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# Drifting fish aggregation devices as a tool to study oceanic marine protected areas

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## ABSTRACT

To meet global conservation targets, there is a growing effort to establish oceanic (waters >200 m depth) marine protected areas (oMPAs). However, despite substantial evidence for benefits of coastal MPAs to fish and fisheries, the effectiveness of oMPAs has been challenging to assess robustly. This is mainly because targeted data collection is expensive, so research often relies on catch data restricted to areas outside oMPA boundaries. Here we explore the use of drifting fish aggregating devices (dFADs) as a novel method to assess the effectiveness of oMPAs. We used acoustic data from 902 dFADs deployed by the fishing industry that drifted across the US Pacific Islands Heritage Marine National Monument around Palmyra Atoll – providing data both inside and outside the oMPA – to study spatial variation in tuna biomass density. Using a generalised additive mixed model with a suite of environmental covariates, we found the relationship between tuna biomass density and many environmental covariates made intuitive ecological sense with respect to known tuna behaviour, providing confidence in the model. We found no measurable increase in tuna biomass density inside the oMPA. This finding could have been influenced by the low fishing pressure around this particular oMPA, and regions with greater contrast in fishing pressure might show different results. This research highlights the utility of dFADs as a cost-effective tool for future studies to assess tuna biomass, especially in regions difficult or costly to sample as oMPAs.

## 1. Introduction

Marine protected areas (MPAs) are a powerful conservation tool for biodiversity (Lubchenco and Grorud-Colvert, 2015). Increasingly, oceanic MPAs (oMPAs), those protected areas beyond the 200-m depth contour of the continental shelf (Blanluet et al., 2023), are being declared to meet objectives of international conservation agreements, including the Kunming-Montreal Global Biodiversity Framework target 3, to protect 30 % of marine areas (https://www.cbd.int/gbf/). To ensure adequate representation of Earth's ecosystems in protected areas, more oceanic habitats will need to be protected (Blanluet et al., 2023). As most oceanic habitats are in the high seas, there is now further opportunity for conservation of these areas with the recent agreement of the UN High Seas Treaty (https://www.un.org/bbnj), which lays the groundwork for a global mechanism to establish MPAs in waters beyond national jurisdiction.

Although oceanic marine protected areas (oMPAs) have broad objectives, including pelagic and benthic biodiversity conservation and potential fisheries benefits, most scientific studies emphasise fisheries benefits (Blanluet et al., 2023; Gilman et al., 2019). While the conservation benefits of coastal MPAs for exploited populations are clear (Gell and Roberts, 2003; Di Lorenzo et al., 2020; Grorud-Colvert et al., 2021), the evidence for benefits of oMPAs is equivocal (Blanluet et al., 2023). The high mobility of pelagic fauna may pose a challenge for area-based

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management (Breen et al., 2015). Further, fisheries data (i.e., catch per unit effort), the main information currently used to sample tuna populations in oceanic environments (Letessier et al., 2017), are limited to fished areas. Thus, following the closure of an oMPA, these studies are limited to sample in the vicinity of the MPA and cannot document the variation of tuna population inside the MPA (Blanluet et al., 2023; White et al., 2020), and direct evaluations of the benefits of oMPAs have been difficult because of the high-cost of fisheries-independent sampling.

To assess the potential conservation benefits of oMPAs, most studies have investigate tuna because they are the main exploited species in oceanic environments (Ortuño Crespo and Dunn, 2017). Tuna fisheries mainly use longlines and purse seines. Over the past 20 years, purse seine fleets have largely moved from free-school searching, using sonars and natural markers such as birds or dolphins to find tuna aggregations, to deploying drifting fish aggregating devices (dFADs) to attract and retain tuna (Fonteneau et al., 2013). A dFAD (Fig. 1B) generally comprise a simple raft equipped with a GPS and a basic echosounder device, and a long tail of net or rope to attract tuna and slow the drift. dFADs are now ubiquitous in the tropical and equatorial zone of the Atlantic, Pacific and Indian Oceans. In the Western Pacific alone, between 40,000 and 60,000 dFADs are deployed each year (Lopez et al., 2020; Escalle et al., 2021a).

Although tuna fishing fleets have substantially benefited from this technological leap (Ehrhardt et al., 2017), conservation and fisheries science could also potentially benefit from this network of drifting platforms (Moreno et al., 2016). For example, dFADs can be used to study tuna aggregation behaviour (Orue et al., 2019b) or build fisheries-independent indicators for stock assessment (Baidai et al., 2020; Escalle et al., 2021b; Uranga et al., 2024). Notably, dFADs cross exclusive economic zones (EEZ) and MPA boundaries alike, making them a promising tool to sample tuna both inside and outside oMPAs. The lack of data within oMPAs because of the reliance on fisheries catch data has been a blind spot in assessing their ecological benefits (White et al., 2020).

Here, we assessed the potential of using dFADs as a sampling platform to investigate tuna biomass density differences inside and outside of an oMPA. We used data from dFADs collected in the vicinity of the protected island of Palmyra Atoll (part of the US "Pacific Islands Heritage Marine National Monument",PIHMNM; Fig. 1A, C). We used data from 902 satellite and echosounder buoys attached to dFADsto explore whether tuna biomass density inside the unfished oMPA was higher than in waters surrounding the MPA which were open to tuna fishing. Data were obtained through the Palmyra "FAD Watch Program", an agreement between The Nature Conservancy (TNC) and several purse seine fishing companies to mitigate dFAD groundings on Palmyra's sensitive coral reef ecosystem.

## 2. Material and methods

The Pacific Remote Islands Marine National Monument (PRIMNM), now the Pacific Islands Habitat and Marine National Monument (PIHMNM), was established around several United States Pacific Island territories, including Palmyra Atoll, in 2009 (Fig. 1A). Following its extension in 2014, it became the third-largest MPA globally in terms of surface area.[1] The PIHMNM's primary objectives include protecting habitats, ecosystems, and biodiversity, reducing human impacts, and supporting exploited fish populations (Office of the Press Secretary, 2014; Blanluet et al., 2023)

The protected area around Palmyra Atoll, part of a broader 53,503 km$^2$ MPA that includes Kingman Reef, was not a major focus for tuna fisheries before or after the establishment of the closed area in 2009. Effort levels in its vicinity are low within the US Exclusive Economic Zone (EEZ), with moderate fishing activity in other nearby zones (Figures S1 and S2, Western and Central Pacific Fisheries Commission (WCPFC) public data). As such, the fisheries context around Palmyra reflects the typical characteristics of many offshore MPAs in the Pacific, including its remoteness (e.g., 5300 km from New Zealand and 1700 km from Hawaii), limited fishing history (Blanluet et al., 2023; Hilborn et al., 2025), and large size, which encompasses a range of habitats from nearshore island environments to depths $>$ 4000 m.

Palmyra Atoll within the PIHMNM was selected for this case study due to the availability of high-resolution dFAD trajectory data associated with the TNC FAD Watch program. Comparable data were not available for other offshore MPAs at the time of the study. While the PRIMNM is indeed relatively small in spatial extent (53,503 km$^2$) compared to the broader migratory range of skipjack tuna, it is representative of many recently implemented offshore MPAs in the Pacific that have been placed in low fishing effort zones (Blanluet et al., 2023), often to minimise conflict with industrial fisheries. Our primary goal was to demonstrate the utility of a new spatial approach for assessing the efficacy of oMPAs. We acknowledge that future application of this method to larger oMPAs with greater baseline fishing pressure would provide a more robust test, pending availability of suitable dFAD data.

### 2.1. Data collection and processing

The dFAD manufacturer Satlink provided the dFAD data in the US EEZ around Palmyra Atoll (a box with ~350 kmsides), which included the PIHMNM protected area and the close vicinity (Fig. 1C). The Kiribati EEZ in the southeast was not sampled. The dataset only includes information from companies that were collaborating on the project, although these companies are likely to own the majority of dFADs in the area, as the primary fishing zones of other companies are farther afield.

