REPORT

Adaptive responses of tropical tuna purse-seiners under temporal regulations

Edgar Torres-Irineo, Michel Dreyfus-León,
Daniel Gaertner, Silvia Salas, Paul Marchal

Received: 30 September 2015 / Revised: 3 February 2016 / Accepted: 8 June 2016 / Published online: 28 June 2016

Abstract The failure to achieve fisheries management objectives has been broadly discussed in international meetings. Measuring the effects of fishery regulations is difficult due to the lack of detailed information. The yellowfin tuna fishery in the eastern Pacific Ocean offers an opportunity to evaluate the fishers' responses to temporal regulations. We used data from observers on-board Mexican purse-seine fleet, which is the main fleet fishing on dolphin-associated tuna schools. In 2002, the Inter-American Tropical Tuna Commission implemented a closed season to reduce fishing effort for this fishery. For the period 1992–2008, we analysed three fishery indicators using generalized estimating equations to evaluate the fishers' response to the closure. We found that purse-seiners decreased their time spent in port, increased their fishing sets, and maintained their proportion of successful fishing sets. Our results highlight the relevance of accounting for the fisher behaviour to understand fisheries dynamics when establishing management regulations.

Keywords Closed season · Eastern tropical Pacific · Fisher behaviour · Purse-seine fishing · Tropical tuna

INTRODUCTION

Acquisition of new technology and increase in vessel size, generally, have resulted on an increase in fleet capacity or efficiency with the associated impacts, such as access to new fishing grounds or catchability improvements (Rijnsdorp et al. 2008; Eigaard et al. 2014; Torres-Irineo et al. 2014). This increase in fishing capacity affects many fisheries around the world resulting in overfishing and economic waste (Clark et al. 2005; Beddington et al. 2007;

FAO 2008; Ye et al. 2013). Management regulations that address the increasing fishing capacity and fishing effort have attempted to limit catches and/or reduce fishing effort through the implementation of measures including total allowable catch, closed seasons, no-take zones, or a combination of the above (Branch et al. 2006). Most of these management measures have not fulfilled their objectives because they can encourage the race for fish and excessive investment by fishers due to inappropriate incentives (Branch et al. 2006; Hilborn 2007; Sumaila et al. 2016). Although the importance of considering the fishers' behaviour when designing management regulations has been emphasized (Salas and Gaertner 2004; Branch et al. 2006; Hilborn 2007; Fulton et al. 2011; Young et al. 2016), fisheries management is still mainly conducted without considering the adaptive fisher's responses.

Among the common tools used to reduce fishing effort and to limit catch, the closed seasons have been used in many types of fisheries. The effectiveness of this measure mainly depends on the species' life traits (seasonal recruitment patterns, growth rates, and natural mortality rates) and on the effects of implementing or modifying the length of the seasonal closure on the fishing effort pattern (Watson et al. 1993). However, the results of such actions do not always reduce fishing effort, because the fishers try to maintain profitable catch levels (Dorn 1998; Branch et al. 2006; Fulton et al. 2011). The expectation of an increase in biomass from the closed season can produce high levels of either nominal or effective fishing effort (Watson et al. 1993).

With the exception of skipjack (*Katsuwonus pelamis*) whose stocks do not show evidence of overfishing, the majority of the stocks of bigeye tuna (*Thunnus obesus*) and yellowfin tuna (*Thunnus albacares*) in the world ocean are fully exploited. In the case of yellowfin tuna in the eastern

Pacific Ocean (EPO), studies have suggested that the stock is in good condition (Hampton et al. 2005; Sibert et al. 2006; Juan-Jorda et al. 2011; IATTC 2015). However, all tropical tuna stocks face growing fishing pressures from overcapacity and the ongoing development of technology (Allen et al. 2010; Lopez et al. 2014). Because of the highly mobile nature of tuna and the global size of tuna fisheries, several regional fishery management organizations (RFMOs) have been established to manage these fisheries within a regional/ocean context. The RFMO for the management of tuna in the eastern Pacific Ocean (EPO) is the Inter-American Tropical Tuna Commission (IATTC). Straddling stocks are shared among exclusive economic zones (EEZs) and high seas, but approximately 40 % of the world's tuna are caught in the high seas, providing a challenge to their conservation and management (Allen et al. 2010). Such a situation poses conservation and management issues of jurisdiction under international law and multilateral cooperation to define property rights and management actions (Aranda et al. 2012). Such management actions need to consider the real and potential impact according to their expected outcome. Some countries have implemented on-board observers to collect information that can allow to better assessments and monitoring.

