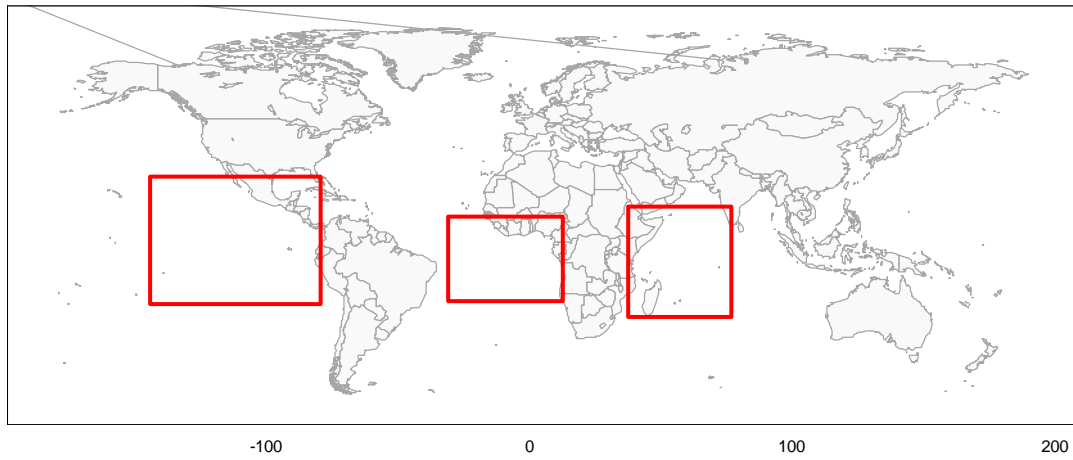
S3. Figure 2 Smoothed fits of covariates modelling the Shannon diversity index: 1) area, 2) SST (Sea surface temperature), 3) Month, 4) Cl. 18 (Chlorophyll 18 days before), 5) WG (Speed of the current) and 6) Therm.Grad (Gradient of the thermocline) variables in Fish Aggregating Device (FAD) fishing mode. The y-axis represents the spline function. Dashed lines indicate approximate 95% confidence bounds.