Satlink dFADs provide data on date, position and fish biomass density. Date and position data were initially every 24 h from July to December 2021, then upgraded from January 2022 to every 4 h, to facilitate recovery operations. Biomass data were obtained every 2 h through the dFAD-mounted SIMRAD echosounders acquisitions. As dFAD biomass and position data were not synchronised, we estimated the position of each biomass measurement at the time the biomass was recorded using a linear interpolation between the previous and the next position. Acquisitions of biomass data comprised an ensemble of 32 pings echo-integrated by layer over 5-min periods (Lopez et al., 2016). The "backscattering volume strength" (Sv) obtained was stored and converted to an estimation of biomass internally using the "target strength" of a horizontally oriented 5-kg skipjack tuna (Satlink, personal communication). The highest biomass value over the 2 h period is then sent to the satellite and added to the dataset.

The echosounder range is from 3 to 115 m, with a 32° beamwidth, separated in 10 layers of 11.2 m, each with an independent biomass density value. To remove plankton and small fish from the acquisition, only Sv values over $-45$ kHz are considered in the echo-integration. Biomass density values $<1$ t by layer are neglected, and the echosounder saturates for biomass density value $>63$ t by layer. Each dFAD is calibrated by the manufacturer in a tank before delivery. Two Satlink buoy types are included in the dataset: the ISL+ characterised by a SIMRAD ES12 transducer and emitting a pulse at 190.5 kHz and 120 W; and the SLX+ (the large majority of the buoys), characterised by a SIMRAD ES16 transducer, emitting a modulated pulse at 200 kHz and 200 W.

Data were collected from 1st August 2021–30 April 2023. During this time, dFADs with at least one position acquired in the sampled area were detected, with some dFADs crossing the area several times over the period. The longest, uninterrupted track in our data set is 65 days, although dFADs averaged 5 days in the sampling area. Following the recommendation of Orue et al. (2019a), we removed every dFAD with a speed $>$ 3 knots, considering that these are likely to be onboard a vessel. We have no previous information on the fishing history and soak time of dFADs before they entered our area. Further, we have no information on

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[1] https://mpatlas.org/large-mpas/, from Marine Conservation Institute

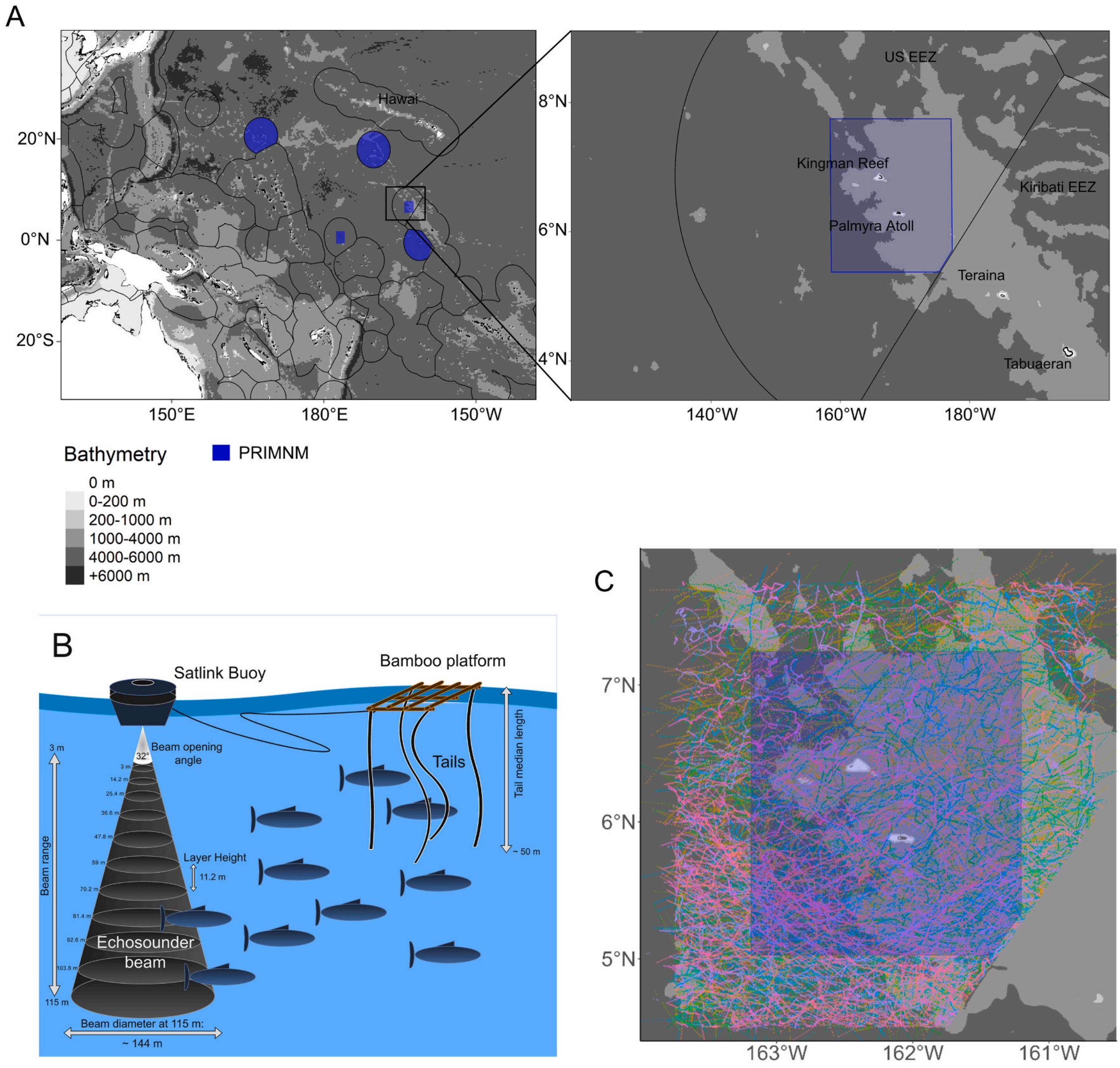

**Fig. 1.** Study context. (A) Map of the "Pacific Islands Habitat and Marine National Monument" (PIHMNM) in the Pacific Ocean, with an inset of the US exclusive economic zone around Palmyra Atoll. (B) A schematic of a drifting fish aggregating device (dFAD). (C) The 902 dFAD trajectories in the current study – the colours are used to help distinguish individual dFAD tracks.

potential fishing events in our dataset. We considered every dFAD that left the oMPA for > 3 days as a new dFAD in our analysis, to take account that it could have been fished whilst outside the area. We also assumed that the fish biomass density measured by the dFADs is predominantly composed of tuna because the dFADs algorithm uses the backscattering of skipjack tuna as a reference Target Strength (Lopez et al., 2016) to transform acoustic data to biomass, and there is strong evidence that most of the biomass recorded around dFADs is from tuna (Lopez et al., 2017a; Orue et al., 2019b), at least for the deeper layers (>20 m, Lopez et al., 2016). Data too close to the Islands (<10 km from their centres) were removed due to the risk of misinterpreting the sea floor as tuna biomass.

For the purposes of this study, we assumed that all satellite buoys in the dataset were attached to dFAD structures. While data from the FAD Watch Program indicate that a small proportion (<5 %) of buoys are recovered without associated raft or netting material—likely due to degradation or detachment over time—these cases are rare. It is possible that buoys drifting without a submerged structure exhibit different movement patterns; however, without consistent metadata confirming attachment status, we were unable to systematically differentiate between buoy-only and dFAD-attached trajectories in our dataset. This remains a potential source of uncertainty, though we consider it unlikely to substantially affect our results given the low frequency of such events.

Acoustic biomass estimates from echo-sounder buoys are widely used by fishers as indicators of tuna presence, but they are imperfect proxies for actual tuna biomass, particularly at the scale of individual buoys (Baidai et al., 2020; Escalle et al., 2021b). These estimates can be influenced by species composition, depth distribution, and behavioural patterns that affect detectability. However, when analysed aggregate across large datasets, these data can provide useful insights into spatial and temporal patterns in tuna association with dFADs (Baidai et al., 2020; Escalle et al., 2021b; Uranga et al., 2024). In this study, we first used high-resolution (2-hourly) data from our large number of buoys to analyse tuna spatial biomass patterns. In a second time, we fitted a statistical model to examine the influence of spatial, temporal, and environmental predictors—including oMPA presence—on tuna biomass.