The eastern Pacific tropical tuna purse-seine fishery

In the EPO, the IATTC has established catch limits for yellowfin and bigeye tuna mainly because of the increase in fleet size. The concern about the increase in the catches of small bigeye by the purse-seine fishery led the IATTC to adopt conservation measures in 1999 to restrict fishing on fish aggregating devices (FAD). However, fishing effort increased continuously, reaching levels above the effort that leads to maximum sustainable yield (F_{MSY}) for both species in the 2000–2001 period. In 2002, the IATTC recognized that the potential production of yellowfin and bigeye tuna could be reduced by this excessive fishing effort. Therefore, the IATTC considered that a limitation on the fishing effort by purse-seine tuna fishing was necessary and consequently implemented a closed season from 1st December to 31st December [resolution: C-02-04]. In 2004, the IATTC adopted a new resolution [C-04-09] “Multi-annual program on the conservation of tuna in the eastern Pacific Ocean for 2004, 2005 and 2006” because of the increasing catches of bigeye tuna by longliners and the continuous increase in fishing capacity. Furthermore, the yellowfin and bigeye tuna stocks were at a level below that which would produce the average maximum sustainable yield. This resolution established two closed seasons for purse-seine fishing, one from 1st August to 11th September

and the other from 20th November to 31st December. Mexico as contracting country in the IATTC complied with both resolutions C-02-04 and C-04-09. For the latter resolution, Mexican tuna purse-seine fleets chose the closed season from 20th November to 31st December. Consequently, since 2002, December has remained closed for Mexican purse-seiners.

Several fleets that target tropical tunas in the EPO use different fishing gears, mainly longline and purse-seine. The main longline fleets are Japanese, Korean, and Taiwanese, but most of the purse-seiners operating in the EPO come from Ecuador, Mexico, and Venezuela. Tropical tuna purse-seiners in the world's oceans mainly fish on free-swimming schools and on FADs. In the EPO, large yellowfin tuna (high market value) are known to be associated with herds of dolphins (Hall 1998). Therefore, in addition to fishing on free-swimming schools (targeting mainly pre-adults of yellowfin tuna) and on FADs (targeting mainly juveniles of yellowfin and bigeye tuna), Mexican purse-seiners take advantage of this association to locate herds of dolphins and perform fishing operations on dolphin-associated tuna schools (Fig. 1). When the presence of tuna is confirmed, the skipper launches four or five speedboats that chase the dolphin herd away, making a wide arc typically at a distance of 100–200 m to the side and behind the herd (Hall 1998).

Different studies have evaluated tuna management in the EPO. These have mainly focused on management objectives, specifically the use of MSY as a management target reference point (Maunder 2002; Maunder and Harley 2006). Other studies have considered the response of stocks to multiple management objectives such as minimizing dolphin mortality, minimizing incidental catch (all species except dolphins), maximizing sustainable yield, and minimizing biological risk for the yellowfin tuna stock (Enríquez-Andrade and Vaca-Rodríguez 2004; Vaca-Rodríguez and Enríquez-Andrade 2006). However, there are no references to how fishers develop adaptive responses to the establishment of closed seasons, which are often used by the IATTC. In this sense, tuna purse-seine fleet dynamics has been studied in the EPO in terms of fishing strategies (Vaca-Rodríguez and Dreyfus-León 2000; Dreyfus-León and Vaca-Rodríguez 2003; Solana-Sansores et al. 2009). The effects of a closed area on the reallocation of fishing effort have also been simulated (Dreyfus-León and Kleiber 2001). In this study, we focused on the Mexican purse-seine fleet as a case study to show the effects of closed seasons on fleet behaviour. We used data collected from observers on-board Mexican tuna purse-seiners operating in the EPO to evaluate the adaptive responses of the fleet to the implementation of a closed season and its effects on catch and fishing effort.

Fig. 1 Spatio-temporal distribution of sets performed on dolphin-associated schools by the Mexican purse-seine fleet in the eastern Pacific Ocean. Data from the PNAAPD observer program

MATERIALS AND METHODS

Fishery indicators

We used data from three sources: (1) the observers' data, from 1992 to 2008, corresponding to 3404 Mexican fishing trips (50 % coverage), which include catches of yellowfin and skipjack tuna for each fishing set, (2) information from departure and return dates of each fishing trip, and (3) monthly time series of climate indices from NOAA, including Sea Surface temperature (SST) anomalies corresponding to the Niño 3 area (5°N–5°S, 150°W–90°W), Niño 1 + 2 (0°–10°S, 90°W–80°W), Niño 3 + 4 (5°N–5°S, 170°W–120°W), Niño 4 (5°N–5°S, 160°E–150°W), and the Southern Oscillation Index (SOI) (<http://www.esrl.noaa.gov/psd/data/climateindices/list/>, accessed July 2013). Observer program data from Mexican tuna purse-seiners operating in the EPO have been collected by the *Programa Nacional de Aprovechamiento del Atún y de Protección de Delfines* (PNAAPD) since 1992. Notice that the Mexican fleet is the main fleet targeting dolphin-associated tuna schools while the other nations mainly fish on FADs. According to the Agreement on the International Dolphin Conservation Program (AIDCP) established in 1992, on-board observers must (1) gather all the information related to fishing operations performed by the purse-seiner in which the observer was assigned (purse-seiner logbook, dates of departure and return, target species catch, bycatch species identification, reports of marine mammals presence, fishing operations); (2) make available to the captain of the purse-seiner assigned all measures established in the AIDCP; (3) make available to the captain the record of dolphin mortality of that vessel; and (4) prepare and provide reports to the corresponding Director of the observer national program. Such on-board observers' activities have been performed since 1992 in all vessels operating in the EPO. Detailed description about observers' activities on-board purse-seiners is available in <http://www.iattc.org/PDFFiles2/AIDCP-amended-Jul-2014.pdf>.