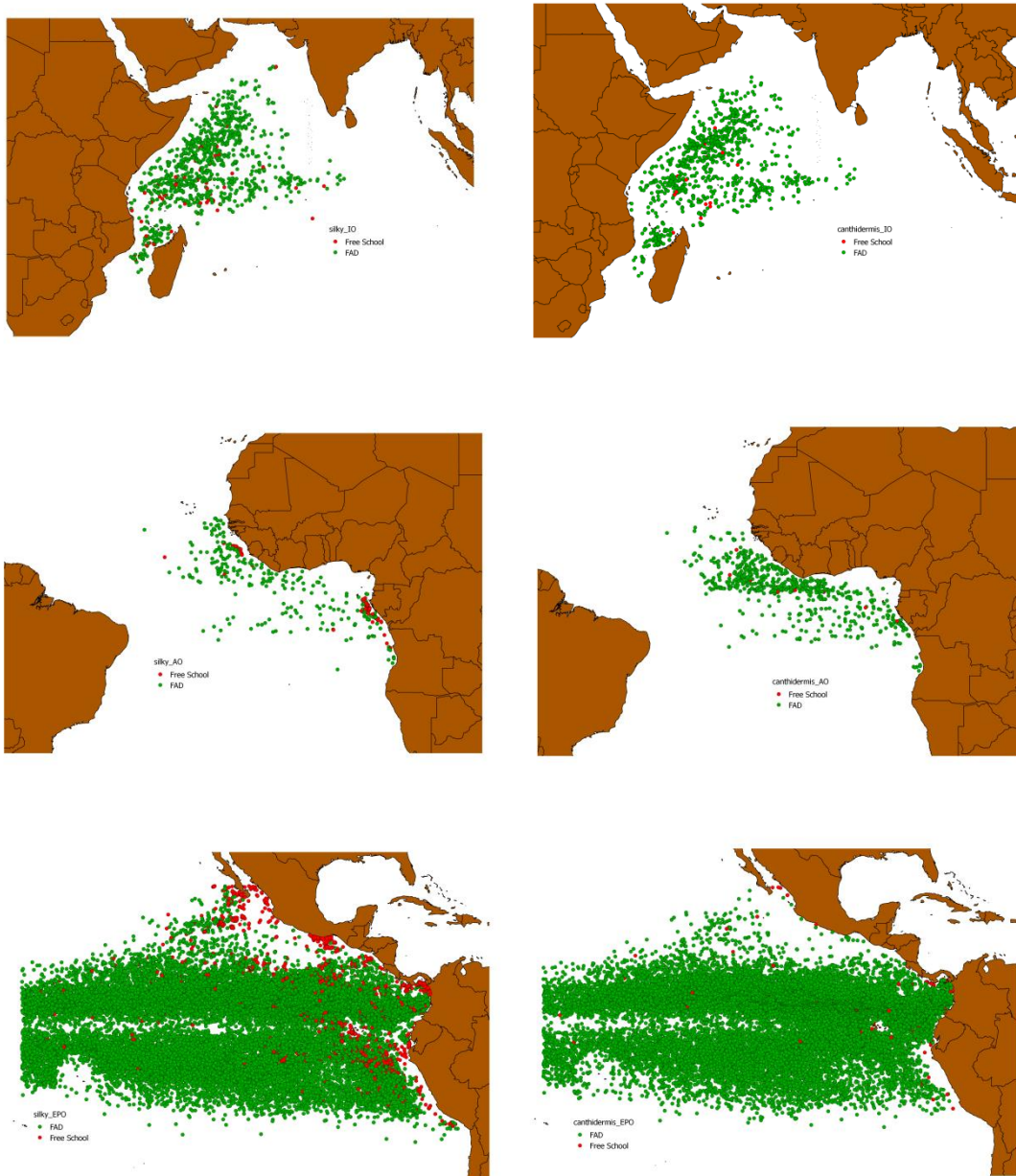


S3. Table 3 Results from Generalized Additive Models (GAMs). Individual contribution of the most important variables to explain the model.

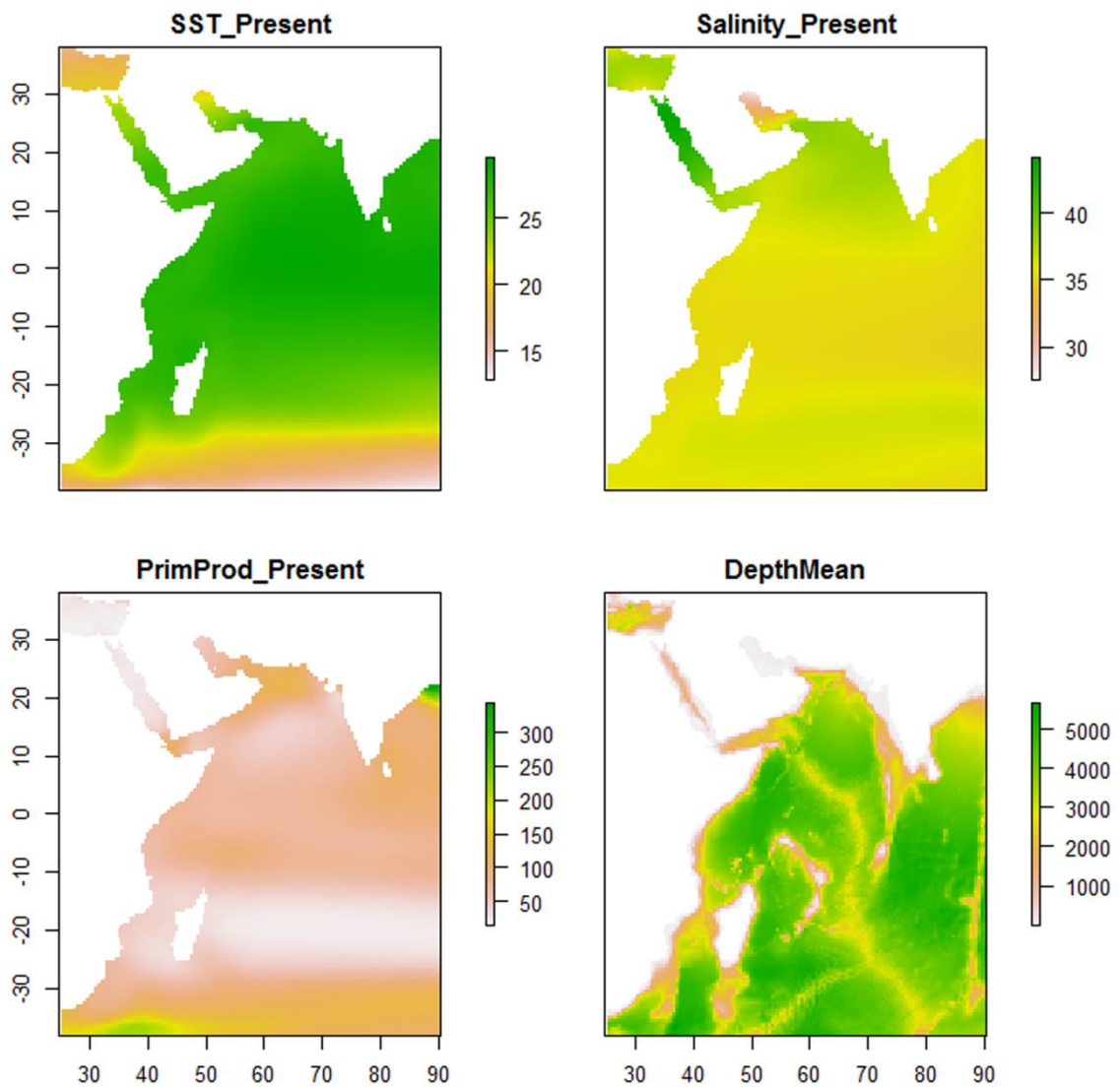
FAD				Free School			
Species richness		Shannon diversity		Species richness		Shannon diversity	
Variables	% Deviance	Variables	% Deviance	Variables	% Deviance	Variables	% Deviance
Area	8.1	Area	6.39	Area	1.55	Area	1.55
Month	16.5	Month	15.4	Month	5.7	Month	5.7
SST	18	SST	12.8	Cl	1.82	Cl	1.82
Cl.18	12	Cl.18	8.94	Sal20	2.34	SST	0.03
WG	1.87	WG	3.23	Therm.Grad	4.45	Therm.Grad	4.45
Therm.Grad	10.7	Therm.Grad	8.31	-	-	-	-

S4. **Figure 1** Areas selected (from left to right) for the application of MaxEnt species distribution model: Eastern Pacific Ocean, Eastern Atlantic Ocean and Western Indian Ocean.

