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The challenge of assessing the effects of drifting fish aggregating devices on the behaviour and biology of tropical tuna

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Abstract :

Fishers have intensively used drifting fish aggregating devices (DFADs) over the last three decades to facilitate their catch of tropical tunas. DFADs increase purse-seine efficiency, potentially increasing tuna fishing mortality. They could also have impacts on tuna natural mortality and reproductive potential, and assessing the consequences of their presence at sea on tuna populations is a challenge. The use of DFADs results in a major increase in the number of floating objects, which are spatially heterogeneous at sea. To date, no converging scientific results exist regarding the effects of DFADs on the large-scale movements and behaviour of tuna, mainly due to the difficulty of disentangling the respective roles of DFADs and environmental factors. Some biological indices show that tuna condition is lower when associated to a floating object than in a free-swimming school. However, it is not clear whether this is the cause or the consequence of the association nor if it has long-term effects on individuals' fitness. Further scientific progress requires (i) the collection of time series of indicators to monitor habitat change, individual behaviour, individual fitness, and population dynamics and (ii) experimental studies to identify the underlying behavioural and biological processes involved in associative behaviour. The extent of the modification of the surface habitat by the massive deployment of DFADs and the current uncertainty of the possible long-term consequences on the individual fitness and dynamics of tuna populations argue for the need for increased awareness of this issue by Regional Fisheries Management Organisations regulating tuna fishing.

Keywords : DFAD, ecological effects, ecological trap, fish behaviour, fisheries management, tuna

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Introduction

Many fish species are known to associate with floating objects (FOBs; Castro et al., 2002; Fréon & Dagorn, 2000), with the first known descriptions of fishers exploiting these associations dating from 200 AD in the Mediterranean Sea by the Roman author Oppian (cited in Taquet, 2013). In particular, the use of FOBs to facilitate the capture of tropical tunas (skipjack SKJ – *Katsuwonus pelamis*; yellowfin YFT – *Thunnus albacares*; and bigeye BET – *T. obesus*), has undergone rapid expansion in recent decades, as a result of the growing importance of these floating structures to the strategy and efficiency of tropical tuna purse seine fleets (Dagorn et al., 2012; Fonteneau et al., 2000, 2013; Leroy et al., 2013; Miyake et al., 2010). Since the onset of the tropical tuna purse seine fishery, fishers took advantage of the associative behaviour of tunas with floating objects and actively searched for natural floating objects (NLOGs) to improve their catches (Greenblatt, 1979 ; Hallier and Parajua, 1999 ; Scott et al. 1999). Towards the end of the 1980s, fishers began to build and deploy man-made drifting fish aggregating devices (DFADs), and to attach radio buoys to locate them (Ariz et al., 1999 ; Hallier and Parajua, 1999 ; Hall et al. 1992 ; Scott et al. 1999 ; Lopez et al., 2014; Marsac et al., 2014; Moreno et al., 2007; Morón, 2001; Stéquert & Marsac, 1986). DFADs are commonly composed of a floating structure (such as a bamboo or metal raft with buoyancy provided by corks, etc.) and a submerged structure (made of ropes, old netting, canvas, weights, etc.). During the last two decades, radio buoys have been replaced by GPS buoys communicating via satellite directly with fishing vessels. In the last decade (2010-2020), most DFADs have been equipped with echo-sounder buoys, providing estimates of aggregated biomass (Lopez et al., 2014). Some fleets also use supply vessels to maintain their DFAD array and to inform the fishing vessels of tuna aggregations (Arrizabalaga et al., 2001; Ramos et al., 2013). DFADs represent very efficient fishing tools that increase the catchability of tunas, leading purse-seine fleets to target preferentially associated schools and expanding their fishing grounds (Lopez et al. 2014, Fonteneau et al. 2015, Lennert-Cody et al. 2019).

Over time, given the growing contribution of purse seine fleets to world tuna catches and the increasing importance of DFAD fishing in the strategy of purse seine fleets, managing DFADs has become a priority for all tuna Regional Fishery Management Organisations (tRFMOs). In this paper we will use “operational” or “active” buoys to designate buoys attached to a FOB that are tracked by one or several purse seine fishing vessel(s). Tuna RFMOs set limits of the number of operational buoys (with the very first limit by the IOTC, Indian Ocean Tuna Commission, in 2015) to mitigate the different risks induced by the deployment and use of DFADs (most recent resolutions: IOTC Res 19/02, ICCAT Rec 22-01, IATTC Res C-21-04, WCPFC CMM 2021-01). Fishing at FOBs was demonstrated to increase by-catch rates, compared to fishing on free-swimming schools (Amandé et al. 2012, Escalle et al. 2018), and to increase the proportion of small BET and YFT (IOTC 2022). As a consequence, spawning capacity and yield per recruit of BET and YFT populations are reduced worldwide by purse-seine vessels setting on DFADs and catching small individuals of these two species (Davies et al. 2014).

Other major DFAD-related measures concern the design of these objects, following the discovery of sharks getting entangled in the netting composing the structure of DFADs (Filmalter et al. 2013). Limiting the pollution induced by DFADs in the ocean is also in front of the agendas of tRFMOs, after realizing the large quantity of plastic used in DFADs and the large numbers of DFAD beaching events in sensitive coastal ecosystems (Escalle et al. 2019, Imzilen et al. 2021, 2022). However, other impacts on tuna populations (unrelated to fishery vulnerability) and ecosystems may be induced by the increased presence of DFADs in their habitat (Marsac et al. 2000, Bromhead et al. 2003, Hallier & Gaertner 2008). Despite the limits on operational buoys, DFADs number in the water has increased (Dagorn et al. 2013a, Maufroy et al. 2017, Imzilen et al. 2021, Dupaix et al. 2021). As such, while logs and branches have always been components of the habitat of tropical tunas (originating from rivers, mangroves or shorelines), the massive use of man-made DFADs has changed their habitat, which could have numerous consequences on tropical tuna's fitness, resulting in population-level impacts. TRFMOs primarily focus on developing management schemes to address the known effects of DFADs on catches (particularly of small YFT and BET, as well as bycatch) or their stranding on coasts. Through the increase of FOB density they induce, DFADs could also impact tropical tuna natural mortality and reproductive potential, hence, altering their individual fitness which could have population-level consequences. Despite the high level of uncertainty on these impacts, assessing them is central as they could act as compounding factors and worsen the increase of fishing mortality induced by DFADs. Hence, there is a need to assess whether DFADs can alter the life history parameters and behaviour of tunas. This will help to determine the magnitude of DFADs impacts on natural mortality relative to those on fishing mortality and to manage the number of DFADs deployed at sea if negative impacts on natural mortality are suspected or demonstrated.

Theoretical background

Fisheries management, as practiced since the 1940s, was based on the ecosystem theory but focused mainly on fishing activity and target fish resources (Garcia et al. 2003). In the early 2000s, following an abundant documentation of the relative failure of conventional fisheries management (Garcia & Grainger 1997; Pauly et al. 2002; Sutinen & Soboil 2003), the need for other frameworks emerged, among which the Ecosystem Approach to Fisheries (EAF; FAO 2003; Garcia et al. 2003). The EAF stresses the need to recognize “more explicitly the interdependence between human well-being and ecosystem health and the need to maintain ecosystems productivity for present and future generations” (Ward et al. 2002). As opposed to conventional fisheries management, EAF calls for the consideration of human activities other than fisheries and the generation of knowledge on ecosystem processes to understand the consequences of human activities (Figure 1, Pikitch et al. 2004). When considering the impact of a fishery on a target species, conventional fisheries management only considered the increase of fishing mortality induced by the removal of individuals, and the impact of such removals on the reproduction (Figure 1). However, fisheries can also modify the habitat of the target species, ultimately impacting their natural mortality and their reproductive potential. For example, habitat modifications induced by fisheries can impact benthic community composition and sensitivity (Neumann et al., 2016), and could also affect fish recruitment (Macura et al., 2019). The EAF framework stresses the need to determine and assess the extent of fisheries impacts not only on the fishing mortality (as done by conventional fisheries management), but also on species habitat and the induced impacts on natural mortality and reproductive potential.