According to Watson et al. (1993), the implementation of a closed seasons might exacerbate the race for fish, i.e. there is an expectation of increase in biomass resulting from the closure, which in turn can promote an increase in fishing effort. Therefore, we estimated the number of days in port (P), considering that this indicator is easily controlled by fishers. We estimated P using data from departure and return dates on a quarterly basis because fishing trips are around 60 days long and do not depart/return on the same date. In addition, to evaluate whether any change in P resulted in an additional effect on the dolphin-associated tuna fishing mode, using observer data, we estimated the number of sets per vessel (E) and the proportion of successful fishing sets on dolphin-associated schools (R) on

an annual basis. Furthermore, since E is the total number of fishing sets which does not reflect how many of these sets were successful (i.e. fishing sets with catch), thus we used R to evaluate whether there was an increase or decrease in the number of successful fishing sets. For instance, if E increased before and after the implementation of the regulation but R remained similar, we would expect an increase in the number of successful fishing sets. We are aware that the number of sets does not necessarily reflect a direct effect of time spent in port by purse-seiners, but they depend on the fishing efficiency and the target species abundance. In the component of the fleet addressed, new technology on-board Mexican purse-seine fleet was mainly implemented during the 1980s (Guillermo Compeán 2015 comm. pers.). Since the introduction of FADs in the tropical tuna purse-seine fishery during the 1990s, the main technological development has mainly been on this fishing mode. Therefore, because Mexican purse-seiners are specialist in fishing on dolphin-associated tuna schools, we assumed that fishing efficiency has remained stable over the analysed period (1992–2008).

On the other hand, we acknowledge that tuna availability depends largely on environmental conditions and given the fact that EPO present high inter-annual variability, we included climate indices in the statistical analysis to taking into account these effects. Despite the potential effect of the mentioned factors, we contend that P would result from an adaptive response of fishers to the implementation of the closed season. We used E and R as a proxy to the closed season effectiveness, since the aim was to reduce fishing effort.

Between 1992 and 2008 a total of 64 Mexican purse-seiners operated in the EPO, most of these vessels operated either before or after the implementation of the closed season. We considered only 22 Mexican purse-seiners operating at least half of the time period that includes the closed season implementation as they operated in the EPO before and after the management regulation; the potential effect of the closed season could be hence more evident.

Adaptive fishers' response analyses

We used generalized estimating equations (GEE) to evaluate the effects of a closed season on the indicators described above (P , E , and R). This method is useful for analysing longitudinal data, i.e. repeated measures from the same cluster (each purse-seiner) which are correlated; since this can increase the risk of Type I errors (Zuur et al. 2009). GEE are similar to generalized linear models but allow for the use of a correlation matrix structure which takes into account the lack of independence of each cluster. The conditional mean

$E(Y_{it}|X_{it}) = \mu_{it}$ is related to independent variables (i.e. linear predictor) through a link function $g(\mu_{it}) = X_{it}\beta$. Our indicators correspond to the vessel i in time t . The variance structure of Y_{it} is given by $\text{var}(Y_{it}|X_{it}) = \mu_{it}$ for count data, and $\text{var}(Y_{it}|X_{it}) = \mu_{it}(1 - \mu_{it})$ for proportional data (Zuur et al. 2009). A correlation between points for the same cluster is specified through a correlation structure. Model parameters are estimated through an iterative process until the model converges, where parameters are consistent and asymptotically normally distributed (Zuur et al. 2009).

In this study, the explanatory variables that comprised the linear predictor were the (1) before (period of years without restriction, i.e. 1992–2001) and after (period of years with restriction, i.e. 2002–2008) closed season periods and (2) environmental effects (i.e. the climate index). We compared two models for each indicator through the Wald test statistic, one including the climate index and the before–after effect, and another with only the before–after effect. We used an auto-regressive correlation structure because we assumed the association between points to be time dependent. Due to missing values of some purse-seiners (i.e. years in which they did not operate), we specified the chronological order of time points of each purse-seiner as suggested in Højsgaard et al. (2006).

GEE for indicators P and E were performed assuming a Poisson error distribution. The Poisson distribution was expected to be most appropriate to describe P and E because these indicators are non-negative integer values without an upper limit (i.e. count variables; Zuur et al. 2009). For the indicator R , the GEE were performed with a binomial error distribution. The binomial distribution is appropriate with proportion variables, for this study, the number of successful fishing sets vs the total number of fishing sets. We performed the GEE using the *geepack* package of the statistical software R (R Core Team 2014).

RESULTS

Fishers' adaptive response to the closed season

The GEE model used to evaluate the effects of climate index on the time (days) spent in port showed no significant effect; therefore, we evaluated only the before–after effect on this fishing indicator. As it can be observed in Table 1 and Fig. 2a, the closed season seem to have an effect on the operations of fishers, thus purse-seiners reduced the number of days in port. Notice that before the closed season, in average, the days in port were around 19, and when the closed season was implemented, the time spent in the port was reduced to around 15 days.

Effects on fishing sets on dolphin-associated tuna schools

The GEE model comparison for number of fishing sets showed a significant effect of both the before–after effect and the SST anomaly for the NIÑO area 3 + 4. The number of sets on dolphin-associated tuna schools (E , in average 2 fishing sets) increased before and after the implementation of the closed season (Table 1; Fig. 2b).

For the proportion of successful fishing sets in terms of the total number of sets on dolphin-associated tuna schools (R), the Wald test statistic showed that it was not necessary to include the climate index in the final model. Therefore, we only evaluated the before–after effect which did not show a significant effect on the proportion of successful fishing sets (Table 1; Fig. 2c).