We used an Inverse Distance Weighted interpolation (IDW, via the 'gstat' package in R; Pebesma, 2004) for generating a map of tuna biomass spatial distributions, aggregated over depth layers. Four different settings of the smoothing parameter - the inverse distance weighting power (idp) - were tested in the IDW function in the R package gstat inverse-distance-weighted map of tuna biomass: 0.25, 0.5, 0.75, and 1. We show the map of tuna biomass density based on the IDW smooth as the deviation from the mean across all depth layers (~3.37 t) for a idp of 0.75 in Fig. 2, when maps for other values of idp are

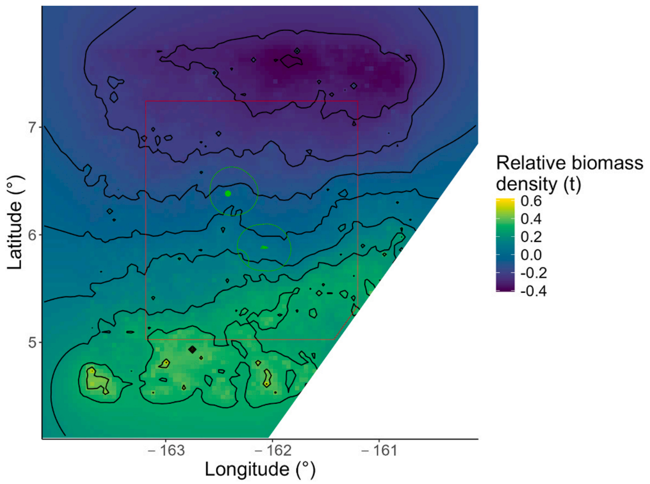

**Fig. 2.** Map of the anomaly in mean tuna biomass (t) in the region. This is based on an inverse distance weighted smoothing (IDW) of the biomass data collected by all the dFADs in the study summed over all depth layers for each 2-hourly interval, after subtracting the mean of 3.37 t. The Pacific Remote Island Marine National Monument (in red) and the position of Kingman Reef and Palmyra Atoll and the National Wildlife Refuge boundaries (in green) are shown.

presented in figure 5 of SI. IDW maps for each year and season are also presented in figure 6 of SI.

### 2.2. Generalised additive mixed model

Tuna biomass density associated with dFADs is influenced by many temporal and spatial environmental variables (Baidai et al., 2020; Capello et al., 2016; Lopez et al., 2017b; Orue et al., 2020). We use a Generalised Additive Mixed Model (GAMM, Wood, 2020) to disentangle the spatial effect of the oMPA from other predictors affecting the tuna biomass density (using the mgcv R package, Wood, 2020). GAMMs are able to handle many non-linear predictors, are relatively robust to collinearity between predictors, and can include cyclic effects such as day-night cycles (Wood, 2020).

We used a GAMM to isolate the potential effect of the oMPA on tuna biomass density whilst adjusting for the effect of a suite of temporal and environmental variables on tuna biomass density. The response variable was the maximum tuna biomass (tonnes) per 2 h time period for each depth layer, corresponding to $n = 199\ 394$ single data points. The GAMM included the dFAD identification number as a random effect to capture individual differences in each dFAD in terms of their physical and acoustic configuration and calibration, deployment history, and the multiple data generated from each dFAD.

Fish catch data are commonly zero inflated (i.e., the data contain an excess of zeros) (Arcuti et al., 2013; Thorson, 2018) and it was same for our fish biomass density data from dFADs. To account for zero inflation, it is typical to use a hurdle model (Thorson, 2018). However, this method can complicate interpretation because two sub-models are combined (Li et al., 2011). We thus used a Tweedie distribution model that could handle zeros and positive data (Li et al., 2011). A Tweedie distribution can be considered a mix of a Poisson (Tweedie power parameter $p = 1$) and a Gamma (Tweedie power parameter $p = 2$) distribution, where $p$ will be fixed by the model between 1 and 2 (Li et al., 2011).

GAMM equation (in R mgcv format, Wood, 2020) are presented in equation 1. We considered four temporal predictors in the GAMM. The first was Time (days), that measure since how long a single dFADs stayed in our dataset. The second was the Time of day (hours), as tuna exhibit a well-known daily aggregation/dispersion behaviour (Fréon and Dagorn, 2000). The third temporal variable was Season, to capture seasonal migrations of tuna (Shadwick et al., 2013), where tuna might leave or return to Palmyra. The last temporal variable was Years, to investigate the inter-annual variability between the two sampling years (August 2021 to July 2022 and August 2022 to July 2023) and potential links of tuna biomass to the El Niño southern oscillation (Lehodey et al., 1997).

We included three spatial predictors in the GAMM. The first was presence in MPA, which represents the presence Inside/Outside of each dFAD position to investigate the potential effect of the oMPA on tuna biomass density. The second spatial predictor was the Depth Layer (m), which represents the different depths that tuna biomass density were recorded. To capture the potential daily migration pattern of tuna, we included an interaction between Depth Layer and Time of day, which could also provide some clue to species composition, as different species prefer different depths (Lopez et al., 2017a). The last spatial predictor included was the distance to the nearest dFAD (km), based on the hypothesis that dFADs in close proximity may share tuna biomass (Stehfest et al., 2013). However, this variable is based only on the dFADs included in our dataset. We acknowledge that other dFADs not captured in our data—such as those from non-U.S. fleets—may also influence tuna distribution in the vicinity, but these cannot be accounted for in this analysis. Two other spatial predictors were considered but removed from the final model as they were highly collinear with other predictors. The first one was the longitude/latitude interaction, which provided inconsistent results with other predictors in the model. The second was bathymetry, but it was highly collinear with the MPA predictor, as the oMPA was centred on two islands.

Environmental oceanographic variables can also affect tuna biomass density and distribution (Lopez et al., 2017b) and are used by fishermen to optimise fishing. We used six environmental predictors in the GAMM, four of which represented surface conditions: Salinity (unitless), Chlorophyll a (mg.m$^{-3}$), Current velocity (m.s$^{-1}$), and Sea surface temperature (°C). Two other environmental predictors were included: Thermocline depth (m) because the position of thermocline is important for many tuna species (Schaefer et al., 2009; Matsumoto et al., 2016); and Moon fraction (unitless) because as moon illumination could potentially affect tuna foraging behavior (Scutt Phillips et al., 2019). Environmental predictors other than Moon fraction were obtained from the model Copernicus (European Union-Copernicus Marine Service, 2016), and had a grid resolution of 0.083°. Moon fraction was calculated using the R package “suncalc”.

An alternative approach using the maximum biomass per dFAD per day as the response variable in a GAMM was also tested. This simplified model yielded results that were qualitatively similar to those from the full depth-resolved analysis. However, model performance was reduced, with a notably lower proportion of deviance explained. This decline likely reflected the loss of temporal and vertical resolution, which are important given diel vertical migration patterns and species-specific depth preferences. As a result, we retained the depth-integrated biomass estimates, which provided greater explanatory power and ecological relevance for our study objectives.

## 3. Results

From August 2021 to July 2023, a total of 902 Satlink buoys associated with dFADs and belonging to the collaborating fishing companies crossed the sampling area boundaries (Fig. 1C). The inverse distance weighted smoothing of the tuna biomass density distribution in the PIHMNM suggested that there was no increase in tuna biomass density in the oMPA compared with immediately adjacent waters (Fig. 2). Mean tuna biomass density (sum over all the depth layers) varied little across the region (+/- 0.4 t), but was highest in the south and lowest in the north, with little observable impact of Palmyra Atoll or the oMPA. However, these data were collected across different temporal (e.g., years, seasons, time of day) and environmental conditions (sea surface temperature and chlorophyll), and from different dFADs that may have been assembled differently, all of which could influence the results.