Noting the increasing number of floating objects being deployed by fishers since the 1990s, some scientists hypothesized that this modifies tropical tuna habitat, leading to an ecological trap and to an increase of their natural mortality (Marsac et al., 2000). An ecological trap occurs when animals are misled by cues that were previously correlated with the habitat quality but no longer are, due to anthropogenic influences (Sherley et al. 2017, Swearer et al. 2021). Such impacts form the basis of the ecological trap theory and result in the preferential selection of low-quality habitats by animals, when better alternatives exist (Battin, 2004; Schlaepfer et al., 2002). It is worth noting that, depending on the definition, an ecological trap can occur without any anthropogenic influence (Robertson & Hutto, 2006; Swearer et al., 2021; Teske et al., 2021). In this paper, we will consider that ecological traps occur because of a sudden anthropogenic change in the environment, i.e. in the case of tropical tuna, the modification of their surface habitat by the increased deployment of DFADs (Gilroy & Sutherland, 2007; Hallier & Gaertner, 2008; Schlaepfer et al., 2002). The ecological trap concept has been proposed regularly in the face of human-induced environmental changes and offers an important framework to assess the impact of human induced habitat changes on species fitness (Hale & Swearer 2016; Swearer et al. 2021).

Although fish associative behaviour with FOBs has been known for almost two millennia (Oppian, 200 AD), the reasons underlying it are still largely unknown, complicating the assessment of DFADs impacts on tuna natural mortality and reproductive potential. To date, two main hypotheses have been retained to explain the associative behaviour of tropical tuna: the *indicator-log* and the *meeting-point* hypotheses (Hall 1992, Dagorn 1995). Based on these two hypotheses, the impacts of DFADs on tropical tuna would differ. The indicator-log hypothesis posits that tuna would associate with FOBs to find rich areas (Hall 1992; Castro et al. 2002). NLOGs are mainly parts of trees and they would indicate rich areas because they originate from rivers and can accumulate in rich frontal zones (Castro et al. 2002; Hallier & Gaertner 2008). The associative behaviour would then result from an evolutionary process where tuna use FOBs to stay in rich waters. Under this behavioural hypothesis, by modifying the distribution and density of FOBs, DFADs could act as ecological traps and retain and/or attract tuna in areas that are detrimental to them, inducing an increase of their natural mortality (Figure 2).

The meeting-point hypothesis states that pelagic species would associate with FOBs to facilitate school formation (Fréon & Dagorn 2000). Provided that tuna can detect floating objects from further away than they can detect other schools, associating with floating objects could increase the probability to encounter other conspecifics. Schooling behaviour can be seen as a trade-off between, on the one hand, increasing protection against predators, encounters of reproduction partners, foraging and swimming efficiency and, on the other hand, increasing detection by predators and inter-individual competition (Rubenstein 1978; Ioannou 2017; Maury 2017). Considering the meeting-point hypothesis, DFADs, by increasing the density of FOBs, could provoke the dispersion of tuna, disturbing schooling behaviour and ultimately impacting their natural mortality (Figure 3, Fréon & Dagorn 2000). It is important to note here that this potential impact on tuna natural mortality does not constitute an ecological trap: by associating with FOBs, tuna try to meet with conspecifics and do not use FOBs as cues to select a habitat. Hence, in the framework of the EAF and to consider all the potential impacts of DFAD fishing on tropical tuna, we need to characterize the extent to which DFADs change the density and distribution of FOBs. We also need to determine if this modification impacts tropical tuna natural mortality and reproductive potential, impact which is behaviourally mediated.

Almost 20 years ago, Demptser & Taquet (2004) made a systematic review of the published literature on FADs and concluded that further research should assess the use of DFADs by pelagic species, the mechanisms underlying their associative behaviour and the ecological consequences of the presence of DFADs at sea on pelagic fish stocks. Since then, several papers reviewed existing evidence and/or proposed future research directions to address the impacts of DFADs on tropical tuna (Dagorn et al. 2013b, Evans et al. 2015, Davies et al. 2014, Fonteneau et al. 2015, Leroy et al. 2013, Taquet 2013, Pons et al. 2023). Yet, most of these papers, except those by Taquet (2013) and Pons et al. (2023), addressed these impacts at a regional scale and all were mainly focussing on the impacts of DFADs on fishing mortality, even though they mentioned potential impacts on natural mortality. A recent review by Pons et al. (2023) assessed the advantages and drawbacks of fishing with DFADs at the global scale. They identified seven sources of concern for FAD fishing, including habitat perturbation generated by DFADs and the risk of DFADs acting as ecological traps. On this question, they highlighted the difficulty of testing the ecological trap hypothesis. The objective and originality of our review paper is not to look at the impacts of fishing at DFADs but to examine in depth if the presence of DFADs in the ocean could impact the natural mortality and reproductive potential of tropical tuna. This particular question has never been fully addressed, precluding management bodies from having a complete view of the current knowledge. To examine the sustainability of DFAD fisheries, in line with the EAF framework, it is therefore essential not only to examine the impact of DFADs on fishing mortality, but also on natural mortality and reproductive potential. The effects induced by DFADs on tuna behaviour and biology could thus act as compounding factors to the already known effects on increasing fishing mortality. An in-depth literature review provides an overview of the state of the art in this area, identifies knowledge gaps, and proposes future research priorities. Following the ecological trap hypothesis framework and the consideration that these impacts are necessarily behaviourally mediated, this paper is structured around four major questions:

i) How much do DFADs change the habitat of tropical tunas?

ii) Do DFADs modify the migration and the schooling behaviour of tropical tunas?

iii) Do DFADs affect the life history parameters of tropical tunas?

iv) What are the scientific challenges to fill the knowledge gaps?

How much do DFADs change the habitat of tropical tunas?

Tropical tuna are circumtropical pelagic fish, preferring relatively warm and stratified waters, with larvae preferring waters above 24°C (Artetxe-Arrate et al., 2021). SKJ, YFT and BET are considered epipelagic species which also exploit the mesopelagic zone, especially during the day when searching for deep scattering prey organisms (Schaefer et al. 2009). Whereas small and large BET are capable of spending long periods of time in the mesopelagic zone, due to their thermal physiology, SKJ and YFT are only able to remain for brief periods of time when exhibiting repetitive bounce diving behaviour. Hence, tropical tuna have distinct ecological niches at different stages of their life-history (Artetxe-Arrate et al., 2021). Tuna habitat can be defined as the surface and sub-surface ocean waters, with all the abiotic (temperature, dissolved oxygen, etc.) and biotic (prey, competitors, etc.) parameters important for their biological functions. Among the components of tuna habitats, floating objects represent very peculiar features. They represent physical discontinuities that tuna are known to associate with, at least at given stages of their life-history (mainly adult SKJ, small YFT and BET). Human activities (logging, coastal development, shipping, etc.) modified the number of floating objects at sea, in some cases even before modern purse-seine tuna fishing began (Caddy & Majkowski, 1996; Thiel & Gutow, 2005). Some of these activities may have consistently increased (coastal development, shipping), whereas others, such as logging, may have varied due to increased global trade and subsequent deforestation of some areas (Caddy & Majkowski, 1996). In addition, environmental changes also affect the production and movement of floating objects (e.g. floods, El Niño events, tsunamis), with global warming supposed to increase the frequency of extreme events. In recent years, the increasing use of DFADs by fishers raised several questions about the sustainability of this practice. The primary concern is the increase in fishing efficiency and mortality induced by DFAD fishing (Dagorn et al. 2013b, IOTC 2022, Pons et al. 2023). However, the increase of the number of floating objects could also induce impacts on tuna behaviour and life history parameters, which are more challenging to address. In the current framework of the ecosystem approach to fisheries (Pikitch et al. 2004), the assessment and management of these impacts is fundamental.

Two types of floating objects (referred to as FOBs) are commonly considered: (i) man-made FADs (which can be drifting, DFADs, or anchored, AFADs) and (ii) natural objects (trees, branches, etc., referred to as NLOGs) or artificial objects (wreckage, nets, washing machines, etc., referred to as ALOGs) that are not deployed for the specific purpose of fishing (collectively called LOGs) (Gaertner et al., 2018). Fishers fish on DFADs and LOGs and can equip any of those objects with a satellite-tracking buoy, becoming therefore a fishing tool monitored by a fishing vessel. For the particular question of habitat change addressed in this study, only DFADs – which are the dominant type of man-made floating objects used in the industrial purse seine fishery (Dagorn et al. 2013a, Maufroy et al. 2017, Dupaix et al. 2021) – are considered and not AFADs.