DISCUSSION

As mentioned before, the increasing concern regarding the worldwide decline in stocks has led to the implementation of stringent management measures to prevent overfishing, focusing on controlling fishing effort. However, controlling effort does not necessarily account for the adaptive strategies of fishers in response to regulations, which can lead to conservation and management failures (Johannes et al. 2000; Arendse et al. 2007; Demestre et al. 2008; García-Carreras et al. 2015).

Closed seasons do not necessarily reduce both nominal and effective effort, as much as anticipated (Branch et al. 2006; Fulton et al. 2011); in short term fishers will respond to environmental variability, market changes, and management regulations in order to increase, or at least to maintain their income and/or catch levels (Salas and Gaertner 2004; Branch et al. 2006; Russo et al. 2015), while in long term, fishers can invest in acquiring new vessels and/or new on-board technology (McIlgorm 2010; Torres-Irineo et al. 2014). Our study provides an example of how fishers can respond to the implementation of seasonal regulations. Similar situations have been reported in several fisheries with unintended impacts on fishing resources (Dorn 1998; Arendse et al. 2007; Demestre et al. 2008; Torres-Irineo et al. 2011). For instance, Arendse et al. (2007) showed that a closed season during the breeding period did not increase the reproductive output of the population through a per-recruit simulation. In another example, Demestre et al. (2008) analysed the use of seasonal closures to minimize the benthic communities' degradation by trawling in the Mediterranean; they found that after the closure, the faunal abundance decreased due to the resumption of fishing activity. In the eastern Atlantic Ocean, Torres-Irineo et al. (2011) found that purse-seiners increased their fishing sets on FADs after the implementation

Table 1 Generalized estimation equation (GEE) model results using the number of days in port, number of fishing sets, and the proportion of successful fishing sets as response variables. Estimates and statistics correspond to the model selected for each indicator. *SE* standard error, *CI* confidence interval (95 %)

Model	Effect	Coefficient	SE	Lower CI	Upper CI	Wald	<i>p</i> value
Days in port	Intercept	2.936	0.053	2.832	3.041	3025.05	<0.001
	Before–after	−0.174	0.059	−0.291	−0.058	8.58	<0.01
Fishing sets	Intercept	3.057	0.033	2.9924	3.121	8635.44	<0.001
	Before–after	0.102	0.033	0.0368	0.167	9.44	<0.01
	SST Anomaly 3–4	0.067	0.019	0.0292	0.104	12.2	<0.001
Proportion of successful fishing sets	Intercept	2.173	0.09	1.996	2.35	576.94	<0.001
	Before–after	−0.014	0.115	−0.238	0.211	0.01	0.9

Fig. 2 Annual average values and standard errors of fishery indicators. Indicator of the number of days in port (a), number of fishing sets on dolphin-associated tuna schools (b), and proportion of successful fishing sets in terms of the total number of fishing sets on dolphin-associated tuna schools (c). *Gray lines* and *dots* correspond to mean values for each vessel analysed, and *black lines* and *dots* are the mean values of the fleet. *Black straight lines* correspond to the mean values of fishery indicators before and after the implementation of the closed season in 2002

of a seasonal closure area. In the case of the Pacific Hake, Dorn (1998) showed how the vessels adjusted their response to a ban to fish at night by increasing their catches during the

day in order to maximize their profits. As Dorn (1998) stated, regulations that ignore the adaptive response of fishers under different conditions may fail to achieve the intended goal.

Our findings suggest that the adaptive fisher's response to the closed season implementation in the tuna fishery in the EPO was to decrease the time spent in port (P). This can be a direct result of hastening fish landing and/or loading of the supplies for the next trip in order to at least maintain the number of fishing sets. It must be kept in mind that tuna availability can affect the time purse-seiners spent in port. For instance, it could be expected that when fishing is good, vessels with high catch of tuna will slow down the unloading process which can result in spending more time in port. Similarly, when tuna availability decreases (e.g. deepening of thermocline), fishers could spend more time in port expecting better environmental conditions to go fishing. In this sense, over the 1992–2001 period (before the closed season), the annual catch of retained yellowfin tuna in the EPO was around 278 000 t (IATTC 2015). In this time period, the time spent in port by Mexican purse-seiners remain around 19 days. During the 2002–2008 period, the second largest on record catch of yellowfin tuna in the EPO (383 279 t) was reached in 2003; for the same year, it was observed the highest number of sets on dolphin-associated tuna schools (IATTC 2015). On the contrary, after the El Niño event during 1982–1983 which affected the tuna catch in the EPO, the lowest catch registered for yellowfin tuna was in 2006 with 166 631 t (IATTC 2015). Despite this change in catch magnitude for the 2002–2008 period, the time spent in port by Mexican purse-seiners remain around 15 days in port. This suggests that the observed decrease in P was an adaptive response of fishers to the implementation of the closed season.