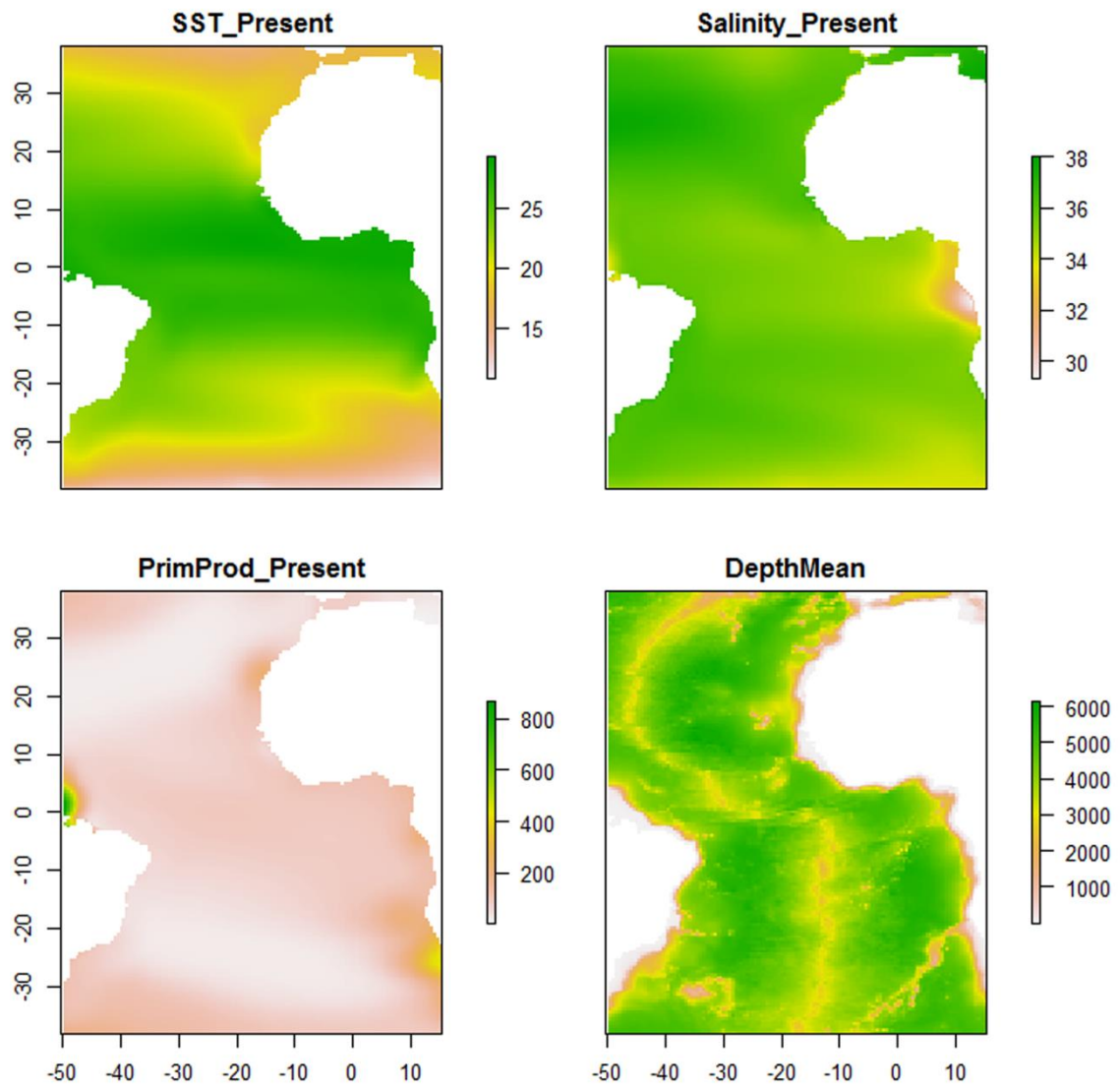




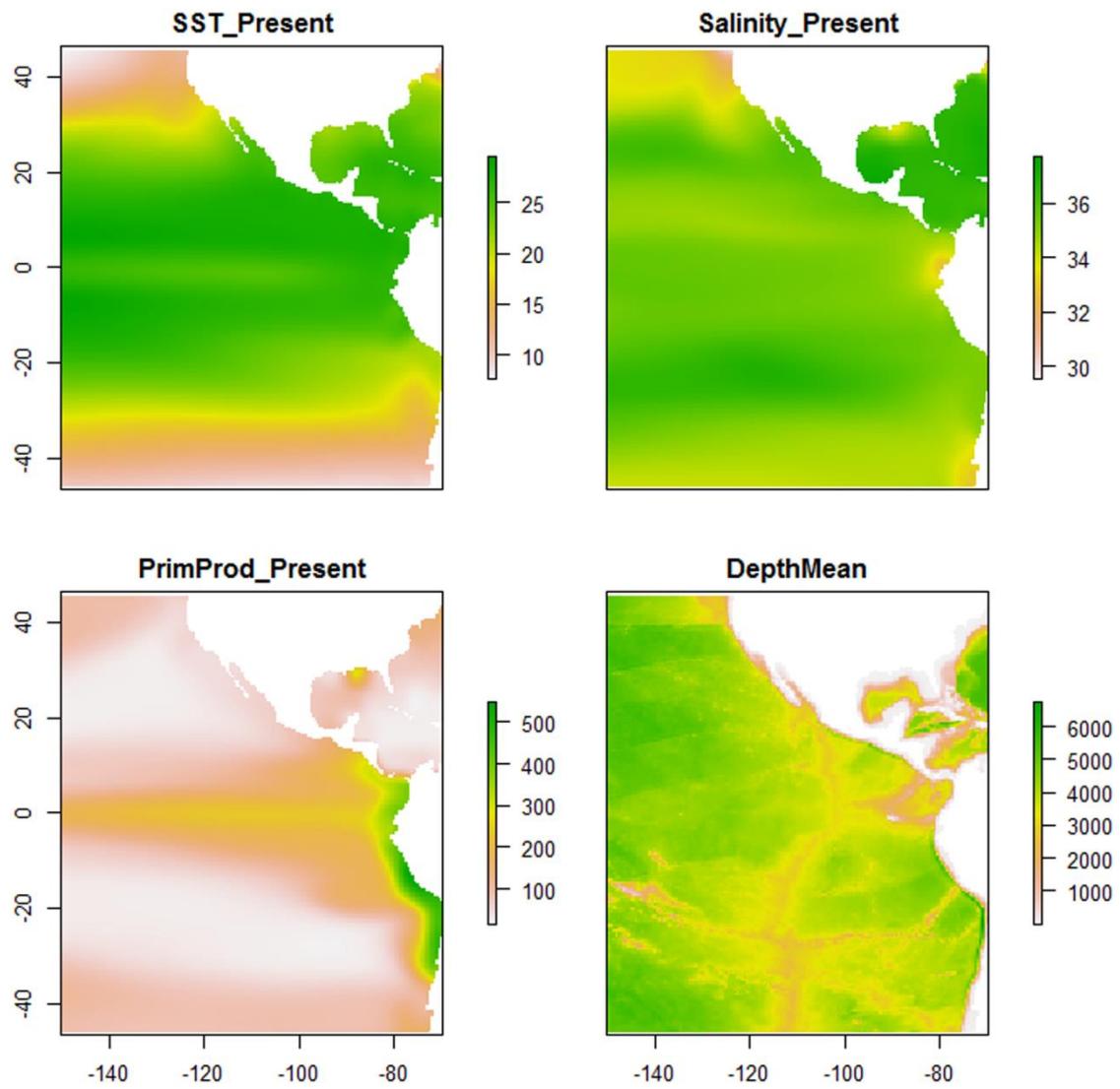
S4. Figure 2 Distribution of sets in FAD and Free School fishing mode for *Carcharhinus falciformis* (first column) and *Canthidermis maculata* (second column) in the Indian (first