DFADs increase the density of FOBs. This change could impact tuna associative behaviour, tuna migrations, tuna fitness, then potentially resulting in an increase of tuna natural mortality and a decrease of reproductive potential and, hence, impacts on tuna populations. Changes in the “FOB component” of habitat due to DFADs can be assessed by estimating and comparing densities of objects (with information on their nature: LOGs or DFADs) and distance between objects (nearest neighbour), with both parameters being closely related. These parameters depend upon the rates at which DFADs are added or removed from the ocean (by sinking, beaching or retrieved by humans), as well as their drift. For every oceanic spatio-temporal unit (e.g. region and season), comparing these parameters with those of natural floating objects and for all types together (natural and artificial) is challenging, the primary concern being to identify the origin of the floating object.

The number of DFADs have regularly increased (Maufroy et al. 2017), but it is necessary to put this in perspective with respect to all floating objects. Using data from observers onboard tuna purse seine vessels in the Indian Ocean (IO), noting all FOBs encountered when the vessel cruises, Dupaix et al. (2021) highlighted a drastic increase in the total number of floating objects in the western IO, from 2006 to 2018, with multiplication factors greater than 2 in every region and reaching as high as 60 in some areas (e.g. Somali area). The entire western IO is affected, with DFADs comprising over 85% of the total FOBs and DFADs contributing to reduce the distances between floating objects (mean distances between DFADs and between NLOGs of 37 km and 89 km, respectively, in 2014-2018). The impact of DFADs on tuna habitat reducing the distance between FOBs was observed in the study both when considering all DFADs or only randomly encountered DFADs (objects which do not belong to the vessel or its fishing company), to account for a potential sampling bias. Phillips et al. (2019a), using data from 2016 and 2017 and Lagrangian simulations in the Western and Central Pacific Ocean (WCPO), also showed an increase in FOB densities induced by DFAD deployments, and observed a shift of the area with the highest FOB densities, from the North-Eastern area of the Bismark Sea to the Tuvalu archipelago. Unfortunately no similar detailed study has been conducted in the other oceans, precluding from estimating the extent of the change of the habitat of tunas due to the addition of new floating objects globally.

Most of the management effort by tRFMOs is focused on the monitoring and control of satellite-tracked buoys attached to floating objects (either to DFADs or to LOGs), emitting positions (and other variables) to vessels and qualified as operational buoys, as this variable is strongly related to fishing effort. This also explains why most scientific studies prioritized the estimate of operational buoys rather than the number of DFADs in the ocean (Table 1). Currently, all tRFMOs have implemented a limit on the instantaneous number of operational satellite buoys per vessel, and, except in the Atlantic Ocean (AO), limited the re-activation of buoys while at sea, but only the IOTC has limited the number of buoys purchased and in stock per year, per vessel (IOTC Res 19/02, ICCAT Rec 22-01, IATTC Res C-21-04, WCPFC CMM 2021-01). This clearly reflects a lack of concerted action worldwide to limit the number of new floating objects deployed in the oceans. Even under the limit of active DFADs at sea per vessel, the actual total numbers of DFADs in the ocean could have increased. So far, few studies have produced estimates of the total number of DFADs deployed annually, with estimations providing a range of 81,000 to 121,000 deployments worldwide, but these global estimates were made a decade ago (Baske et al., 2012; Gershman et al., 2015; Scott & Lopez, 2014). As a comparison, AFADs seem to be less numerous worldwide (13,000 AFADs estimated in Scott & Lopez 2014), although there may be few areas with very high densities of AFADs, such as Indonesia (5,000-10,000, Proctor et al. 2019), the Philippines or Papua New Guinea.

In practice, despite efforts by tRFMOs to require the submission of DFAD data, accurately determining a simple indicator such as the total number of DFADs that are drifting in the world’s oceans is a major challenge. The easiest way would be to monitor the number of deployments through logbooks or onboard observers or set up a FAD register (see Res 23/02 of the IOTC). The number of operational buoys does not correspond to the number of DFADs in the water (and/or deployed) as some buoys can be attached to LOGs, can be deactivated, and some DFADs may lack positional trackers, but it can be used as a proxy to illustrate the trend in numbers. Therefore, as the number of operational buoys does not effectively limit DFAD deployments, the number of DFADs in the water and/or deployments could be larger than the limits adopted by the tRFMOs. Under the assumption that the number of natural floating objects remains relatively constant, the increasing number of electronic buoys used reflects an increase of the number of FOBs. In recent years, DFAD deployments were stable in the WCPO (2011-2019; Escalle et al. 2020), decreased in the IO (2016-2021; IOTC, 2022), increased in the Eastern Pacific Ocean (EPO, 2015-2020; Lopez et al. 2021) and buoy deployments increased in the AO (2007-2013; Maufroy et al. 2017). Hence, a characterisation of DFAD deployment trends at the global scale is needed. However, the clear trend in the number of DFAD sets or DFAD catches (Floch et al., 2019;

FIRMS Global Tuna Atlas cited in IOTC, 2021; Restrepo et al., 2017) suggests that DFAD deployment has also increased.

Do DFADs modify the migration and the schooling behaviour of tropical tunas?

DFADs may affect both the movements of tunas and their schooling behaviour. Large-scale movements of tunas can be impacted in the following two ways: (i) DFADs could cause tunas to relocate to new areas and (ii) they could increase residence times in some areas. If DFADs were to have an impact on tuna's large-scale movements, it could increase their natural mortality by retaining or relocating them in unsuitable areas or disturbing their migration (Marsac et al. 2000). Although we are currently not able to quantify, and even demonstrate, such impacts, they could result in population-scale effects. Ideally, the best approach for investigating such potential effects would be to compare the large-scale movement patterns of tunas before and after the period in which the increase of DFAD numbers occurred (i.e. before or after the 1990's). Historical data to assess large-scale movement patterns before fishers started to massively deploy DFADs, necessary for this type of analysis, exist only in the WCPO (Kim 2015) and in the EAO (Cayré et al. 1986) and we do not know of any long-term study that compared movement patterns before and after DFAD use increased.

Effects on individual large-scale movements

Wang et al. (2014) found that the spatial dynamics of free-swimming school sets in the WCPO were influenced by the onset of El Niño Southern Oscillation (ENSO) events, while these events had no effects on the location of floating-object-associated school sets. This result does not allow us to conclude on the impact of DFADs on population movements, as catch data reflects the movements of the available catchable portion of the stocks and the catchability of different set types (e.g. DFAD sets catching smaller individuals than the free-school sets), and not the true movements of fish.

Hallier & Gaertner (2008) analysed conventional tagging data of SKJ and YFT in the Eastern Atlantic Ocean (EAO). Different migratory directional patterns and displacement rates were observed between fish recaptures associated with DFADs and those in free-swimming schools. Displacement rates were significantly larger for both YFT and SKJ recaptured in association with DFADs (13 and 15 nm/day, respectively) than those recaptured in free-swimming schools (3 and 4.5 nm/day, respectively), which suggests that DFADs could relocate tunas to new areas. In the IO, Stehfest and Dagorn (2010) found similar results for SKJ, YFT and BET, but with lower displacement rates differences than in the AO. Hallier and Gaertner (2008) interpreted these results as indicating significant modifications of migratory patterns due to associations with DFADs, suggesting an influence of DFAD association strong-enough to disturb tropical tuna migratory patterns. However, Stehfest and Dagorn (2010) argue that it could only reflect an artefact of the non-uniform distribution of DFAD fishing. Also, authors of both studies agree that school type at recapture might not be representative of the associative history of individuals before their recapture. Using an advection-diffusion model, Kim (2015) also showed that including a DFAD attraction component to the model better fitted SKJ tagging data in the WCPO, suggesting an effect of DFADs on SKJ migratory patterns. Comparing DFAD induced movements in the 2000s with those in the 1990s, they showed that the rising DFAD density increased this modification of migration patterns. These studies were the only ones to assess differences of movement patterns induced by DFADs and, due to species and ocean differences, more studies would be needed to interpret these results at a global scale.

DFADs potential to modify large-scale movements of tunas can be investigated through archival tags by comparing tuna movements with the general drift patterns of DFADs. In the equatorial EPO, evaluation of archival tag data sets from 96 BET (54-159 cm in length, 1-5.5 years of age) tagged between 2000 – 2005 (Schaefer et al., 2009; Schaefer & Fuller, 2010) did not support the hypothesis that the most probable BET tracks were related to the general drift patterns of DFADs. This suggests that the large-scale spatial dynamics of BET are not strongly influenced by DFADs at the densities and conditions found in the EPO. However, in the Central Pacific Ocean (CPO), a predominantly eastward extensive dispersion of BET tagged with conventional tags and archival tags was observed (Schaefer et al., 2015). The authors explain the strong regional fidelity of BET in the equatorial EPO by the high concentration of food, leading to their residence and retention in that area. In the equatorial CPO, the strong eastward-flowing North equatorial countercurrent and BET searching for higher prey concentrations could explain the predominantly eastward dispersion of BET.