Learning about fisher response to changes in their environment (climate, market, regulations) when an intervention has been in place is important (Dorn 1998; Johannes et al. 2000; Young et al. 2016). In this study, even though our analysis is based on data from on-board observers, additional information obtained by fishers' interviews could be very useful to corroborate these findings. Nonetheless, it is worth to note that the IATTC in 2004 recognized that regulations placed on purse-seiners fishing on dolphins-associated tuna schools had probably affected the way these vessels operate, especially since the late 1980s. Notwithstanding, the proxies used in this study to evaluate the closed season effect showed that the objective was not totally fulfilled. Given the fact that fishing operations are dynamics and adaptive (Dorn 1998; Salas et al. 2004; García-Carreras et al. 2015), it is necessary to take into consideration fishers' responses to alleviate the fishing pressure on the resources (Torres-Irineo et al. 2011).

The establishment of spatio-temporal regulations is usually based on breeding or spawning periods of target species (Arendse et al. 2007; van Overzee and Rijnsdorp 2015). According to Arendse et al. (2007), closed seasons can be a useful management tool if reproductive outputs of individuals are negatively affected by fishing activity. van Overzee and Rijnsdorp (2015) consider that closed seasons that aim to protect spawning seasons can contribute to fisheries sustainability depending on the complexity of the spawning system which varies among target species. In the EPO, yellowfin spawning occurred continuously throughout the year with no pronounced seasonal patterns in intensity (Knudsen 1977; Schaefer 1998). In the present case, the closed season has been established to control fishing effort, rather than to protect spawners or juveniles. Accordingly, the three proxy measures used in this study (P , E , and R) suggest that these management measures led to behavioural changes in fishers to maintain or increase their fishing effort.

Regardless of the purpose of the implementation of a closed season, it is necessary to consider relationships between closure length, closure timing, stock dynamics, and fleet dynamics (Watson et al. 1993). According to Branch et al. (2006), the implementation of a closed season aiming to control fishing effort could increase the fishing efficiency and capacity of fleets, particularly in profitable fisheries, leading to further restrictions in future closed seasons. In this sense, it would be expected that Mexican purse-seiners had invested in acquiring new technology to increase their fishing power after the closed season implementation. However, there are no records of major introduction of new on-board technology by Mexican purse-seiners after the closed season. Worldwide, the major improvements of on-board technology of tuna purse-seiners have been observed for FAD-fishing since the early 1990s (Lopez et al. 2014; Torres-Irineo et al. 2014); hence the adaptations seem to be done at the operational level. Furthermore, as stated before, the introduction of technology is likely expected to affect directly the purse-seiners' activities at sea, i.e. fishing sets, and to a lesser extent the time spent in port. For instance, due to the continuous increase in purse-seine capacity, despite regulation measures, in 2011, the IATTC implemented the resolution [C-11-01] which established two closed seasons each of 2 months. Hence, there is no unique recommendation for success when implementing a closed season or any management regulation because objectives differ across RMFOs (van Overzee and Rijnsdorp 2015). Closed seasons could be implemented together with limited-entry programs (Branch et al. 2006), however the implementation

must be considered on a case by case scheme, even within the same fishery.

CONCLUSIONS

Given the regional context of each tuna RFMO, it has been difficult to reach a consensus in terms of regulatory measures. In the EPO, for the yellowfin tuna fishery, longliners are mainly from Japan, the Republic of Korea, and Taiwan. Most of the dolphin-associated schools sets are operated by Mexican and Venezuelan purse-seine fleets, and most of the FADs sets are performed by Ecuadorian purse-seiners. Therefore, any regulation of the allocation of effort among these methods would require agreement among the States concerned, building on a management strategy evaluation framework (Maunder 2002). It is important to understand that closed seasons do not only affect fishing on dolphin-associated schools but all tropical tuna fisheries (i.e. longline, pole-and-line and purse-seine fisheries). However, it is difficult for a RFMO to reallocate the total effort among the different international fleets. Such a reallocation may be perceived to favour one group/country over another one, even if this is supported by a scientifically rationale objective (Maunder 2002).

Several authors have emphasized the importance of accounting for fishers' behaviour and their response to different incentives based on their traditional knowledge and experiences, including fisheries management (Johannes et al. 2000; Branch et al. 2006; Hilborn 2007; Poos et al. 2010; van Putten et al. 2012). Understanding both the incentives and behaviour of fishers is a crucial step towards designing management measures. Simulation analyses can help to evaluate possible fishers' responses before implementing management measures (Dorn 1998; Batsleer et al. 2013). In this regard, the indicators used in this study can be used as input data to perform simulations. The present study highlights the relevance of understanding the fishers' adaptive responses to the management system which can make it possible to identify areas for improvements for a continued sustainable and beneficial use of tropical tuna.

Acknowledgments We thank anonymous referees for suggestions that helped to improve the paper. The fisheries data analysed in this publication were collected by the *Programa Nacional de Aprovechamiento del Atún y de Protección de Delfines* (PNAAPD). Data collection is supported by the research fund FIDEMAR, which is formed by the National Chamber of the Fishing Industry (CANAINPESCA), the Federal Government (CONAPESCA-INA-PESCA), and the Mexican foundation for the preservation of marine wildlife (FUMDAMAR). This study was part of the Ph.D. thesis conducted by the first author (ETI) at the University of Montpellier 2 (ED SIBAGHE) and funded by *Consejo Nacional de Ciencia y Tecnología* (CONACYT), Mexico, scholarship No. 199730.