line), Atlantic (second line) and Pacific (third line) Ocean.



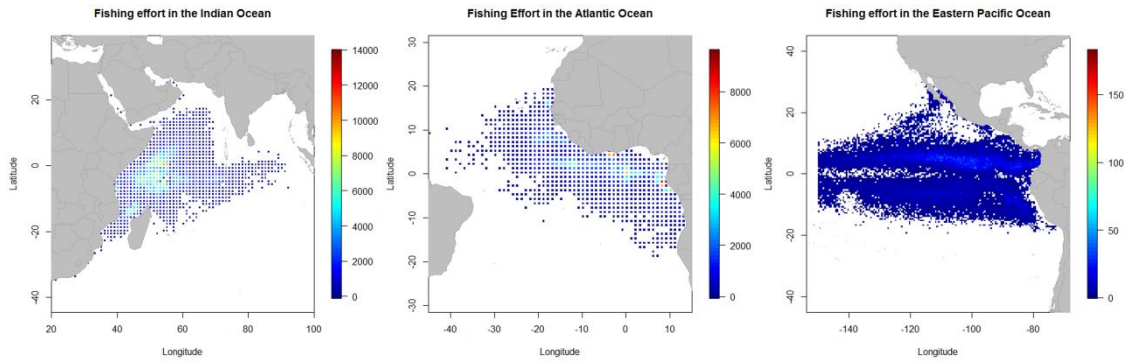
S4. Figure 3a Environmental variables in the Western Indian Ocean: Sea surface temperature (SST), Salinity, Primary Production (PrimProd) and Depth Mean.