Effects on individual fine-scale movements

The possibility of DFADs influencing tuna movements could be evaluated by determining the impact of DFADs on tuna's fine-scale movements. First, if DFADs increase the percentage of the time tuna spend associated with floating objects, it will increase their availability to fishers. It can therefore have an impact by increasing catchability and fishing mortality. In addition, a modification of fine-scale tuna movements could also result in population-scale impacts by inducing larger-scale movement changes resulting in an increase in natural mortality. In this section, we focus on the modifications of tuna fine-scale movements induced by DFADs and on how these changes could result in large-scale movement modifications. Fine-scale movements can be assessed through the measurement of the time tuna spend associated with DFADs and the time they spend unassociated (or between two DFAD associations). It could be considered that the longer tunas remain associated with DFADs, the larger the influence DFADs could have on their large-scale movements.

Acoustic tags and archival tags (only when a species exhibits a distinct vertical behaviour when associating with a floating object, as observed for BET or sometimes YFT) have been used by scientists to measure these parameters (Table 2). Passive acoustic tagging studies on DFADs revealed that the majority of residence times of tunas (i.e. continuous periods of time spent associated with a given DFAD) were of a few days. Mean values ranged from 0.2 to 4.6 days for SKJ (Dagorn et al., 2007; Govinden et al., 2021; Matsumoto et al., 2014, 2016), from 1.0 to 6.6 days for YFT and 1.4 to 10 days for BET (Dagorn et al., 2007; Govinden et al., 2021; Matsumoto et al., 2016, Phillips et al. 2019b). Long associations, however, have been observed on rare occasions – *e.g.* 27 days for YFT in the IO (Govinden et al., 2021) and up to 18, 50 and 30 days for SKJ, YFT and BET respectively, in the WCPO (Phillips et al. 2017, Phillips et al. 2019b). A recent study in the EAO (Tolotti et al., 2020) reported significantly larger mean residence times for the three tuna species, from 9 days

(SKJ) to 19 days (YFT) and 25 days (BET), with record values of 55 days and 600 km travelled associated to a DFAD for both BET and YFT.

These studies suggest that residence times at a single DFAD vary between oceanic regions and species. Without more studies, it is difficult to assess whether the long DFAD associations observed are restricted to specific areas and time periods, or if they can often occur. In fact, even short residence times at single DFADs as those observed in the Indian and Pacific oceans do not prove that arrays of DFADs cannot influence large-scale movements. In an array of DFADs, a tuna can “switch” from one DFAD to a neighbouring one, which could retain it in the array. It is therefore important to also measure the time tunas spend between two associations (or unassociated), or in other words, the total percentage of time a tuna spends associated over long periods. This variable is likely to depend on the density of all floating objects in the area. So far, very few durations between two DFAD associations have been measured using acoustic tags because it is difficult to locate and exhaustively instrument with acoustic receivers all DFADs in an area.

In the WCPO, 25 BET, 6 YFT and 2 SKJ displayed “homing” behaviour by returning to the same DFAD with absences greater than a day (Phillips et al. 2019b). Most of these absences were short for BET (median: 3.2 days) and longer for YFT (median: 10.5 days) but with a low sample size not allowing to be conclusive. In the other tropical oceans, even fewer tunas were observed performing such homing behaviour: one BET in the AO (out of 23 tagged fish, Tolotti et al., 2020), one YFT and two SKJ in the IO (out of 31 and 17 tagged fish respectively, Govinden et al., 2021), and these absences lasted less than two days.

Because BET and sometimes YFT exhibit different vertical behaviour patterns when associated or non-associated with floating objects (Holland and Brill 1990, Abascal et al. 2018), archival tags have been used to assess residence times at and between floating objects, and therefore percentage of days associated with floating objects, without the need to instrument all objects with acoustic receivers. Using satellite archival tagging data where individual BET tracks could be recorded over several months or even years, the percentage of time associated with floating objects was estimated to be between 4 % and 17 %

depending on the size of the fish and the oceanic region (Fuller et al., 2015; Phillips et al., 2017; Schaefer & Fuller, 2010, Leroy et al. 2013, Schaefer & Fuller 2002). Associative and non-associative behaviour with floating objects have also been described with archival tags for YFT (Phillips et al., 2017; Schaefer et al., 2009; Schaefer & Fuller, 2013, Leroy et al. 2013), with estimates of the percentage of time spent associated with floating objects between 10% and 23%. These percentages are much lower than those estimated from acoustic telemetry data (e.g. 75 % for small BET based on the measurements in Phillips, et al. 2019b).

This inconsistency between studies using different tagging methods could result from the size of tagged individuals or the way the percentage of time spent by tuna associated and non-associated is calculated. Individuals monitored with archival tags were generally larger (fork length: 50-146 cm YFT and 46-102 cm BET in Phillips et al. 2017, 51-134 cm BET in Fuller et al. 2015, 88-134 cm BET in Schaefer & Fuller 2002, 54-159 cm BET in Schaefer & Fuller 2010) than those marked with passive acoustic tags (38-90 cm BET in Phillips et al. 2019), even though size ranges largely overlap. This suggests that small BET spend a higher proportion of their time associated with FOBs than large individuals. This agrees with observed size distributions of DFAD catches, where smaller individuals are caught, and with the negative correlation between BET individual length and percentage of time associated found by Schaefer & Fuller (2002). However, Schaefer et al. (2009) found lower association percentages with archival tags on small tunas (10.4 and 15.9 % of the time associated for 51-60 cm FL YFT and 65-99 cm FL BET respectively) than the work of Phillips et al. (2019) with acoustic tagging. This could suggest a potential bias in the different methodologies that need to be further investigated. A small percentage of time associated with floating objects would indicate no or little influence of DFADs, while a high percentage could indicate a potentially significant influence of DFADs which could result in impacts on large-scale movements.

We are therefore far from understanding the effects of different densities of floating objects on tuna fine-scale movements nor the link between fine-scale and large-scale movements. Most electronic tagging efforts have been done on YFT and to a lesser extent BET, but more behavioural data are clearly needed for all three tropical tuna species. One of the main difficulty is to disentangle the effects of DFADs from the impacts of other external signals (e.g. prey density) which can also influence tuna associative behaviour (Lopez et al. 2017, Nooteboom et al. 2023, Schaefer et al., 2009, Schaefer & Fuller, 2010).

Effects on schooling behaviour

DFADs could also affect schooling behaviour, which can have a wide range of consequences on the life-history parameters and the movements of tunas. Dagorn & Fréon (1999) and Fréon & Dagorn (2000) suggested that tuna could associate with floating objects for social advantages such as facilitating the formation of larger schools. Tuna associative behaviour would have been selected because schooling behaviour provides several evolutionary advantages. It can be seen as an evolutionary trade-off between (i) increasing protection against predators, swimming and foraging efficiency, mating, and (ii) increasing detection by predators and intra- and inter-specific competition (Rubenstein 1978; Ioannou 2017; Maury 2017). Hence, if tuna use FOBs for social behaviour, the number of FOBs could affect the size of schools and therefore reduce their evolutionary advantages, which could impact both tuna survival and reproduction, resulting in population-scale impacts. To date no result has been obtained on tropical tuna from DFADs regarding this question. If floating objects facilitate the schooling behaviour of tunas, then the deployment of large numbers of DFADs may have effects on school size, either by facilitating the formation of large (but less) schools or decreasing school size with DFADs offering too many aggregation sites (Figure 3, Dagorn et al., 2010). DFADs could also modify the size structure of tuna schools, allowing the formation of large aggregations composed of several unassociated schools of different size structures (Wang et al. 2012). Sempo et al. (2013) modelled the impact of the increasing deployment of DFADs on the distribution of social fish species such as tunas. They demonstrated that for social species, increasing the number of DFADs does not necessarily lead to an increase in the total amount of tuna associated with DFADs, a non-intuitive result. Capello et al. (2022) also showed that the number of DFADs with associated schools and the size of associated schools were not linearly related to the total number of DFADs and that this relationship varied according to the considered social scenario.

Do DFADs modify the life-history parameters of tropical tunas?

The increasing number of DFADs at sea also raises questions regarding their effect on the feeding strategy of tropical tuna, and related energy-dependent traits such as tuna health (monitored for example by body condition), growth, reproduction and natural mortality.