REFERENCES

- Allen, R., J. Joseph, D. Squires, and E. Stryjewski. 2010. Introduction. In *Conservation and management of transnational tuna fisheries*, ed. R. Allen, J. Joseph, and D. Squires, 1–10. Amsterdam: Wiley-Blackwell.
- Aranda, M., H. Murua, and P. de Bruyn. 2012. Managing fishing capacity in tuna regional fisheries management organisations (RFMOs): Development and state of the art. *Marine Policy* 36: 985–992. doi:10.1016/j.marpol.2012.01.006.
- Arendse, C.J., A. Govender, and G.M. Branch. 2007. Are closed fishing seasons an effective means of increasing reproductive output? A per-recruit simulation using the limpet *Cymbula granatina* as a case history. *Fisheries Research* 85: 93–100. doi:10.1016/j.fishres.2007.01.001.
- Batsleer, J., J.J. Poos, P. Marchal, Y. Vermard, and A.D. Rijnsdorp. 2013. Mixed fisheries management: protecting the weakest link. *Marine Ecology Progress Series* 479: 177–190. doi:10.3354/meps10203.
- Beddington, J.R., D.J. Agnew, and C.W. Clark. 2007. Current problems in the management of marine fisheries. *Science* 316: 1713–1716. doi:10.1126/science.1137362.
- Branch, T.A., R. Hilborn, A.C. Haynie, G. Fay, L. Flynn, J. Griffiths, K.N. Marshall, J.K. Randall, et al. 2006. Fleet dynamics and fishermen behavior: Lessons for fisheries managers. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 1647–1668. doi:10.1139/f06-072.
- Clark, C.W., G.R. Munro, and U.R. Sumaila. 2005. Subsidies, buybacks, and sustainable fisheries. *Journal of Environmental Economics and Management* 50: 47–58. doi:10.1016/j.jeem.2004.11.002.
- Demestre, M., S. de Juan, P. Sartor, and A. Ligas. 2008. Seasonal closures as a measure of trawling effort control in two Mediterranean trawling grounds: Effects on epibenthic communities. *Marine Pollution Bulletin* 56: 1765–1773. doi:10.1016/j.marpolbul.2008.06.004.
- Dorn, M.W. 1998. Fine-scale fishing strategies of factory trawlers in a midwater trawl fishery for Pacific hake (*Merluccius productus*). *Canadian Journal of Fisheries and Aquatic Sciences* 55: 180–198.
- Dreyfus-León, M., and P. Kleiber. 2001. A spatial individual behaviour-based model approach of the yellowfin tuna fishery in the eastern Pacific Ocean. *Ecological Modelling* 146: 47–56. doi:10.1016/S0304-3800(01)00295-2.
- Dreyfus-León, M.J., and J.G. Vaca-Rodríguez. 2003. An age-structured stochastic model of the yellowfin tuna (*Thunnus albacares*) Eastern Pacific fishery. *Océánides (La Paz, B.C.S.)* 18: 23–31.
- Eigaard, O.R., P. Marchal, H. Gislason, and A.D. Rijnsdorp. 2014. Technological development and fisheries management. *Reviews in Fisheries Science & Aquaculture* 22: 156–174. doi:10.1080/23308249.2014.899557.
- Enríquez-Andrade, R.R., and J.G. Vaca-Rodríguez. 2004. Evaluating ecological tradeoffs in fisheries management: A study case for the yellowfin tuna fishery in the Eastern Pacific Ocean. *Ecological Economics* 48: 303–315. doi:10.1016/j.ecolecon.2003.09.009.
- FAO. 2008. *Fisheries management. 3. Managing fishing capacity*. Vol. 3. FAO Technical Guidelines for Responsible Fisheries 4. Rome.
- Fulton, E.A., A.D.M. Smith, D.C. Smith, and I.E. van Putten. 2011. Human behaviour: The key source of uncertainty in fisheries management. *Fish and Fisheries* 12: 2–17. doi:10.1111/j.1467-2979.2010.00371.x.
- García-Carreras, B., P. Dolder, G.H. Engelhard, C.P. Lynam, G.A. Bayliss-Brown, and S. Mackinson. 2015. Recent experience with effort management in Europe: Implications for mixed fisheries.