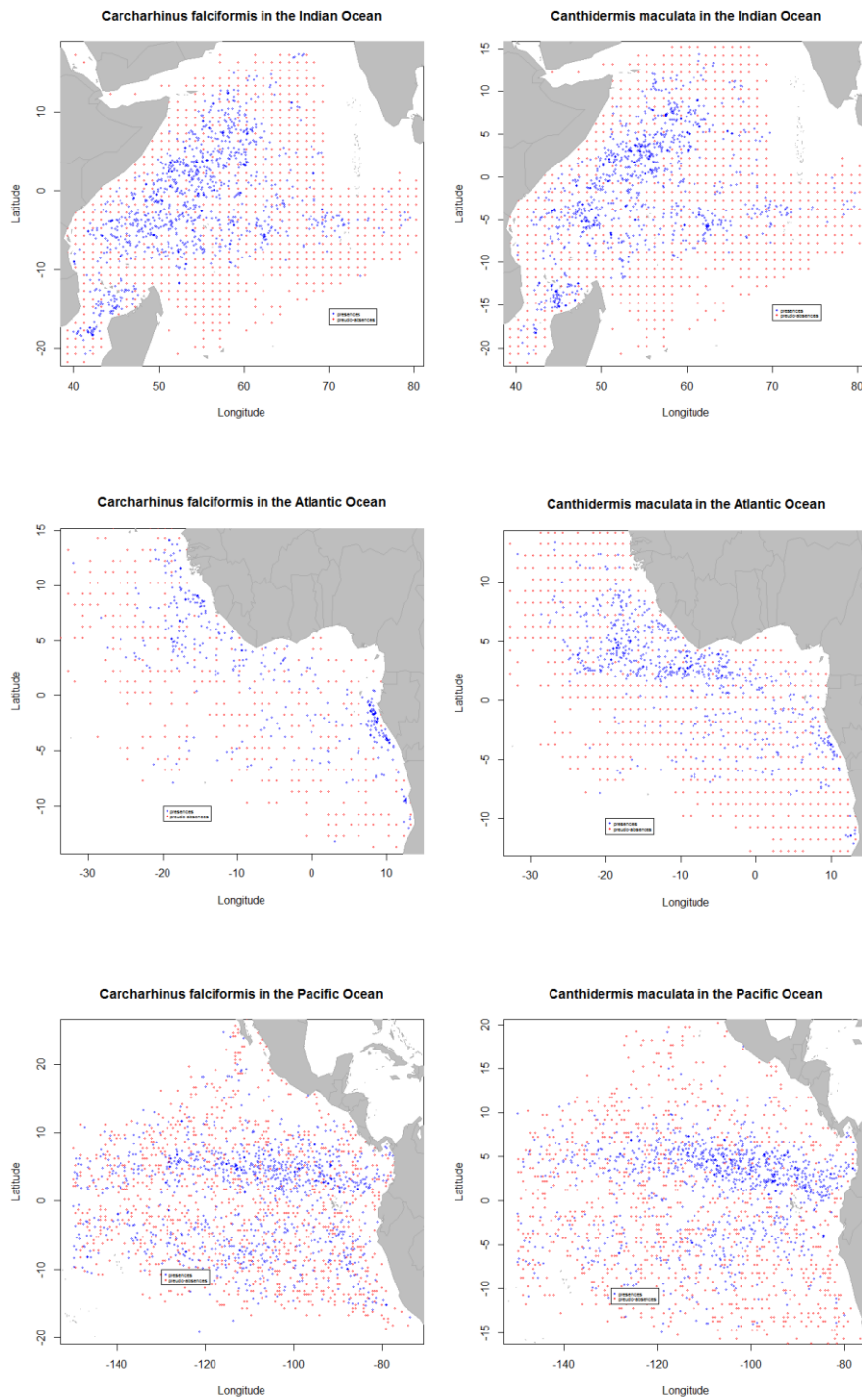
S4. Figure 3b Environmental variables in the Eastern Atlantic Ocean: Sea surface temperature (SST), Salinity, Primary Production (PrimProd) and Depth Mean.