Effects on feeding

In his review on DFAD impacts on tropical tunas, Taquet (2013) recommended comparative analyses of stomach contents on tropical tunas. Such analyses have shown that small-sized tunas may not feed while associated with DFADs in the Atlantic (Hallier & Gaertner, 2008; Ménard et al., 2000), Indian (Grande et al., 2013; Jaquemet et al., 2011; Zudaire et al., 2015, Malone et al. 2011, Hallier & Gaertner, 2008) and Western and Central Pacific (Machful et al., 2021) oceans. Small YFT and SKJ captured in DFAD-associated schools had a higher fraction of empty stomachs, lower stomach fulness or daily food rates (in the EAO; Hallier & Gaertner 2008, Ménard et al. 2000; and in the IO, Hallier & Gaertner 2008), and lower prey weight (in the IO; Grande et al. 2013, Zudaire et al. 2015) than those captured in free-swimming schools. These results support the hypothesis that the quantity of prey present in DFAD assemblages is not sufficient to sustain the dietary requirements of large aggregations of small-sized tuna commonly found at DFADs (several tens of tons) (Fréon & Dagorn, 2000). Hence, if tuna were to spend more time associated with FOBs, due to the increase in the number of FOBs induced by the deployment of DFADs, it could impact their feeding behaviour, potentially resulting in an increase in their natural mortality. However, evidence is still too scarce to allow the determination and quantification of this potential increase of natural mortality. Also, except in Hallier & Gaertner (2008), the influence of the sampling time of tunas on the stomach content was not taken into account. Purse seine vessels mainly fish on DFADs at dawn (Forget et al., 2015) and on free-swimming schools during daytime. First, feeding activities are believed to often take place in the early evening on organisms performing diel vertical migration between the deep scattering layer and the surface (Schaefer & Fuller, 2002), resulting in prey being fully digested by the time the fish are caught and sampled, at dawn. Second, free-swimming schools of tunas are almost exclusively caught when actively feeding at the sea surface, hence higher levels of stomach fullness are to be expected. Nevertheless, the association of tunas with DFADs could also affect the composition and quality of their diet, as shown for YFT in the Western IO (WIO) and WCPO and for SKJ in the WCPO (Zudaire et al. 2015, Allain et al. 2010). Differences of diet composition were observed for these species, that may be due to their associative behaviour despite the above-mentioned sampling bias, with associated tuna in the WCPO feeding on shallower prey than free-swimming tunas (Allain et al. 2010), which is in agreement with YFT staying closer to the surface when associated (Holland and Brill, 1990, Schaefer et al. 2009).

Independently of the trophic role of DFADs, the deployment and the drift trajectories of DFADs could create new zones of high floating object densities, which may be unfavourable for the foraging success of tunas, resulting in an increase of natural mortality (Marsac et al. 2000). In the Western Indian Ocean, Jaquemet et al. (2011) found that in “rich” forage areas, DFADs have no impact on the feeding pattern of tunas, whereas in “poor” forage areas, tunas associated with DFADs had lower stomach fullness compared to tunas in free-swimming schools. The authors suggested that the impact of DFADs on feeding success could be location-dependent, leading them to emphasize the possible detrimental effect on the condition of tuna associated with DFADs if associated tunas drift towards areas with poor forage resources. However, such an effect relies on the assumption that a tuna’s probability to depart from a DFAD is independent of their local environment which seems in disagreement with behavioural studies (Fuller et al. 2015, Nooteboom et al. 2023).

In the Pacific Ocean, Hunsicker et al. (2012) observed that predation on SKJ and YFT by large pelagic fishes sampled from DFAD sets was greater than for those captured via other fishing methods (e.g. free-swimming schools). These authors concluded that by aggregating small-sized SKJ, YFT, and BET, DFADs enhance their vulnerability to predators such as sharks and billfishes, and thus increase natural mortality of small sized tunas. The foraging arena theory (Ahrens et al. 2012), considers that individuals alternate between vulnerable and invulnerable states, being only part of their time available to their predators. If the risk of being predated increases when associated with a FOB, by increasing the time they spend associated, DFADs could increase the time tropical tuna spend in a “vulnerable” state which would increase their mortality by predation. To date, the study by Hunsicker et al. (2012) is the only study assessing the impact of DFADs on tuna vulnerability to predators, hence additional data from other regions would be needed for further testing these assumptions.

Effects on body condition

Individual condition can be seen as a proxy of individual’s fitness, as it can impact both the individual survival and reproduction (Lloret et al. 2014). Tuna condition has been investigated using different methods: biometric condition factors (e.g. plumpness), and biochemical indices (e.g., fat and water contents, lipid class composition). Gaertner et al. (1999) in a preliminary investigation did not find evidence of a morphometric difference between free-swimming school or DFAD-caught tunas in the EAO. But Marsac et al. (2000) in the EAO and Hallier & Gaertner (2008) in the WIO found that individuals associated with DFADs were in lower condition than those in free-swimming schools, using morphometric indicators (thorax width or girth, plumpness of fish) as fish health indicators. This result suggests that DFADs, by reducing individual condition, could increase tuna natural mortality and/or impact their reproduction (specifically for SKJ who also associate to DFADs when they are mature). Robert et al. (2014) measured the condition of SKJ using BIA (Bioelectrical Impedance Analysis), a non-invasive field tool that estimates body water content (inversely correlated with body fat content), and determines total lipid and main lipid class concentrations. They confirmed the lower condition of SKJ associated with floating objects compared to those in free-swimming schools. Because the studied area (Mozambique Channel, WIO) is naturally rich with NLOGs and had undergone little habitat modifications due to DFADs at the time of the study (Dagorn et al., 2013a, Dupaix et al. 2021), the authors concluded that before the use of DFADs, tunas associated with logs could have also been in lower condition than tunas in free-swimming schools. These results can mean that (1) a lower measured condition could reflect normal variations and does not necessarily imply detrimental physiological consequences, or (2) some specific areas where NLOGs have always been in high numbers could also have negatively impacted the condition of tunas that passed through and stayed in these areas.

As a lower condition measured at DFADs does not necessarily imply longer-term detrimental consequences for tuna, there is a need to monitor tuna condition and other biological parameters on a longer term and determine if they are influenced by the density of DFADs in the area. Dupaix et al. (2023), using length-weight data from 1987 to 2018 in the WIO, found no decreasing trend of YFT condition over the studied period, during which the number of DFADs has increased. Hence, this study, using one morphometric indicator as a proxy for condition (Le Cren's relative condition factor), suggests the absence of a long-term impact of DFADs on YFT condition, under the conditions encountered in the WIO in the last three decades. Nevertheless, it should be noted that other factors could also have counteracted potential negative effects of DFADs on tuna condition.

Studies that investigated potential DFAD impacts on tuna condition mainly suggest that the condition of associated tuna is lower than that of free-swimming tuna. These results are reinforced by the example of the preparation of katsuobushi (shaved dried SKJ) in Japan. Indeed the Japanese tuna industry prefers SKJ caught on DFADs as they have less fat than those from free-swimming schools (Nishida, pers. comm.). However, Sardenne et al. (2016), when comparing biometric and biochemical indicators found inconsistencies due to a high variability of biometric indicators with season and ontogeny. They concluded that biometric indicators measured on whole tuna (e.g. thorax girth, fish plumpness, Le Cren's K_n) should be interpreted with caution as they may not always reflect the energetic condition measured in the tissues of the fish. Experimental validation of the condition factors used is needed to determine the potential impacts and the underlying mechanisms of the difference in tuna condition. For example, condition factors could be calibrated and validated by monitoring them during fasting experiments on captive tuna, although measuring some of them regularly in experimental conditions could represent a methodological challenge.

Effects on reproduction and growth

DFADs, by decreasing tropical tuna condition, could also impact reproductive potential, which could decrease population resilience. In the WIO, Zudaire et al. (2014, 2015) found (i) a significantly higher proportion of energy-rich fish prey in the diet (stomach contents; Zudaire et al., 2015), as well as (ii) significantly higher total lipid concentrations and triacylglycerol to sterol (TAG:ST) ratio, indicators of energetic condition, in the gonads of YFT females caught in free-swimming schools compared to females associated with DFADs (Zudaire et al., 2014). This can be interpreted as simply reflecting differences in prey availability and feeding activity and thus differential lipid incorporation to tissues between DFAD-associated and non-associated tunas. It could also highlight higher energetic investment to reproduction in free-swimming YFT due to a higher condition (i.e., better health), keeping in mind the potential bias provoked by an uneven size distribution between school types in these studies. However, the study failed to demonstrate a direct effect on the fecundity, most likely due to the low number of actively spawning females analysed and the high inter-individual fecundity variability observed in YFT (Pecoraro et al., 2017).