- Fisheries Research* 169: 52–59. doi:[10.1016/j.fishres.2015.04.010](https://doi.org/10.1016/j.fishres.2015.04.010).
- Hall, M.A. 1998. An ecological view of the tuna–dolphin problem: Impacts and trade-offs. *Reviews in Fish Biology and Fisheries* 8: 1–34.
- Hampton, J., J.R. Sibert, P. Kleiber, M.N. Maunder, and S.J. Harley. 2005. Fisheries: Decline of Pacific tuna populations exaggerated? *Nature* 434: E1–E2. doi:[10.1038/nature03581](https://doi.org/10.1038/nature03581).
- Hilborn, R. 2007. Managing fisheries is managing people: What has been learned? *Fish and Fisheries* 8: 285–296.
- Højsgaard, S., U. Halekoh, and J. Yan. 2006. The R Package geepack for generalized estimating equations. *Journal of Statistical Software* 15: 1–11.
- IATTC. 2004. Fishery Status report. Tunas and billfishes in the Eastern Pacific Ocean in 2003. 2. IATTC.
- IATTC. 2015. Fishery status report. Tunas, billfishes and other pelagic species in the Eastern Pacific Ocean in 2014. 13. IATTC.
- Johannes, R.E., M.M. Freeman, and R.J. Hamilton. 2000. Ignore fishers' knowledge and miss the boat. *Fish and Fisheries* 1: 257–271.
- Juan-Jorda, M.J., I. Mosqueira, A.B. Cooper, J. Freire, and N.K. Dulvy. 2011. Global population trajectories of tunas and their relatives. *Proceedings of the National Academy of Sciences* 108: 20650–20655. doi:[10.1073/pnas.1107743108](https://doi.org/10.1073/pnas.1107743108).
- Knudsen, P.F. 1977. Spawning of yellowfin tuna and the discrimination of subpopulations. *Inter-American Tropical Tuna Commission Bulletin* 17: 117–169.
- Lopez, J., G. Moreno, I. Sancristobal, and J. Murua. 2014. Evolution and current state of the technology of echo-sounder buoys used by Spanish tropical tuna purse seiners in the Atlantic, Indian and Pacific Oceans. *Fisheries Research* 155: 127–137. doi:[10.1016/j.fishres.2014.02.033](https://doi.org/10.1016/j.fishres.2014.02.033).
- Maunder, M.N. 2002. The relationship between fishing methods, fisheries management and the estimation of maximum sustainable yield. *Fish and Fisheries* 3: 251–260. doi:[10.1046/j.1467-2979.2002.00089.x](https://doi.org/10.1046/j.1467-2979.2002.00089.x).
- Maunder, M.N., and S.J. Harley. 2006. Evaluating tuna management in the eastern Pacific Ocean. *Bulletin of Marine Science* 78: 593–606.
- McIlgorm, A. 2010. Economic impacts of climate change on sustainable tuna and billfish management: Insights from the Western Pacific. *Progress in Oceanography* 86. CLimate Impacts on Oceanic TOP Predators (CLIOTOP) CLIOTOP CLIOTOP International Symposium, 187–191. doi:[10.1016/j.pocan.2010.04.024](https://doi.org/10.1016/j.pocan.2010.04.024).
- Poos, J.J., J.A. Bogaards, F.J. Quirijns, D.M. Gillis, and A.D. Rijnsdorp. 2010. Individual quotas, fishing effort allocation, and over-quota discarding in mixed fisheries. *ICES Journal of Marine Science: Journal du Conseil* 67: 323–333.
- R Core Team. 2014. R: A language and environment for statistical computing, Vienna, Austria.
- Rijnsdorp, A.D., J.J. Poos, F.J. Quirijns, R. HilleRisLambers, J.W. De Wilde, and W.M. Den Heijer. 2008. The arms race between fishers. *Journal of Sea Research* 60: 126–138. doi:[10.1016/j.seares.2008.03.003](https://doi.org/10.1016/j.seares.2008.03.003).
- Russo, T., J. Pulcinella, A. Parisi, M. Martinelli, A. Belardinelli, A. Santojanni, S. Cataudella, S. Colella, et al. 2015. Modelling the strategy of mid-water trawlers targeting small pelagic fish in the Adriatic Sea and its drivers. *Ecological Modelling* 300: 102–113. doi:[10.1016/j.ecolmodel.2014.12.001](https://doi.org/10.1016/j.ecolmodel.2014.12.001).
- Salas, S., and D. Gaertner. 2004. The behavioural dynamics of fishers: Management implications. *Fish and Fisheries* 5: 153–167.
- Salas, S., U.R. Sumaila, and T. Pitcher. 2004. Short-term decisions of small-scale fishers selecting alternative target species: A choice model. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 374–383. doi:[10.1139/f04-007](https://doi.org/10.1139/f04-007).
- Schaefer, K.M. 1998. Reproductive biology of yellowfin tuna (*Thunnus albacares*) in the eastern Pacific Ocean. *Inter-American Tropical Tuna Commission Bulletin* 21: 205–272.
- Sibert, J., J. Hampton, P. Kleiber, and M. Maunder. 2006. Biomass, size, and trophic status of top predators in the Pacific Ocean. *Science* 314: 1773–1776. doi:[10.1126/science.1135347](https://doi.org/10.1126/science.1135347).
- Solana-Sansores, R., I. Dicante, and L.P. Arredondo-Urbe. 2009. Dinámica de la flota atunera mexicana del Océano Pacífico Oriental. *Hidrobiológica* 19: 225–232.
- Sumaila, U.R., C. Bellmann, and A. Tipping. 2016. Fishing for the future: An overview of challenges and opportunities. *Marine Policy* 69: 173–180. doi:[10.1016/j.marpol.2016.01.003](https://doi.org/10.1016/j.marpol.2016.01.003).
- Torres-Irineo, E., D. Gaertner, A.D. de Molina, and J. Ariz. 2011. Effects of time-area closure on tropical tuna purse-seine fleet dynamics through some fishery indicators. *Aquatic Living Resources* 24: 337–350. doi:[10.1051/alr/2011143](https://doi.org/10.1051/alr/2011143).
- Torres-Irineo, E., D. Gaertner, E. Chassot, and M. Dreyfus-León. 2014. Changes in fishing power and fishing strategies driven by new technologies: The case of tropical tuna purse seiners in the eastern Atlantic Ocean. *Fisheries Research* 155: 10–19. doi:[10.1016/j.fishres.2014.02.017](https://doi.org/10.1016/j.fishres.2014.02.017).
- Vaca-Rodríguez, J.G., and M.J. Dreyfus-León. 2000. Analysis of the fishing strategies of the yellowfin tuna (*Thunnus albacares*) Eastern Pacific Fishery based on Monte Carlo simulations of a density-dependent matrix model. *Ciencias Marinas* 26: 369–391. doi:[10.7773/cm.v26i3.600](https://doi.org/10.7773/cm.v26i3.600).
- Vaca-Rodríguez, J.G., and R.R. Enríquez-Andrade. 2006. Analysis of the eastern Pacific yellowfin tuna fishery based on multiple management objectives. *Ecological Modelling* 191: 275–290. doi:[10.1016/j.ecolmodel.2005.04.025](https://doi.org/10.1016/j.ecolmodel.2005.04.025).
- Van Overzee, H.M.J., and A.D. Rijnsdorp. 2015. Effects of fishing during the spawning period: Implications for sustainable management. *Reviews in Fish Biology and Fisheries* 25: 65–83. doi:[10.1007/s11160-014-9370-x](https://doi.org/10.1007/s11160-014-9370-x).
- Van Putten, I.E., S. Kulmala, O. Thébaud, N. Dowling, K.G. Hamon, T. Hutton, and S. Pascoe. 2012. Theories and behavioural drivers underlying fleet dynamics models: Theories and behavioural drivers. *Fish and Fisheries* 13: 216–235. doi:[10.1111/j.1467-2979.2011.00430.x](https://doi.org/10.1111/j.1467-2979.2011.00430.x).
- Watson, R.A., D.J. Die, and V.R. Restrepo. 1993. Closed seasons and tropical penaeid fisheries: A simulation including fleet dynamics and uncertainty. *North American Journal of Fisheries Management* 13: 326–336.
- Ye, Y., K. Cochrane, G. Bianchi, R. Willmann, J. Majkowski, M. Tandstad, and F. Carocci. 2013. Rebuilding global fisheries: The World Summit Goal, costs and benefits. *Fish and Fisheries* 14: 174–185. doi:[10.1111/j.1467-2979.2012.00460.x](https://doi.org/10.1111/j.1467-2979.2012.00460.x).
- Young, M.A.L., S. Foale, and D.R. Bellwood. 2016. Why do fishers fish? A cross-cultural examination of the motivations for fishing. *Marine Policy* 66: 114–123. doi:[10.1016/j.marpol.2016.01.018](https://doi.org/10.1016/j.marpol.2016.01.018).
- Zuur, A.F., E.N. Ieno, N. Walker, A.A. Saveliev, and G.M. Smith. 2009. *Mixed effects models and extensions in ecology with R Statistics for Biology and Health*. New York: Springer.