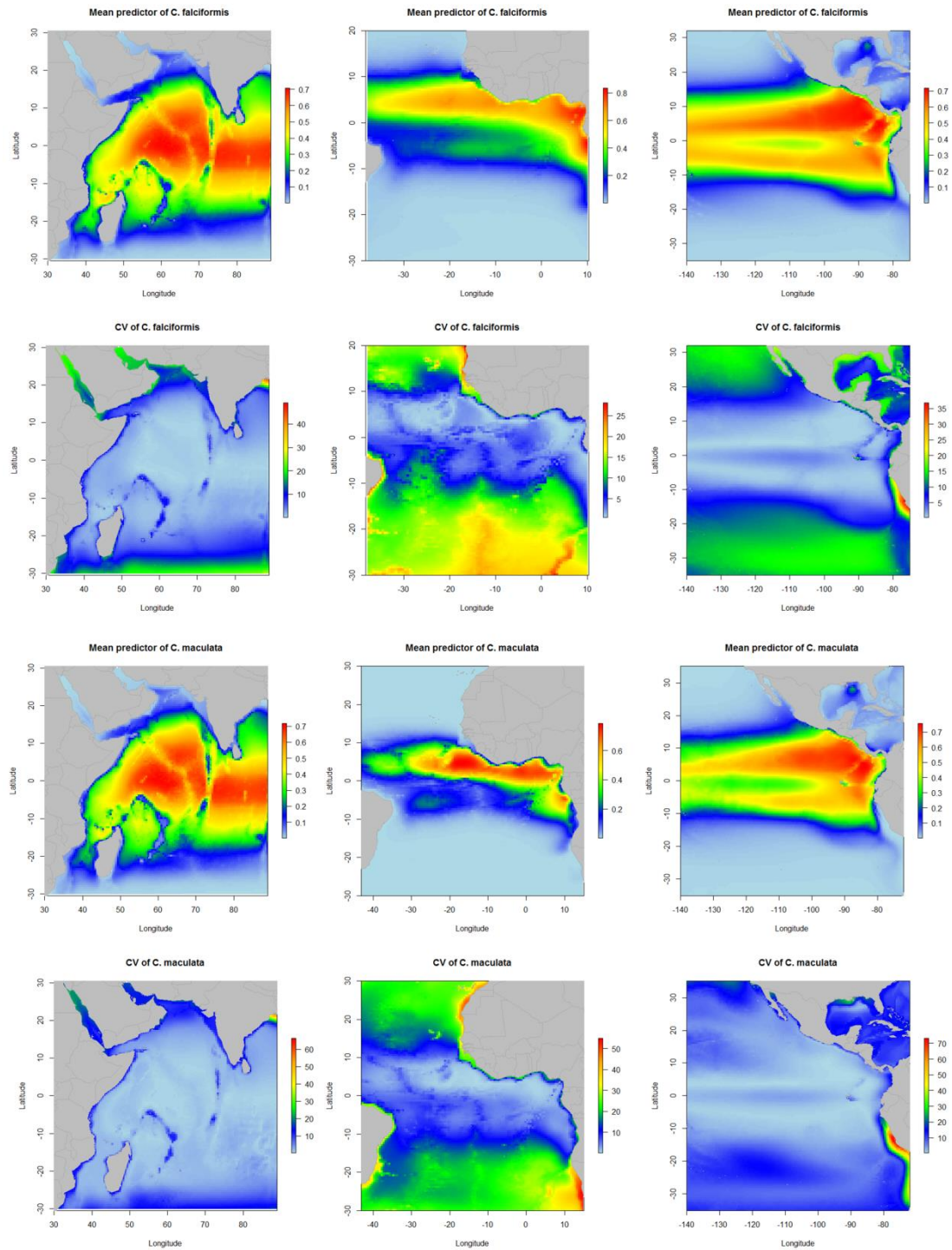
S4. Figure 3c Environmental variables in the Eastern Pacific Ocean: Sea surface temperature (SST), Salinity, Primary Production (PrimProd) and Depth Mean.



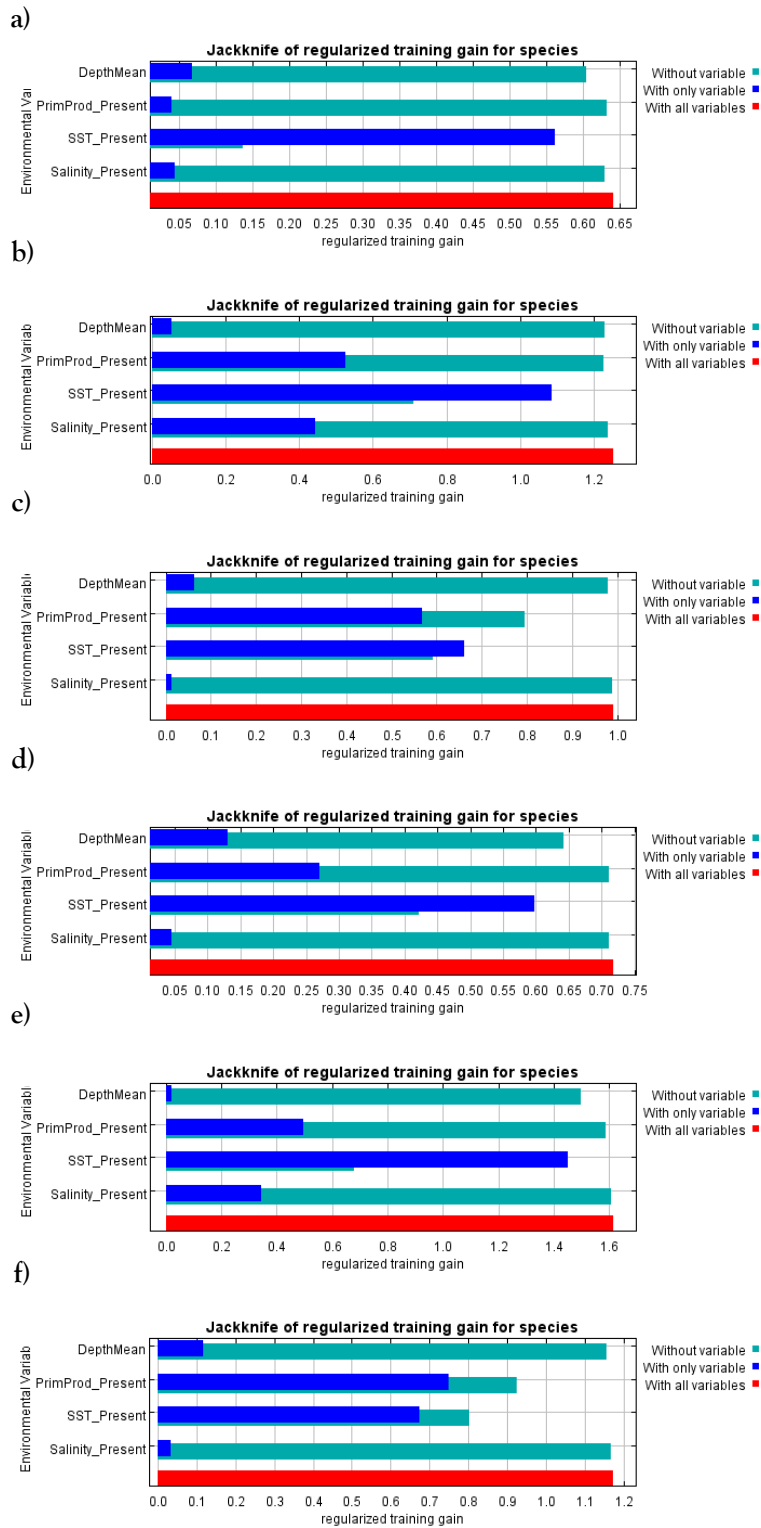
S4. Figure 4 Distribution of the total fishing effort for both by-catch species in the Western Indian Ocean (2003-2010, by fishing days), Eastern Atlantic Ocean (2003-2011, by fishing days) and Eastern Pacific Ocean (1993-2011, by total number of sets).