Similarly, Ashida et al. (2017) investigated the difference in reproductive traits of female SKJ, of similar size distribution, between school types in the WCPO, highlighting a significant higher proportion of mature females in free swimming schools, characterised by higher relative condition factor, than associated with DFADs. However, as for YFT in the IO (Zudaire et al. 2014), no significant effect of the school type was observed on the WCPO SKJ fecundity, which corroborates previous results observed for WIO SKJ (Grande, 2013; Grande et al. 2014). Also, an investigation of the reproductive dynamics of SKJ in the EPO based on the histological evaluations of ovaries from 3732 females indicated spawning was observed for fish captured in both unassociated and floating object sets (Schaefer and Fuller 2019). The lack of relationship between condition and fecundity of SKJ could be related to their energy allocation and reproductive strategies. SKJ tuna females fuel their gametes with energy gained concomitantly during reproduction (i.e., income breeding strategy, Grande et al. 2016). However, YFT females can store additional energy reserves prior to spawning, which define them as income-capital breeder (Zudaire et al., 2014) unlike SKJ. Therefore, as

SKJ females exhibit better condition when free swimming, it can be assumed that their reproductive efficiency is lower when associated with DFADs, but the same conclusion cannot be made for YFT.

Using tagging data collected in the EAO, Hallier & Gaertner (2008) estimated and compared the growth rates of SKJ and YFT associated with DFADs versus free-swimming schools. Released and recaptured SKJ associated with DFADs had a significantly lower growth rate than those in free-swimming schools, but the difference was not significant for YFT (though it was lower, as for SKJ). However, the history experienced by individual fish between release and recapture was unknown. The “experimental” design could not be controlled as the time one specimen spent associated with DFADs and in free-swimming schools is not available.

What are the scientific challenges to fill the knowledge gaps?

DFADs have been representing one of the key management priorities and challenges of tRFMOs over the last decade. Since fishers started using them, DFADs numbers continuously increased until first management measures limiting the number of operational buoys were adopted in the mid-2010s (Song & Shen 2022). The massive use of DFADs in all oceans has been generating major concerns on the sustainability of this fishing mode. DFADs increase the catchability of tropical tunas leading to large catches of small BET and YFT (Dagorn et al., 2013b; Fonteneau et al., 2013), generate more bycatch, including vulnerable species such as some shark species, silky (*Carcharhinus falciformis*) and oceanic whitetip (*Carcharhinus longimanus*) sharks (Dagorn et al., 2013b; Fonteneau et al., 2013; Leroy et al., 2013), and can strand on coastal areas causing damage to marine habitats (Imzilen et al., 2021; Maufroy et al., 2015, Escalle et al. 2019). Although there is increasing knowledge and literature on DFADs, the issue of their impacts on tuna natural mortality and reproductive potential remains an open scientific question. Several pieces of evidence demonstrate that DFADs increase tuna catchability, increasing their fishing mortality (Davies et al. 2014; Wain et al. 2021). However, if impacts on tuna natural mortality and reproductive potential were to be demonstrated at the population level, DFAD impacts could be even greater. Furthermore, these impacts, added to the increase of fishing mortality, could have cumulative effects on tuna populations. All knowledge collected and reviewed on the behaviour and life-history parameters of tunas at DFADs clearly reveals a lack of converging scientific results on the long term consequences on tuna (at the individual and/or population levels) of increased numbers of floating objects. Therefore, if DFADs seem to affect the short-term condition of tropical tunas, we are not currently able to conclude whether DFADs affect the movements and/or other life-history parameters of tunas in a way that could significantly affect the fitness of individuals and the demography of their populations. As such, there is a need to improve our observation and understanding of this associative phenomenon to determine with certainty the impacts of DFADs on the life-history parameters and behaviour of tropical tuna, quantify the magnitude of these impacts and provide evidence-based advice.

A major gap in tuna and DFAD science is the lack of time series of key parameters such as the numbers of DFADs and natural floating objects, residence and absence times at DFADs as well as large movements between oceanic regions, school sizes, condition and reproduction indices. The first research priority in this context is to initiate or continue time series of such indicators (Capello et al. 2023). Setting long-term monitoring programs in every ocean appears to be a priority, as effects of DFADs could vary depending on the species, the characteristics of each ecosystem and on the density of floating objects. Moreover, it would facilitate comparative analyses between oceans to better understand the drivers of tuna associative behaviour. The collection of some parameters will require dedicated scientific surveys (e.g. electronic tagging, biological sampling) while others (e.g. numbers of DFADs and natural objects, biological condition factors) have started to be routinely collected by tRFMOs through FAD-specific data requirements included in conservation and management measures (Grande et al. 2018, Báez et al. 2022, Song & Shen 2022) as well as government and industry initiatives (e.g., routine fishery monitoring and at-sea observer programs).

Another research priority is to develop experimental studies to identify the biological and behavioural processes involved in tuna associative behaviour. The only scientific consensus is the fact that in a given area, conditions of tunas associated with floating objects often seem to be lower than those of fish in free-swimming schools. However, the different indicators used to assess tuna condition are not always well correlated (Sardenne et al. 2016), and experimental studies are needed to validate them against proper benchmarks, allowing to determine how representative they are of individuals' health. Then, understanding how fast these indicators change with the fish's associative behaviour appears essential. This could also be achieved through studies on captive tropical tunas (e.g., Estess et al. 2017), but non-lethal observations should be promoted (e.g. BIA) in order to track changes throughout the fish lifespan. No evidence exists suggesting whether the lower condition at DFADs is the consequence or the cause of their association with DFADs. Often the robustness of the findings of investigation on the life-history parameters of tunas is hampered by the lack of knowledge of the time spent associated with a DFAD or in an array of DFADs by each specimen analysed. The history of each individual tuna is a hidden variable that must be taken into account in statistical analyses, which is a challenge. Studies combining behavioural observations (tagging) and condition of the individuals (e.g. BIA or biochemical analyses of biopsies made at the time of tagging) should then be encouraged. Ideally, tags equipped with physiological sensors would clearly help understanding the interplay between associative behaviour and tuna physiology. Such tags, however, are only starting to be developed.

Studies on AFADs could provide insights to the questions addressed in this manuscript: as argued by Dagorn et al. (2010), AFADs also alter the natural environment (by adding floating objects to the ocean). However, it remains questionable if they are comparable due to the fact that AFADs are generally located nearshore, with corresponding particular oceanographic conditions, and they do not move with water masses. Papua New Guinea, the Philippines and Indonesia are examples of areas with very high numbers of AFADs (Proctor et al. 2019) and as such, these dense arrays of AFADs could generate the same concerns on tuna life-history parameters and behaviour that those described for DFADs. Understanding the behaviour of tunas around AFADs can also improve our general understanding of tunas around all types of floating objects and help design new, well focused studies for DFADs. For practical reasons, more studies have been performed on the behaviour of tuna at AFADs than at DFADs (e.g. Dagorn et al., 2007; Govinden et al., 2013; Holland et al., 1990; Ohta & Kakuma, 2005; Rodriguez-Tress et al., 2017). They provided estimates of residence times between two AFAD associations and therefore of the percentage of time spent associated to AFADs (e.g. Pérez et al., 2020; Robert et al., 2013b; Rodriguez-Tress et al., 2017), which still needs to be further explored at DFADs. For example, Pérez et al. (2020) used acoustic tagging data on AFAD arrays to demonstrate that when inter-AFAD distance decreases, tuna visit more AFADs, spend less time travelling between AFADs and more time associated with them. Concerning DFADs, as actual densities of drifting floating objects are difficult to obtain, studies using a modelling approach based on experimental data should be promoted (Pérez et al. 2022, Capello et al. 2023). These studies should investigate the consequences of changes in floating object density on tuna school sizes and associative behaviour. These modelling studies could be complemented and/or calibrated by studies which use data from echosounder buoys deployed by fishers on floating objects. Recent methodological advances allowed the prediction of tuna presence or absence under FOBs (Baidai et al., 2020; Orue et al., 2020). Using an extensive dataset from echosounder buoys in the WCPO (more than 3.8 million transmissions), Escalle et al. (2021c) determined different profiles of acoustic signals related to different types of aggregations. Other studies also show that multi-frequency echosounder buoys could allow the discrimination of tropical tuna species under DFADs (Moreno et al. 2019, Sobradillo et al. 2023). These new methodological developments, in combination with tagging data, both conventional and electronic, and modelling approaches offer promising perspectives for the study of tuna aggregation behaviour under FOBs and the potential impact of DFAD density on tuna schooling behaviour.