AUTHOR BIOGRAPHIES

Edgar Torres-Irineo (✉) is Professor at the Faculty of Sciences of the Universidad Nacional Autónoma de México within the unit UMDI located in Sisal, Yucatán, México. His research interests include fishing fleet dynamics, fisher behaviour, and fisheries management. Address: UMR MARBEC, IRD, Centre de Recherche Halieutique Méditerranéenne et Tropicale, Avenue Jean Monnet, BP 171, 34200 Sète, France. Address: CONACYT, Unidad Multidisciplinaria de Docencia e Investigación, Facultad de Ciencias, Universidad Nacional Autónoma

de México, 97130 Sisal, Yucatan, Mexico.
e-mail: etorresir@conacyt.mx; edgar.torres82@gmail.com;
edgar.torres@mda.cinvestav.mx

Michel Dreyfus-León is a Professor at the National Institute of Fisheries and the Faculty of Marine Sciences at the University of Baja California in Mexico. His research interests include the understating of fishers' behaviour through the use of artificial intelligence tools, and the management of tropical tuna fisheries in Mexico.

Address: Instituto Nacional de la Pesca, Facultad de Ciencias Marinas, UABC, Ensenada, Mexico.

Address: 511 E. San Ysidro Blvd 2430, San Ysidro, CA 92173-3150, USA.

e-mail: dreyfus@cicese.mx

Daniel Gaertner is a Researcher at the *Institut de recherché pour le développement* within the research unit MARBEC located in Sète, France. His research interests include tropical tunas' stock assessment, fishing strategies, and analysis of capture-recapture data.

Address: UMR MARBEC, IRD, Centre de Recherche Halieutique

Méditerranéenne et Tropicale, Avenue Jean Monnet, BP 171, 34200 Sète, France.

e-mail: daniel.gaertner@ird.fr

Silvia Salas is a Professor at the Department of Marine Resources at Cinvestav Mérida. His research interests include fishing fleet dynamics, socio-economics of small-scale fisheries, and fisheries management.

Address: Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional, Km 6 Antigua Carretera a Progreso, Cordemex, CP 97310 Mérida, Yucatán, Mexico.

e-mail: ssalas@mda.cinvestav.mx; marquez.silvia@gmail.com

Paul Marchal is a Professor at the Ifremer institute in the *Laboratoire Ressources Halieutiques de Boulogne*. His research interests include fish stock assessment and mixed fisheries modelling mainly in the North Sea.

Address: Channel and North Sea Fisheries Department, IFREMER, 150 Quai Gambetta, BP 699, 62321 Boulogne s/mer, France.

e-mail: paul.marchal@ifremer.fr