After adjusting for temporal and environmental covariates, as well as accounting for the random effect of individual dFADs in the GAMM, we found a statistically significant difference in predicted tuna biomass density inside versus outside the oMPA ($p = 0.0043$). However, the direction of the effect was opposite to expectations: mean tuna biomass density inside the oMPA was slightly lower ($0.100 \pm 0.013$ t) than outside ($0.102 \pm 0.013$ t) (Fig. 3a). While statistically significant, the effect size is minimal and unlikely to be ecologically meaningful. This result reinforces the interpretation that there is no observable increase in tuna biomass density within the oMPA.

The most significant predictor of tuna biomass density in the GAMM was the interaction between the Depth layer and Time of day. We found tuna biomass density around dFADs to be significantly driven by the day/night cycle (Fig. 3d), with tuna biomass density associated with dFADs peaking at sunrise (5 am), declining during the day, and lowest just before nightfall (~4 pm). The greatest amplitude in the daily cycle was deeper in the water column, and there was a strong decrease in the amplitude shallower, with the surface layer exhibiting little change. There was also a slight shift in timing of the biomass density peak with depth: deeper layers peak around 5 am, whereas mid layers (from 36.6 m to 81.4 m) peaked between 3 am and 5 am.

Other temporal predictors in the GAMM were less important. Tuna biomass density over Time (Fig. 3e) was marked by a peak in the first few days each dFAD entered the study region, followed by a decrease over time. Tuna biomass density varied significantly seasonally (Fig. 3c), with a peak during summer (July-September) and a low during winter (January-March), with spring and autumn having intermediate biomass density. There is also a significant difference in tuna biomass density between the two years of sampling (Fig. 3b), with greater biomass in 2021–2022 than in 2022–2023.

There were several important environmental predictors in the GAMM. Tuna biomass density was significantly related with Current velocity (Fig. 3h), with higher biomass density with faster currents $> 0.5$ m $s^{-1}$. Tuna biomass density was also related to Thermocline depth (Fig. 3l), with a deeper thermocline associated with higher tuna biomass density. Tuna biomass density was significantly, positively and near-linearly related to Chlorophyll (Fig. 3j), Moon illumination (Fig. 3f) and Salinity (Fig. 3i), but there was little effect of Sea surface temperature. Finally, there was a proximity effect among dFADs, with lower tuna biomass density when Distance to nearest dFADs was $< 50$ km apart (Fig. 3g).

## 4. Discussion

To test whether the dFAD acoustic data of tuna biomass density could be used to assess the potential efficacy of oMPAs, we developed a GAMM to estimate biomass density in the PIHMNM marine reserve and the surrounding waters within the United States exclusive economic zone. While we found no observable effect of the oMPA on tuna biomass density, the interpretability of many of the covariates in the GAMM suggests that the bioacoustic data from the dFADs reflect real trends in tuna biomass density and therefore was sufficiently robust to observe changes in tuna biomass density inside and outside the oMPA. This study is the first to investigate the biomass density of tuna inside and outside an oMPA using bioacoustic data from dFADs, and will hopefully lead to similar studies of other oMPAs in the future.

### 4.1. *No detectable effect of the MPA on tuna biomass*

There have been contradictory results from studies investigating the effect of oMPAs on tuna biomass density, with some studies reporting tuna spillover (Boerder et al., 2017; Medoff et al., 2022) and others not (Chan, 2020; Gilman et al., 2020; Hampton et al., 2023; Hilborn et al., 2025), although all these studies used fisheries catch data. Tuna are highly mobile and migratory, and previous work has called into question the utility of oMPAs given the relatively small size of oMPAs (e.g., ~230 km side squares for the PIHMNM that surround Palmyra) compared to the potential daily range of tuna species associated with dFADs (skpijack *Katsuwonus pelamis*: ~80 km.$d^{-1}$; yellowfin *Thunnus albacares*: ~110–135 km.$d^{-1}$, bigeye tuna *Thunnus obesus*: ~110 km.$d^{-1}$; based on their mean swimming speed and directed movement, Shadwick et al., 2013). Others have questioned the utility of MPAs in general due to the displacement (not reduction) of fishing effort (Hilborn, 2018). Lack of evidence of differences in biomass inside and outside of oMPAs could also be a consequence of low fishing effort in the vicinity of many oMPAs before and after their closing (White et al., 2020).

Given the relatively low levels of fishing effort in the US EEZ around PIHMNM (see Supplementary Material S2 and S3), we might not expect to see significant differences in biomass inside and outside of PIHMNM. This was borne out through our analysis, which shows no evidence of tuna spillover from Palmyra and Kingman PIHMNM in the immediate vicinity of the oMPA, consistent with study of the same ecosystem based on Catch Per Unit Effort (CPUE) data (Gilman et al., 2020) and satellite positions of fishing vessels (White et al., 2020). Although we might expect a greater potential effect of an oMPA in heavily fished areas (Quinn and Deriso, 1999), low levels of fishing effort are common in many oceanic areas (White et al., 2020), so the results here might not be atypical of the case for other oMPAs. Increasing target tuna populations is usually not a direct objective of the marine reserve, nor is the marine reserve placed to provide protection to a critical life history stage of tuna (e.g., a spawning aggregation), both of which might influence the biomass seen inside vs outside the protected area. However, as was seen with the levels of fishing effort, this is not abnormal: most oMPAs are not directly designated or sited with the purpose of conserving pelagic populations (Blanluet et al., 2023).

The present study also showed that tuna biomass density around dFADs decreased slowly over time (based on the Time predictor, Fig. 3e). If there was more tuna inside than outside the oMPA, we might expect dFADs to aggregate more tuna as they crossed the MPA boundary and an increase in tuna biomass density over time whilst in the MPA. Thus, our results suggest that there was no increase in tuna biomass density after dFADs entered the MPA. Further, the overall decrease of biomass density with time suggests that dFADs did not “drain” tuna from the MPA. However, clear interpretation of the Time predictor is challenging because we did not know the last time each dFAD was fished and the residence time of tuna. This information was not readily available in the current study but could be key in future studies.

### 4.2. *The robustness of using dFADs for understanding drivers of tuna biomass*

There is compelling evidence that the bioacoustic data in the current study was sufficiently informative to understand drivers of tuna biomass density, and thus detect changes in tuna biomass density inside the oMPA. This is because many of the observed relationships were consistent with known tuna ecology. For example, tuna biomass density associated with dFADs peaked at sunrise (5 am, Fig. 3d), consistent with other work that shows tuna at that time form coherent schools in close proximity to dFADs (Schaefer and Fuller, 2013). During most daylight hours, we found that tuna stay in deeper layers around the dFAD and above the thermocline, as found by Matsumoto et al. (2016). During the early evening, we noted that tuna biomass density around the dFADs declined, likely because tuna disperse from the vicinity of dFADs for opportunistic foraging on the migrating deep scattering layer (Schaefer et al., 2009).

We also found that tuna biomass density was concentrated in deeper layers, suggesting that populations in the area comprise larger tuna species and individuals (Lopez et al., 2017b). Generally, larger tuna species such as yellowfin and bigeye tuna gather in deeper layers around dFADs, whereas smaller tuna species, such as skipjack, aggregate in shallow layers (Shadwick et al., 2013; Lopez et al., 2016). However, this