Tuna RFMOs set limits on the number of operational buoys (IATTC: up to 340 depending on the vessel size, Res C-21-04; ICCAT: 300 in Rec 22-01; IOTC: 300 in Res 19/02; WCPFC: 350 in CMM 2021-01). These limits are essentially set to control the fishing effort and the catches of tunas and non-target species, hence to control fishing mortality. How such limits also act on the number of deployed DFADs and the potential impacts of DFADs on tuna's natural mortality, is unknown. In theory, all purse seine vessels could use at least the same amount of DFADs than the maximum number of operational buoys authorized in each of the regions. Multiplying this maximum number of operational buoys authorized per vessel by the number of large-scale purse seine vessels in each ocean provides a global authorized limit of about 238,000 operational buoys (details of the calculation in Supplementary Materials 1). This number is about twice higher than the estimate of the global number of DFADs deployments made by Gershman et al. (2015), based on data from 2013. Hence, it would mean that the global purse seine fishery could have increased the number of DFADs in the ocean while still respecting the current limits on the number of active buoys. Most tRFMOs now require that DFAD identification, characteristics, deployment date and deployment location are reported (e.g. ICCAT Rec 22-01; IOTC Res. 19/02; IATTC C-21-04). Some studies evidenced different regional trends of DFAD deployments (IOTC, 2022, Escalle et al. 2020, Lopez et al. 2021, Floch et al., 2019; Maufroy et al., 2017), but no study assessed this trend on a global scale after 2013 (Gershman et al., 2015). Tuna RFMOs should continue to collect and make fine-scale DFAD data available to scientists to allow regular estimations of the extent of the habitat modifications generated by DFADs, which should be addressed at a global scale.

Conclusion

This study reviews the current state of knowledge on how DFADs could also impact natural mortality and reproduction additionally to their impact on fishing mortality. To summarize the questions formulated:

(1) although the deployment of DFADs has undoubtedly modified the habitat of tropical tunas, the extent of this modification still needs to be better characterized in some regions. This characterization can be achieved through the continued monitoring of indicators (e.g. spatialized DFAD and NLOG densities, DFAD/NLOG ratio) collected by tRFMOs.

(2) studies assessing the impacts of DFADs on tuna large-scale movements show contradictory results. Strong ocean and species-specific variability is observed for the proportion of time spent associated with FOBs. However, the effect of the methodology used (archival tagging vs acoustic tagging) should be investigated. To date, besides theoretical

studies, no evidence has been shown on the impact of DFADs on associative and schooling behaviour.

(3) DFADs probably impact tuna short-term condition, but it does not necessarily imply a longer-term detrimental effect and should be confirmed with long-term time series of validated condition indicators. The results on the impacts of DFADs on other life-history parameters are inconclusive.

(4) The main conclusion of this work is the lack of clear converging scientific results on the impacts of DFADs on the natural mortality and reproductive potential of tropical tuna. It should therefore be underlined that scientific efforts should not only focus on the effects of DFADs on catches (target and non-target species) but should also address other possible impacts, such as density dependent effects on the behaviour and life-history parameters of tunas. This current lack of converging results justifies a major and urgent scientific effort, in terms of data collection, experimental research and modelling to tackle definitively whether the increased deployment of DFADs could lead to impacts on tropical tuna populations, additionally to the impacts on fishing mortality.

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Data availability statement

Data used in the supplementary material were obtained from Justel-Rubio et al. (2023) and the following website: https://www.iattc.org/en-US/Management/Vessel-register (accessed 2023/03/14)

Conflict of Interest

The authors have no conflict of interest to declare.

Author contribution statement

A.Dupaix, F.Ménard, J.D.Filmalter and L.Dagorn conducted the literature search and wrote the first version of the manuscript with suggestions from all the co-authors. All co-authors participated in the revisions of the manuscript.

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Tables

Table 1: Summary of main findings from previous studies on the numbers of monitored floating objects or the number of DFADs used in large-scale tropical tuna purse seine fisheries.

Area	Period	Indicator	Associated number of vessels	Estimation	Reference
All oceans	2006-2011	DFADs deployed yearly		47,000-103,000	Baske et al. (2012)
	2010s	DFADs deployed yearly		91,000	Scott & Lopez (2014)
	2013	DFADs deployed yearly		81,000-121,000	Gershman et al. (2015)
Atlantic Ocean	1998	Radio buoys	45 vessels	3,000	Ménard et al. (2000)
	2004-2014	Buoys deployed yearly	Per vessel (French PS fleet)	From 41 (2004) to 200 (2014)	Fonteneau et al. (2015)
	2007-2013	Monthly active buoys		From 1,289 (2007) to 8,856 (2013)	Maufroy et al. (2017)

Indian Ocean	2003-2005	Daily active buoys	45 vessels	2,100	Moreno et al. (2007)
	2007-2013	Monthly active buoys		From 2,679 (2007) to 10,929 (2013)	Maufroy et al. (2017)
	2010-2012	Daily active buoys	34 vessels	3,750-7,500	Filmalter et al. (2013)
	2010-2014	Quarterly active buoys	25 vessels	1,200	Chassot et al. (2014)
	2013	Quarterly active buoys	19 vessels	6,015	Delgado de Molina et al. (2014)
	2013	DFADs deployed yearly	19 vessels	12,813	Delgado de Molina et al. (2014)
	2016-2021	DFADs deployed yearly	Whole ocean	10,514 to 24,550	IOTC (2022)
Western and Central Pacific Ocean	2011-2019	Daily active buoys	Per vessel	45-75	Escalle et al. (2021)
	2011-2019	DFADs deployed	268 to 322 vessels	20,000-40,000	Escalle et al. (2020, 2021a)

		yearly	(whole WCPO)		
	2016-2019	Buoys deployed yearly	Whole WCPO	31,000 to 39,500	Escalle et al. (2020)
	2016-2020	Buoys deployed yearly	187 to 235 vessels	16,000 to 22,000	Escalle et al. (2021b)
Eastern Pacific Ocean	2018-2020	Daily active buoys	100 to 140 vessels	8,000-11,000	Lopez et al. (2021)
	2015-2020	DFADs deployed yearly	100 to 140 vessels	20,000 to 40,000	Lopez et al. (2021)

Table 2: Summary of main findings from previous studies on tuna individual CRT and CAT assessed under anchored and drifting FADs. CRT: Continuous Residence Time – continuous bouts of time spent at the same FAD without any absence longer than 24h. CAT: Continuous Absence Time – the time between two associations with a FAD. FL: fork length, YFT: *Thunnus albacares*, SKJ: *Katsuwonus pelamis*, BET: *Thunnus obesus*).

FAD type	Study location	Metric	Findings	Reference
Drifting	Eastern Atlantic Ocean	CRT	YFT (34-82 cm FL): average of 19.15 days (maximum value of 55 days) SKJ (39-61 cm FL): average of 9.19 days (maximum value of 15 days) BET (45-61 cm FL): average of 25.31 days (maximum value of 55 days)	Tolotti et al. (2020)
	Mozambique Chanel (Western Indian Ocean)	CRT	YFT (29-60 cm FL): between 0.00-26.72 days with median at 9.98 days SKJ (47-57 cm FL): between 0.09-18.33 days with median at 4.47days BET (54-56 cm FL): between 0.00-6.56 days with median at 3.89 days	Govinden et al. (2010)
	Western and Central Pacific Ocean	CRT	SKJ (46-60 cm FL): median of 1 day (maximum value of 18 days) YFT (36-98 cm FL): median of 2 days (maximum value of 50 days) BET (38-90 cm FL): median of 10 days (maximum value of 30 days)	Phillips et al. (2019b)
		CAT	BET (38-90 cm FL): median of 3.2 days (maximum value of 48.2 days)	
	Equatorial Central Pacific Ocean	CRT	SKJ (36-65 cm FL) : from 0.0 to 6.4 days (with average value at 2.3 days)	Matsumoto et al. (2014)
		CRT	SKJ (34.5–65.0 cm FL): less than 7 days YFT (31.6–93.5 cm FL): less than 7 days BET (33.5–85.5 cm FL): less than 7 days	Matsumoto et al. (2016)
Anchored	Philippines (Indian Ocean)	CRT	Juvenile YFT (19–31 cm FL) : between 1 and 6 days	Mitsunaga et al., (2012)
	Maldives Islands (Indian Ocean)	CRT	SKJ (37−54 cm FL) : 0.20-3.75 days YFT (35−53 cm FL) : 0.61-0.70 days	Govinden et al. (2013)
	Mauritius islands (Indian Ocean)	CRT	SKJ (41 -59 cm FL) : 2.5 days YFT (46 -81cm FL) : 9.6 days BET (48 - 60 cm FL) : 5.2 days	Rodriguez-Tress et al. (2017)
		CAT	SKJ (41 -59 cm FL) : 2.9 days YFT (46 -81cm FL) : 1.4 days BET (48 - 60 cm FL) : 0.8 days	
	Hawaii islands	CRT	Small YFT (30-39 cm FL) : 13.58 days	Robert et al. (2012)