S4. Figure 5 Distribution of presences and the pseudo-absences generated for *Carcharhinus falciformis* and *Canthidermis maculata* in the Indian (above), Atlantic (middle) and Eastern Pacific Oceans (below).



S4. Figure 6 Mean predictor with 5 MaxEnt run with k-fold method (first and third line) and coefficient of variation (cv) (second and fourth line) for *Carcharhinus falciformis* (first and second line) and *Canthidermis maculata* (third and fourth line).

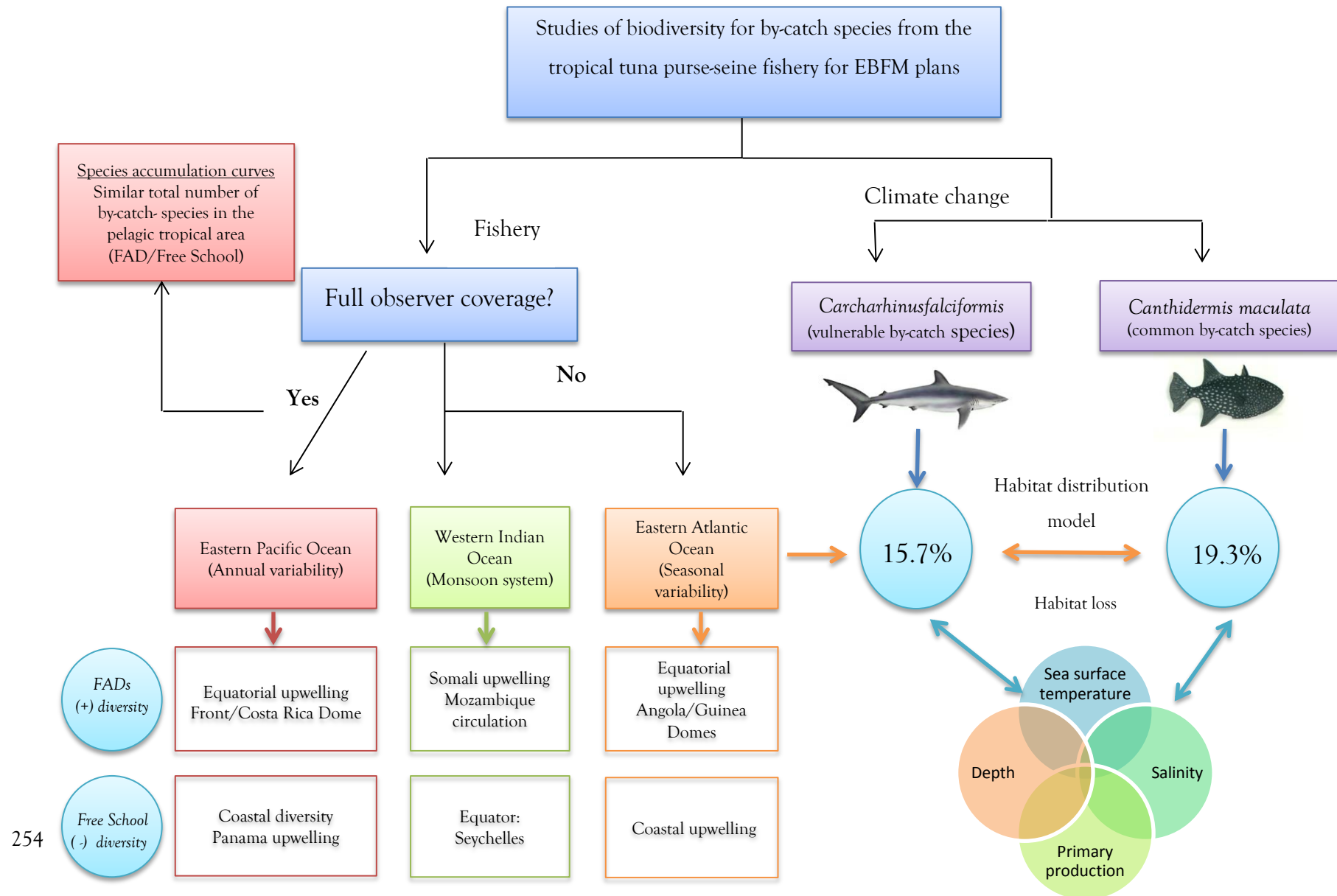


S4. Figure 7 Contribution of the environmental variables to the MaxEnt model based on a jackknife procedure, providing the explanatory power of each variable when used in isolation for *Carcharhinus falciformis* in the Indian (a), Atlantic (b) and Eastern Pacific Ocean (c) and for *Canthidermis maculata* in the Indian (d), Atlantic (e) and Eastern Pacific Ocean (f).

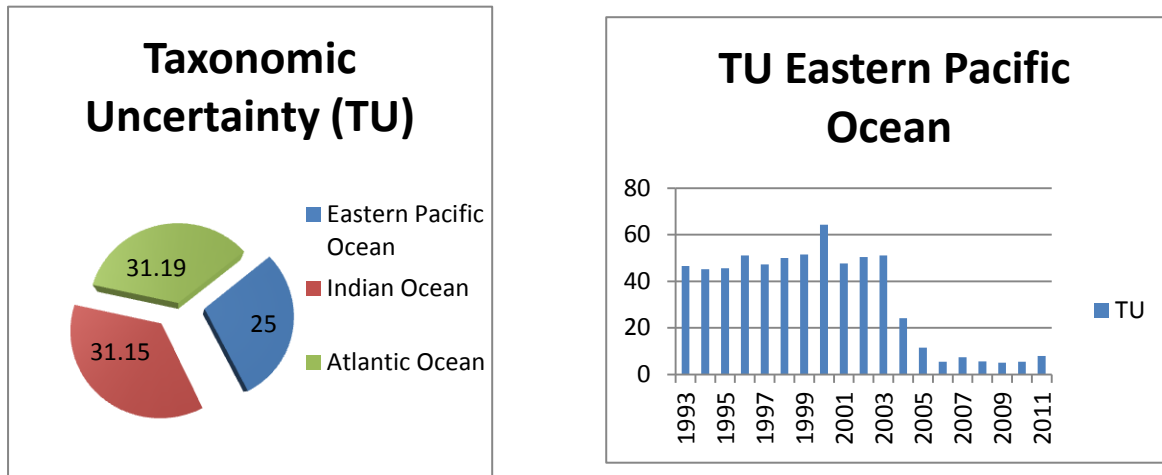
S4. Table 1 Spearman correlation between environment variables in each ocean: SST (sea surface temperature), SAL (salinity), PRIM (primary production) and DEPTH.

Indian Ocean				
	SST	SAL	PRIM	DEPTH
SST	1.00			
SAL	-0.18	1.00		
PRIM	-0.18	0.02	1.00	0.00
DEPTH	-0.02	-0.22	0.00	1.00
Atlantic Ocean				
	SST	SAL	PRIM	DEPTH
SST	1.00			
SAL	-0.21	1.00		
PRIM	0.29	-0.55	1.00	-0.23
DEPTH	0.05	0.05	-0.23	1.00
Eastern Pacific Ocean				
	SST	SAL	PRIM	DEPTH
SST	1.00			
SAL	0.32	1.00		
PRIM	0.19	-0.41	1.00	0.00
DEPTH	-0.04	-0.19	0.00	1.00

S5. Figure 1 Scheme with the different scenarios of biodiversity and the effect of the Climate Change.



S5. **Figure 2** Taxonomic Uncertainty (TU) in the Indian, Atlantic and Pacific Oceans (left). Evolution of TU by years in the Eastern Pacific Ocean (right).



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In the tropical area, 60% of global tuna catches are performed by purse seine gear but their exploitation affects not only target species populations (such as tunas) but also by-catch species (such as billfishes, turtles, sharks, etc...). To date, fishery management has been ineffective because it has been focused on protecting single target species with a substantial cost included. In contrast, and with the introduction of the Ecosystem Approach to Fisheries Management (EAFM) which takes into account that species are integrated with the environment and cannot be managed in isolation, is one of the solutions to reduce the by-catch levels and to maintain the marine biodiversity. However, up to date, works about the biodiversity of by-catch species on tropical purse-seine fishery are scarce. Despite the growing literature on biodiversity, little information is yet available for marine biodiversity in general and for this specific group of species in particular. The most important studies published to date include different levels of marine diversity without including comparisons between tropical oceans. This Thesis presents scientific research results about the structure, diversity and habitat preferences (at global and local scale) of the by-catch communities from the tropical tuna purse-seine fishery in the Western Indian Ocean, Eastern Pacific Ocean and Eastern Atlantic Ocean. The present work also develops a habitat distribution model to describe the potential habitat of two different by-catch species and their change on the habitat distribution under the A2 scenario of climate change.

Nerea Lezama Ochoa