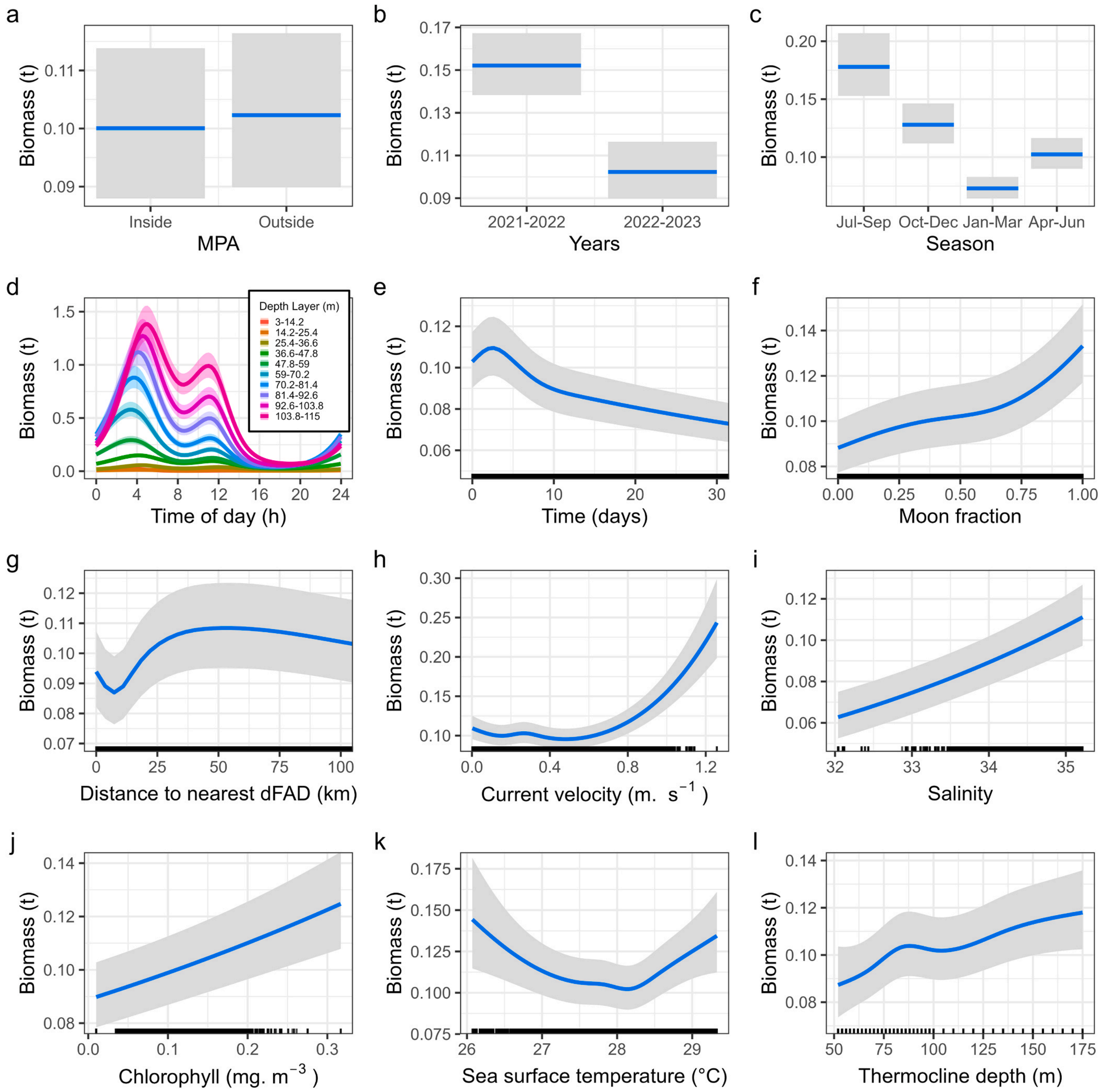

**Fig. 3.** Variation in tuna biomass (y-axis) as a function of the predictors in the Generalised Additive Mixed Model (GAMM). Confidence bands shown in grey. Tuna biomass is similar inside and outside the oMPA. Note that the larger the y-axis range in the GAMM, the more important the predictor.

separation of species/size by depth is less clear in the Central Pacific Ocean (Matsumoto et al., 2016).

Furthermore, a greatest tuna biomass density was observed in summer and autumn, which is consistent with the known longitudinal seasonal migration of skipjack tunas whereby the centre of skipjack biomass in the central Pacific Ocean is generally located further east in winter (~140°E) and further west in summer (Lehodey et al., 1997) closer to our sampling area (~160°W). This seasonal skipjack migration is strongly influenced by the El Niño-Southern Oscillation (ENSO), with stocks typically shifting eastward during El Niño and westward during La Niña events (Lehodey et al., 1997). Thus, skipjack abundance near Palmyra would be expected to decrease during La Niña conditions. However, our highest tuna biomass estimates occurred in 2021–2022, during a strong La Niña[2] (McGowan and Theobald, 2023), which suggests that local biomass dynamics may not have followed large-scale regional patterns. Given the relatively small size of our study area in the context of skipjack distribution, such deviations from expected ENSO-driven trends highlight the importance of considering local variability alongside basin-scale processes.

Most environmental predictors in the GAMM were relatively weak

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[2] https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php

but several were interpretable. We found increased tuna biomass density around dFADs at full moon (higher light levels) and lower biomass density at new moon (Fig. 3f). This is consistent with data on bigeye tuna, which have stronger hunting behaviour at new than full moon (Scutt Phillips et al., 2019), presumably foraging in low light and aggregating around dFADs in better light conditions. Higher tuna biomass density appeared to coincide with higher chlorophyll levels (Fig. 3j), which could be an index of greater prey availability (Mugo et al., 2010). Our finding that tuna biomass increased with distance to the nearest dFAD up to ~50 km (Fig. 3g) supports the 'tuna school fragmentation hypothesis' (Sempo et al., 2013), which posits that high densities of dFADs can divide aggregations into smaller groups. This pattern suggests that tuna may distribute their biomass among multiple nearby dFADs when they are closely spaced (Stehfest et al., 2013; Scutt Phillips et al., 2019). Beyond ~50 km, this effect appears to plateau, indicating that tuna are less likely to move between widely spaced dFADs. This has important implications given the high density of dFAD deployments in parts of the western and central Pacific Ocean (Escalle et al., 2021a). Such spatial concentration may alter tuna aggregation behavior, potentially reducing catchability at individual dFADs and influencing estimates of local biomass. Our results highlight the need to consider dFAD spacing in both fishery management and ecological studies of tuna dynamics based on dFADs.

### *4.3. Caveats*

Our approach differs from much of the existing literature on dFAD-derived biomass estimation (e.g. Santiago et al., 2019; Baidai et al., 2020; Escalle et al., 2021b; Precioso et al., 2022) in that we did not have access to full life-history metadata for individual dFADs (e.g. time since deployment, fishing set events) or species-validated catch data from logbooks. These limitations preclude precise biomass estimation or species-specific analyses. However, our objective was not to estimate absolute tuna abundance, but rather to assess relative variation in biomass density across space, particularly in relation to oMPA boundaries. This allows us to avoid the more complex data filtering and transformation often required to isolate unfished or early-stage dFADs (e.g. Santiago et al., 2019; Uranga et al., 2024). While we interpret variation in patterns in biomass, we caution that absolute biomass values derived from buoy data should be treated with care, given the known biases and uncertainties associated with echo-sounder readings.

As with all studies relying on acoustic data from dFADs (Orue et al., 2019b; Escalle et al., 2021b; Precioso et al., 2022), biomass density estimates must be interpreted with caution. The low-cost echosounders mounted on buoys are not designed for precise biomass estimation: they operate at lower spatial and temporal resolution compared to scientific echosounders, and their data are further compressed for satellite transmission, amplifying potential noise and error (Diallo et al., 2019). In addition, the echo-integration algorithm used by Satlink software is configured to estimate aggregations of skipjack tuna, using a reference target strength based on 5 kg individuals of this species, which lacks a swimbladder. This can lead to bias in biomass estimates when other species such as yellowfin or bigeye tuna—both of which have swimbladders—are present, particularly at greater depths.

It is also important to note that these buoys do not report biomass values below 1 tonne per layer, which may lead to underestimation of biomass when smaller aggregations are present (Navarro-García et al., 2021). Conversely, biomass can be overestimated when non-tuna species are detected or when tuna are not tightly aggregated (Wang et al., 2012). Moreover, buoy-derived estimates are highly variable on short time scales (day-to-day), reflecting not only true movement dynamics of fish under dFADs but also methodological limitations (Lopez et al., 2017b; Diallo et al., 2019). While we retained all vertical layers in our analysis to preserve internal consistency and data volume, we acknowledge that both overestimation and underestimation of biomass are possible, and this should be considered when interpreting our results. Echosounder buoys only detect tuna aggregated beneath dFADs, which represents a fraction of the total biomass in the area. The dynamics of tuna aggregation—including residence time, attraction behaviour, and turnover—remain poorly understood and may vary with oceanographic conditions, tuna behaviour, and local dFAD density (Dagorn et al., 2013). As such, the relationship between dFAD-associated biomass and total tuna abundance at the seascape scale remains uncertain and may be confounded in areas with high dFAD saturation.