			Large YFT (63-68 cm FL): 9.44 days	
		CAT	4 days for small YFT and 1.65 days for large YFT	
	(Pacific Ocean)	CRT	4 behavioural modes reported for YFT (54 to 95 cm FL) : - Brief association : 13.1 minutes - Short association: 2.9 days - Two long association modes : 13.8 and 23.2 days	Robert et al. (2013a)
		CAT	2 behavioural modes: - Short: 2.8 days - Long: infinite	
	South-western Taiwan (Pacific Ocean)	CRT	YFT (35–81 cm FL) : average of 2.1 days (maximum value to 31 days)	Weng et al. (2013)
	Okinawa Island (Pacific Ocean)	CRT	YFT (40-119 cm FL): median of 7.9 days (maximum value to 55 days) BET (50-77 cm FL): median of 7.0 days (maximum value to 34 days)	Ohta & Kakuma (2005)
	Palau Islands (Pacific Ocean)	CRT	YFT (50-60cm FL): mean of 16 days (maximum value to 123 days) YFT (60-100cm FL): mean of 2 days (maximum value to 33 days)	Filous et al., (2020)

Figures

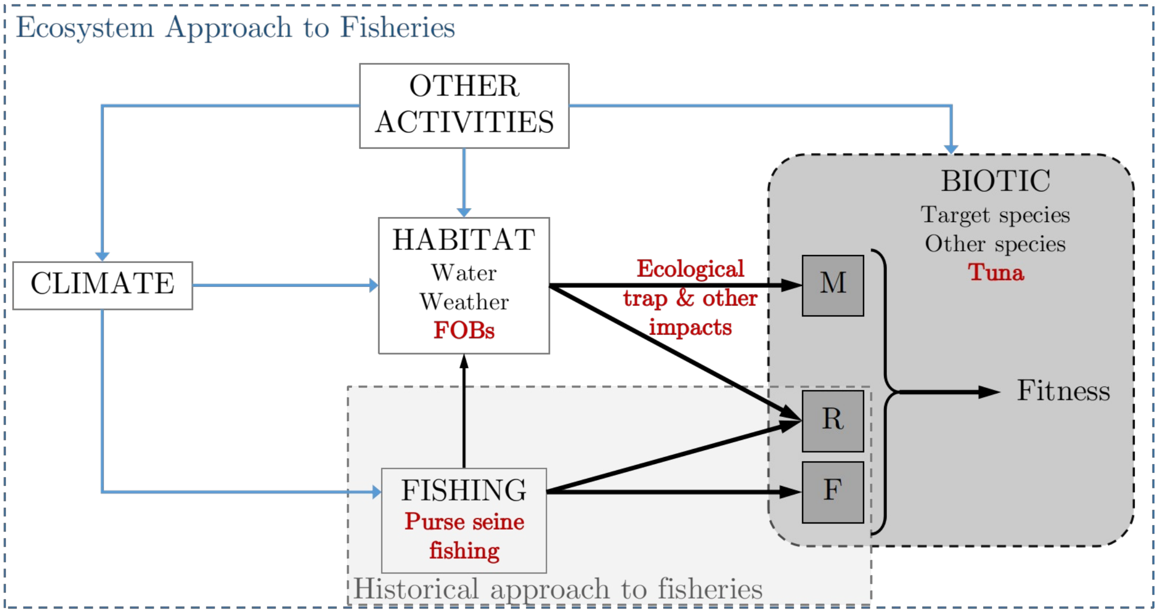

Figure 1: Drifting Fish Aggregating Devices impacts on tropical tuna natural mortality and reproductive potential in the framework of the Ecosystem Approach to Fisheries. Words in red refer to the specific case study developed in this paper. FOB: floating object; M: Natural mortality; R: Reproductive potential; F: Fishing mortality.

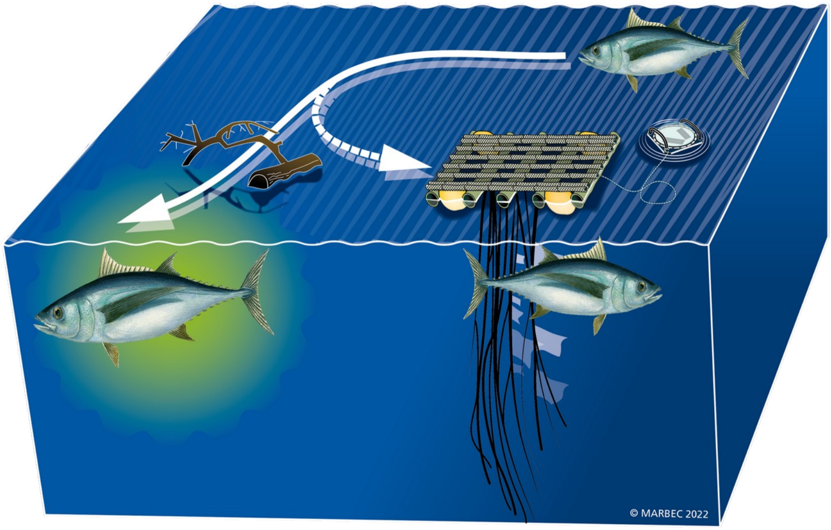

Figure 2: Schematic representation of the ecological trap hypothesis applied to Drifting Fish Aggregating Devices (DFADs), as originally formulated. Under this hypothesis, before DFADs introduction, when only natural floating objects (NLOGs) were present, floating objects were indicators of productive areas. Hence, by associating with floating objects, tuna selected high quality habitats. DFAD massive deployment modified the distribution of floating objects (FOBs), which are not representative of rich areas anymore. By associating with FOBs, tunas can be attracted to or retained in habitats of lesser quality.

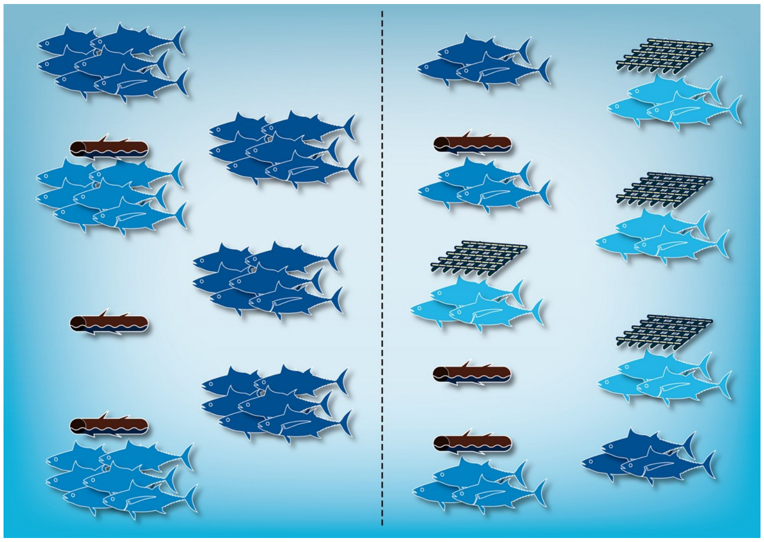

Figure 3: Schematic representation of potential effects of Drifting Fish Aggregating Devices (DFADs) on tuna schooling behaviour. The left side represents an ocean with natural floating objects (NLOGs) only (no DFAD), while the right side represents an ocean with both NLOGs and DFADs, i.e. more floating objects (FOBs). Dark blue represents tuna in free-swimming schools, intermediate blue tuna associated with NLOGs and light blue tuna associated with DFADs. An increase in FOB density (right panel) could lead both to (i) more tuna associated to FOBs and less free-swimming schools, (ii) more numerous but smaller FOB-associated schools.