We must also not that each observation by a dFAD is not truly independent of other observations from the same dFAD, as tuna are following the platform and each dFAD is simultaneously an observing and aggregating device. However, including the random effect for dFAD in the GAMM and the large number of dFADs in the dataset (n = 902) helps minimise this limitation.

### *4.4. dFADs as a scientific tool*

The interpretability of many of the predictors in the model suggest dFADs could be a robust tool for examining the efficacy of oMPAs for enhancing tuna biomass. As existing methods such as using fisheries data make it difficult to sample within oMPAs, dFADs could provide an effective alternative (Moreno et al., 2016; Blanluet et al., 2023). Tagging studies of tuna in oMPAs are an alternative, but they are limited by the low number of tagged animals, the high tag cost, and the relatively short tag lifetime (Letessier et al., 2017; Richardson et al., 2018). Although research vessels are ideally suited to sampling inside and outside oMPAs, collecting data over long time scales and in remote ocean locations is expensive. dFADs, already widely present in many ocean areas, are potentially a powerful and low-cost approach to sample tuna inside and outside oMPAs.

The current work is the first we know of to investigate the effect of oMPAs on tuna inside and outside an oMPA, at similar temporal and spatial scales to CPUE studies. At a larger scale, using the dFAD network to investigate tuna populations throughout an entire ocean could bring unparalleled insights into tuna movement, behaviour and aggregation dynamics (Moreno et al., 2016). However, dFADs also have negative ecological consequences, including potentially increasing the overexploitation of tuna resources (Dagorn et al., 2013), damaging coral reefs following collisions (Escalle et al., 2019), and causing marine pollution (Churchill, 2021). However, answering scientific questions to help better manage the ocean, using data from dFADs that are already being deployed by the fishing industry, is unlikely to increase their number. In fact, the current collaboration between TNC and several purse seine fishing companies has had the positive environmental outcome of reducing the impact of dFAD groundings on Palmyra's sensitive coral reef ecosystem. This is because once the dFADs drifted into the vicinity of the atoll, they were tracked so they could be retrieved prior to impact on the reef. For now over 50 dFADs were intercepted by TNC staff offshore (within a 6 nautical mile recovery zone) of Palmyra Atoll through the life of the Palmyra FAD watch Program, in order to stop them from having adverse impacts on the sensitive coral reef ecosystem. These efforts have strongly reduced dFAD grounding at Palmyra

## 5. Conclusion

This study presents a new method to sample tuna inside and outside oMPAs, which will hopefully be applied more frequently in the future. We found no discernable benefit of the oMPA to tuna biomass, which may be a consequence of the limited fishing immediately outside the area. More studies of oMPAs using dFADs, particularly in areas that are heavily fished, are necessary to answer the question of whether oMPAs enhance tuna stocks. Despite the objectives of oMPAs often including benefits to tuna fisheries (Kaplan et al., 2014), the primary objective of oMPAs, including the PIHMNM (Office of the Press Secretary, 2014), are to protect pelagic and benthic biodiversity and their ecosystem services (Blanluet et al., 2023). Palmyra Atoll has already proven to provide conservation benefits for sharks (White et al., 2017; Gilmour et al., 2025) and seabirds (Young et al., 2015; Gilmour et al., 2025), but potential benefits for the broader pelagic ecosystem in PIHMNM are largely unknown. Ultimately, benefits of oMPAs should be judged based on all their objectives, not just those pertaining to tuna fisheries.

## Equations

**Equation 1.** : We use the R package mgcv (Wood, 2020) to fit the GAMM. The GAMM included smooth terms s(), with k the upper limit of the degrees of freedom associated with the smooth, the basis spline bs is the type of splines of the smooth; we use the cubic regression spline for environmental variables, the cyclic cubic regression spline for time of day because its periodic, and random effects as “re”.

Biomass ~ s(time_in_dataset, k = 6, bs = "cr") + s(Chl, k = 6, bs = "cr") + s(sal, k = 6, bs = "cr") + s(temperature, k = 6, bs = "cr") + s(thermocline_depth, k = 6,bs = "cr") + s(current_velocity, k = 6, bs = "cr") + s(time_day, k = 6, by = Depth_layer, bs = "cc") + s(FAD_Name, bs = "re") + s(Moon_Illumination, k = 6, bs = "cr") + s(distance_to_nearest_dFAD, k = 6, bs = "cr") + Depth_Layer + season + years + presence_in_MPA

## CRediT authorship contribution statement

**Everett Jason:** Writing – review & editing, Formal analysis. **Wolff Nicholas:** Writing – review & editing, Formal analysis. **Kydd Pollock:** Writing – review & editing, Formal analysis. **Arthur Blanluet:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Richardson Anthony:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Sandra Neubert:** Writing – review & editing, Formal analysis. **Dunn Daniel:** Writing – review & editing, Formal analysis. **Game Edward:** Writing – review & editing, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

## Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Fishing companies provided tuna data in an agreement with The Nature Conservancy. Otherwise, there are no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2025.107474.

## Data availability

The authors do not have permission to share data.

## References

Arcuti, S., Calculli, C., Pollice, A., D’Onghia, G., Maiorano, P., Tursi, A., 2013. Spatio-temporal modelling of zero-inflated deep-sea shrimp data by Tweedie generalized additive. Statistica 73, 87–101.

Baidai, Y., Dagorn, L., Amande, M.J., Gaertner, D., Capello, M., 2020. Machine learning for characterizing tropical tuna aggregations under Drifting Fish Aggregating Devices (DFADs) from commercial echosounder buoys data. Fish. Res. 229, 105613. https://doi.org/10.1016/j.fishres.2020.105613.

Blanluet, A., Game, E.T., Dunn, D.C., Everett, J.D., Lombard, A.T., Richardson, A.J., 2023. Evaluating ecological benefits of oceanic protected areas. Trends Ecol. Evol., S0169534723002343 https://doi.org/10.1016/j.tree.2023.09.003.

Boerder, K., Bryndum-Buchholz, A., Worm, B., 2017. Interactions of tuna fisheries with the Galápagos marine reserve. Mar. Ecol. Prog. Ser. 585, 1–15. https://doi.org/10.3354/meps12399.

Breen, P., Posen, P., Righton, D., 2015. Temperate marine protected areas and highly mobile fish: a review. Ocean Coast. Manag. 105, 75–83. https://doi.org/10.1016/j.ocecoaman.2014.12.021.

Capello, M., Deneubourg, J.L., Robert, M., Holland, K.N., Schaefer, K.M., Dagorn, L., 2016. Population assessment of tropical tuna based on their associative behavior around floating objects. Sci. Rep. 6, 36415. https://doi.org/10.1038/srep36415.

Chan, H.L., 2020. Economic impacts of Papahānaumokuākea Marine National Monument expansion on the Hawaii longline fishery. Mar. Policy 115, 103869. https://doi.org/10.1016/j.marpol.2020.103869.

Churchill, R., 2021. Just a harmless fishing fad—or does the use of FADs contravene international marine pollution law? Ocean Dev. Int. Law 52, 169–192. https://doi.org/10.1080/00908320.2021.1901342.

Dagorn, L., Holland, K.N., Restrepo, V., Moreno, G., 2013. Is it good or bad to fish with FAD s? What are the real impacts of the use of drifting FAD s on pelagic marine ecosystems? Fish Fish 14, 391–415. https://doi.org/10.1111/j.1467-2979.2012.00478.x.

Di Lorenzo, M., Guidetti, P., Di Franco, A., Calò, A., Claudet, J., 2020. Assessing spillover from marine protected areas and its drivers: a meta-analytical approach. Fish Fish 21, 906–915. https://doi.org/10.1111/faf.12469.

Diallo, A., Baidai, Y., Mannocci, L., Capello, M., 2019. Towards the derivation of fisheries-independent abundance indices for tropical tuna: Report on biomass estimates obtained from a multi-frequency echosounder buoy model (M3I+) (No. WPTT. IOTC, pp. 21–54.

Ehrhardt, N., Brown, J.E., Pohlot, B.G., 2017. Desk Review of FADs fisheries development in the WECAFC region and the impact on stock assessments (Desk Review No. WECAFC/SAG/VIII/2017/5). Western Central Atlantic Fishery Commission (WECAFC), Merida, Mexico.

Escalle, L., Hare, S.R., Vidal, T., Brownjohn, M., Hamer, P., Pilling, G., 2021a. Quantifying drifting fish aggregating device use by the world’s largest tuna fishery. ICES J. Mar. Sci. 78, 2432–2447. https://doi.org/10.1093/icesjms/fsab116.

Escalle, L., Scutt Phillips, J., Brownjohn, M., Brouwer, S., Sen Gupta, A., Van Sebille, E., Hampton, J., Pilling, G., 2019. Environmental versus operational drivers of drifting FAD beaching in the Western and Central Pacific Ocean. Sci. Rep. 9, 14005. https://doi.org/10.1038/s41598-019-50364-0.

Escalle, L., Vidal, T., Vanden Heuvel, B., Clarke, R., Hare, S., Hamer, P., Pilling, G., 2021b. Project 88 final report: acoustic FAD analyses. WCPFC.

European Union-Copernicus Marine Service, 2016. Global Ocean 1/12° Physics Analysis and Forecast updated Daily. https://doi.org/10.48670/MOI-00016.

Fonteneau, A., Chassot, E., Bodin, N., 2013. Global spatio-temporal patterns in tropical tuna purse seine fisheries on drifting fish aggregating devices (DFADs): taking a historical perspective to inform current challenges. Aquat. Living Resour. 26, 37–48. https://doi.org/10.1051/alr/2013046.

Fréon, P., Dagorn, L., 2000. Review of fish associative behaviour: toward a generalisation of the meeting point hypothesis. Rev. Fish. Biol. Fish. 10, 183–207. https://doi.org/10.1023/A:1016666108540.

Gell, F.R., Roberts, C.M., 2003. Benefits beyond boundaries: the fishery effects of marine reserves. Trends Ecol. Evol. 18, 448–455. https://doi.org/10.1016/S0169-5347(03)00189-7.

Gilman, E., Chaloupka, M., Fitchett, M., Cantrell, D.L., Merrifield, M., 2020. Ecological responses to blue water MPAs. PLoS ONE 15, e0235129. https://doi.org/10.1371/journal.pone.0235129.

Gilman, E., Kaiser, M.J., Chaloupka, M., 2019. Do static and dynamic marine protected areas that restrict pelagic fishing achieve ecological objectives? Ecosphere 10. https://doi.org/10.1002/ecs2.2968.

Gilmour, M.E., Pollock, K., Adams, J., Block, B.A., Caselle, J.E., Filous, A., Friedlander, A.M., Game, E.T., Hazen, E.L., Hill, M., Holmes, N.D., Lafferty, K.D., Maxwell, S.M., McCauley, D.J., Schallert, R., Shaffer, S.A., Wolff, N.H., Wegmann, A., 2025. Multi-species telemetry quantifies current and future efficacy of a remote marine protected area. Glob. Change Biol. 31, e70138. https://doi.org/10.1111/gcb.70138.

Grorud-Colvert, K., Sullivan-Stack, J., Roberts, C., Constant, V., Horta e Costa, B., Pike, E.P., Kingston, N., Laffoley, D., Sala, E., Claudet, J., Friedlander, A.M., Gill, D.A., Lester, S.E., Day, J.C., Gonçalves, E.J., Ahmadia, G.N., Rand, M., Villagomez, A., Ban, N.C., Gurney, G.G., Spalding, A.K., Bennett, N.J., Briggs, J., Morgan, L.E., Moffitt, R., Deguignet, M., Pikitch, E.K., Darling, E.S., Jessen, S., Hameed, S.O., Di Carlo, G., Guidetti, P., Harris, J.M., Torre, J., Kizilkaya, Z., Agardy, T., Cury, P., Shah, N.J., Sack, K., Cao, L., Fernandez, M., Lubchenco, J., 2021. The MPA Guide: a framework to achieve global goals for the ocean. Science 373, eabf0861. https://doi.org/10.1126/science.abf0861.

Hampton, J., Lehodey, P., Senina, I., Nicol, S., Scutt Phillips, J., Tiamere, K., 2023. Limited conservation efficacy of large-scale marine protected areas for Pacific skipjack and bigeye tunas. Front. Mar. Sci. 9, 1060943. https://doi.org/10.3389/fmars.2022.1060943.

Hilborn, R., 2018. Are MPAs effective? ICES J. Mar. Sci. 75, 1160–1162. https://doi.org/10.1093/icesjms/fsx068.

Hilborn, R., Fitchett, M., Hampton, J., Ovando, D., 2025. When does spillover from marine protected areas indicate benefits to fish abundance and catch? Theor. Ecol. 18 (1). https://doi.org/10.1007/s12080-024-00596-2.

Kaplan, D.M., Chassot, E., Amandé, J.M., Dueri, S., Demarcq, H., Dagorn, L., Fonteneau, A., 2014. Spatial management of Indian Ocean tropical tuna fisheries: potential and perspectives. ICES J. Mar. Sci. 71, 1728–1749. https://doi.org/10.1093/icesjms/fst233.

Lehodey, P., Bertignac, M., Hampton, J., Lewis, A., Picaut, J., 1997. El Niño Southern Oscillation and tuna in the western Pacific. Nature 389, 715–718. https://doi.org/10.1038/39575.

Letessier, T.B., Bouchet, P.J., Meeuwig, J.J., 2017. Sampling mobile oceanic fishes and sharks: implications for fisheries and conservation planning: Sampling of oceanic predators. Biol. Rev. 92, 627–646. https://doi.org/10.1111/brv.12246.

Li, Y., Jiao, Y., He, Q., 2011. Decreasing uncertainty in catch rate analyses using Delta-AdaBoost: an alternative approach in catch and bycatch analyses with high percentage of zeros. Fish. Res. 107, 261–271.

Lopez, J., Moreno, G., Boyra, G., Dagorn, L., 2016. A model based on data from echosounder buoys to estimate biomass of fish species associated with fish aggregating devices. Fish. Bull. 114, 166–178. https://doi.org/10.7755/FB.114.2.4.

Lopez, J., Moreno, G., Ibaibarriaga, L., Dagorn, L., 2017a. Diel behaviour of tuna and non-tuna species at drifting fish aggregating devices (DFADs) in the Western Indian Ocean, determined by fishers' echo-sounder buoys. Mar. Biol. 164, 44. https://doi.org/10.1007/s00227-017-3075-3.

Lopez, J., Moreno, G., Lennert-Cody, C., Maunder, M., Sancristobal, I., Caballero, A., Dagorn, L., 2017b. Environmental preferences of tuna and non-tuna species associated with drifting fish aggregating devices (DFADs) in the Atlantic Ocean, ascertained through fishers' echo-sounder buoys. Deep Sea Res. Part II Top. Stud. Oceanogr. 140, 127–138. https://doi.org/10.1016/j.dsr2.2017.02.007.

Lopez, J., Román-Verdesoto, M.H., Lennert-Cody, Cleridy E., Maunder, M., Vogel, N., 2020. Float. Object Fish. Indic. https://doi.org/10.13140/RG.2.2.21748.17286.

Lubchenco, J., Grorud-Colvert, K., 2015. Making waves: the science and politics of ocean protection. Science 350, 382–383. https://doi.org/10.1126/science.aad5443.

Matsumoto, T., Satoh, K., Semba, Y., Toyonaga, M., 2016. Comparison of the behavior of skipjack ( *Katsuwonus pelamis*), yellowfin ( *Thunnus albacares*) and bigeye ( *T. obesus*) tuna associated with drifting FADs in the equatorial central Pacific Ocean. Fish. Oceanogr. 25, 565–581. https://doi.org/10.1111/fog.12173.

McGowan, H., Theobald, A., 2023. Atypical weather patterns cause coral bleaching on the Great Barrier Reef, Australia during the 2021–2022 La Niña. Sci. Rep. 13, 6397. https://doi.org/10.1038/s41598-023-33613-1.

Medoff, S., Lynham, J., Raynor, J., 2022. Spillover benefits from the world's largest fully protected MPA. Science 378, 313–316. https://doi.org/10.1126/science.abn0098.

Moreno, G., Dagorn, L., Capello, M., Lopez, J., Filmalter, J., Forget, F., Sancristobal, I., Holland, K., 2016. Fish aggregating devices (FADs) as scientific platforms. Fish. Res. 178, 122–129. https://doi.org/10.1016/j.fishres.2015.09.021.

Mugo, R., Saitoh, S.-I., Nihira, A., Kuroyama, T., 2010. Habitat characteristics of skipjack tuna (Katsuwonus pelamis) in the western North Pacific: a remote sensing perspective: Skipjack tuna habitat from RS & GIS in western NP. Fish. Oceanogr. 19, 382–396. https://doi.org/10.1111/j.1365-2419.2010.00552.x.

Navarro-García, M., Precioso, D., Gavira-O'Neill, K., Torres-Barrán, A., Gordo, D., Gallego-Alcalá, V., Gómez-Ullate, D., 2021. Aggregation times of tuna schools to fads estimated by echosounder. DATA (No. IOTC-2021-WGFAD02-INF04). IOTC.

Office of the Press Secretary, 2014. FACT SHEET: President obama to designate largest marine monument in the world off-limits to development. The White House.

Ortuño Crespo, G., Dunn, D.C., 2017. A review of the impacts of fisheries on open-ocean ecosystems. ICES J. Mar. Sci. 74, 2283–2297. https://doi.org/10.1093/icesjms/fsx084.

Orue, B., Lopez, J., Moreno, G., Santiago, J., Soto, M., Murua, H., 2019b. Aggregation process of drifting fish aggregating devices (DFADs) in the Western Indian Ocean: who arrives first, tuna or non-tuna species? PLoS ONE 14, e0210435. https://doi.org/10.1371/journal.pone.0210435.

Orue, B., Lopez, J., Moreno, G., Santiago, J., Boyra, G., Uranga, J., Murua, H., 2019a. From fisheries to scientific data: a protocol to process information from fishers' echo-sounder buoys. Fish. Res. 215, 38–43. https://doi.org/10.1016/j.fishres.2019.03.004.

Orue, B., Lopez, J., Pennino, M.G., Moreno, G., Santiago, J., Murua, H., 2020. Comparing the distribution of tropical tuna associated with drifting fish aggregating devices (DFADs) resulting from catch dependent and independent data. Deep Sea Res. Part II Top. Stud. Oceanogr. 175, 104747. https://doi.org/10.1016/j.dsr2.2020.104747.

Pebesma, E.J., 2004. Multivariable geostatistics in S: the gstat package. Comput. Geosci. 30, 683–691. https://doi.org/10.1016/j.cageo.2004.03.012.

Precioso, D., Navarro-García, M., Gavira-O'Neill, K., Torres-Barrán, A., Gordo, D., Gallego, V., Gómez-Ullate, D., 2022. TUN-AI: tuna biomass estimation with machine learning models trained on oceanography and echosounder FAD data. Fish. Res. 250, 106263. https://doi.org/10.1016/j.fishres.2022.106263.

Quinn, T.J., Deriso, R.B., 1999. Quantitative fish dynamics. Oxford University Press.

Richardson, A.J., Downes, K.J., Nolan, E.T., Brickle, P., Brown, J., Weber, N., Weber, S. B., 2018. Residency and reproductive status of yellowfin tuna in a proposed large-scale pelagic marine protected area. Aquat. Conserv. Mar. Freshw. Ecosyst. 28, 1308–1316. https://doi.org/10.1002/aqc.2936.

Santiago, J., Uranga, J., Quincoces, I., Orue, B., Grande, M., Murua, H., Merino, G., Urtizberea, A., Pascual, P., Boyra, G., 2019. A novel index of abundance of juvenile yellowfin tuna in the Indian Ocean derived from echosounder buoys. IOTC2019WPTT 21–47.

Schaefer, K.M., Fuller, D.W., 2013. Simultaneous behavior of skipjack (Katsuwonus pelamis), bigeye (Thunnus obsesus), and yellowfin (T. albacares) tunas, within large multi-species aggregations associated with drifting fish aggregating devices (FADs) in the equatorial eastern Pacific Ocean. Mar. Biol. 160, 3005–3014. https://doi.org/10.1007/s00227-013-2290-9.

Schaefer, K.M., Fuller, D.W., Block, B.A., 2009. Vertical Movements and Habitat Utilization of Skipjack (Katsuwonus pelamis), Yellowfin (Thunnus albacares), and Bigeye (Thunnus obesus) Tunas in the Equatorial Eastern Pacific Ocean, Ascertained Through Archival Tag Data, in: Tagging and Tracking of Marine Animals with Electronic Devices, Reviews: Methods and Technologies in Fish Biology and Fisheries. Springer Netherlands, Dordrecht, pp. 121–144. https://doi.org/10.1007/978-1-4020-9640-2_8.

Scutt Phillips, J., Peatman, T., Escalle, L., Leroy, B., Smith, N., 2019. Electron. tagging Mitig. bigeye Yellow tuna Juv. purse seine Fish.

Sempo, G., Dagorn, L., Robert, M., Deneubourg, J., 2013. Impact of increasing deployment of artificial floating objects on the spatial distribution of social fish species. J. Appl. Ecol. 50, 1081–1092. https://doi.org/10.1111/1365-2664.12140.

Shadwick, R.E., Schiller, L.L., Fudge, D.S., 2013. Physiology of swimming and migration in tunas. Swimming Physiology of Fish: Towards Using Exercise to Farm a Fit Fish in Sustainable Aquaculture. Springer, pp. 45–78.

Stehfest, K.M., Patterson, T.A., Dagorn, L., Holland, K.N., Itano, D., Semmens, J.M., 2013. Network analysis of acoustic tracking data reveals the structure and stability of fish aggregations in the ocean. Anim. Behav. 85, 839–848. https://doi.org/10.1016/j.anbehav.2013.02.003.

Thorson, J.T., 2018. Three problems with the conventional delta-model for biomass sampling data, and a computationally efficient alternative. Can. J. Fish. Aquat. Sci. 75, 1369–1382. https://doi.org/10.1139/cjfas-2017-0266.

Uranga, J., Lopez, J., Grande, M., Lennert-Cody, C.E., Quincoces, I., Maunder, M.N., Aires-da-Silva, A., Merino, G., Murua, H., Santiago, J., 2024. Echosounder buoy derived tropical tuna biomass indices in the Estern Pacific Ocean (8th Meeting No. FAD-08-02). IATTC Ad-Hoc Permanent Working Group on FADs, La Jolla, California (USA).

Wang, X., Xu, L., Chen, Y., Zhu, G., Tian, S., Zhu, J., 2012. Impacts of fish aggregation devices on size structures of skipjack tuna Katsuwonus pelamis. Aquat. Ecol. 46, 343–352. https://doi.org/10.1007/s10452-012-9405-0.

White, T.D., Carlisle, A.B., Kroodsma, D.A., Block, B.A., Casagrandi, R., De Leo, G.A., Gatto, M., Micheli, F., McCauley, D.J., 2017. Assessing the effectiveness of a large marine protected area for reef shark conservation. Biol. Conserv. 207, 64–71. https://doi.org/10.1016/j.biocon.2017.01.009.

White, T.D., Ong, T., Ferretti, F., Block, B.A., McCauley, D.J., Micheli, F., De Leo, G.A., 2020. Tracking the response of industrial fishing fleets to large marine protected areas in the Pacific Ocean. Conserv. Biol. 34, 1571–1578. https://doi.org/10.1111/cobi.13584.

Wood, S.N., 2020. Inference and computation with generalized additive models and their extensions. Test 29, 307–339.

Young, H.S., Maxwell, S.M., Conners, M.G., Shaffer, S.A., 2015. Pelagic marine protected areas protect foraging habitat for multiple breeding seabirds in the central Pacific. Biol. Conserv. 181, 226–235. https://doi.org/10.1016/j.biocon.2014.10.027.