Title 1: The challenge of assessing the effects of drifting fish aggregating devices on the behaviour and biology of tropical tuna

Title 2: Effects of drifting fish aggregating devices on biology and behaviour of tropical tuna

Running title: Effects of DFADs on tropical tuna (33 characters including space **< 40**)

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Abstract (236 words**< 250)**

Though fisheries have intensively used drifting fish aggregating devices (DFADs) over the last three decades to facilitate their catch of tropical tunas, assessing the consequences of the presence of DFADs at sea on tuna behaviour and biology is a challenge. The use of DFADs has resulted in a major increase in the number of floating objects, which are spatially heterogeneous at sea. To date, no scientific consensus exists 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. It is not possible, however, to elucidate whether this is the cause or result of the association, or if it affects the fitness of individuals in the long term. Further scientific progress would require (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 the 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 (6 max): DFAD, ecological effects, ecological trap, fish behaviour, fisheries management, tuna

Table of contents

Introduction

How much do DFADs change the habitat of tropical tunas?

Do DFADs modify the migration and the schooling behaviour of tropical tunas?
Effects on individual movement
Effects on schooling behaviour

Do DFADs modify the biology of tropical tunas?
Effects on feeding
Effects on body condition
Effects on reproduction and growth

What are the scientific challenges to fill the knowledge gaps?

Acknowledgements

Data availability statement

References

Tables

Figures

Introduction

Many fish species are known to associate with floating objects (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 Dempster & Taquet, 2004). In particular, the use of floating objects to facilitate the capture of tropical tunas (skipjack – *Katsuwonus pelamis*; yellowfin – *Thunnus albacares*; and bigeye – *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 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, allowing these fleets to manage much more efficiently their DFAD stock (Arrizabalaga et al., 2001; Ramos et al., 2013). DFADs represent very efficient fishing tools that increase the catchability of tunas. 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 23/02, ICCAT Rec 22-01, IATTC Res C-21-04, WCPFC CMM 2021-01). Other major DFAD-related measures concerned 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 (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. 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.

Changing a habitat can positively or negatively impact the ecology of wild animals inhabiting it. For example, artificial habitats could benefit some reef species (Lee et al. 2018). Contrarily, alterations could also reduce habitat quality, e.g. by reducing the number of shelters or nests for some species, or by decreasing their food resources (often through the alteration of the habitat of these resources themselves, Mullu 2016). In some cases, animals may be misled by cues that were previously correlated with the habitat quality but no longer are, due to anthropogenic influences. 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, it is also considered that 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). While this theory has been proposed regularly in the face of anthropogenic environmental modifications and their impacts on various species, few studies have empirically demonstrated the existence of such traps (Battin, 2004; Swearer et al., 2021).

Noting the increasing number of floating objects being deployed by fishers during the 1990s, scientists hypothesized that the increase in the number of DFADs could lead to an ecological trap, altering the ecological value of floating objects for tropical tunas associated to DFADs (Marsac et al., 2000). It is hypothesized that large numbers of DFADs may alter certain biological characteristics of epipelagic populations associated with them: migration, schooling behaviour, growth, fish condition and bioenergetics, predation and natural mortality (Figures 1 & 2). TRFMOs primarily focus on developing management schemes to address the known effects of DFADs on catches (particularly of small yellowfin and bigeye tunas, as well as sharks) or their stranding on coasts. However, there is also a need to assess whether DFADs, through their presence on the ocean, can alter the biology and behaviour of tunas, so as to manage the number of DFADs deployed at sea if negative impacts are suspected or demonstrated. The objective of this paper is to review the current knowledge on the effects of DFADs on the behaviour and biology of tropical tunas, identify knowledge gaps, and propose future research priorities. 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 modify the biology of tropical tunas?

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

How much do DFADs change the habitat of tropical tunas?

Natural floating objects have always occurred in the habitats occupied by tunas. Such natural objects are primarily tree trunks or branches that were washed down rivers into the ocean. Human activities (logging, coastal development, shipping, etc.) also modified the number of floating objects encountered by tunas, in some cases even before modern purse-seine tuna fishing began (Caddy & Majkowski, 1996; Thiel & Gutow, 2005). Some of these trends may have been consistently positive (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. It should be noted that the current largest tuna purse seine fishery in the world was first developed in the western Pacific by Japanese exploratory fishing cruises that perfected methods for seining tuna schools found in association with natural floating logs that later evolved into DFAD based effort in all oceans (Watanabe 1988). In recent years, the large and persistent increase in the number of DFADs deployed by fishers raised the question of the impacts of this practice on the tropical tuna habitat. It is therefore essential to assess the extent to which DFADs have changed the habitat of tunas, in comparison to the historic pristine state when only natural floating objects existed.

Two types of floating objects (referred to as FOBs) are commonly considered: (i) man-made FADs (which can be drifting or anchored) 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.

Habitat changes 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 (e.g. logs, whether equipped or not with buoys, operational or not) and for all types together (natural and artificial) is challenging. The primary concern here is to identify the origin of the floating object, which could either be man-made (DFADs), natural (NLOG) or artificial discard (ALOG).

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, 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 whole western IO is impacted, with DFADs representing more than 85% of the overall FOBs. Since 2014, even the Mozambique Channel, an area known to have a large number of natural objects (Dagorn et al., 2013a), is impacted showing a higher number of DFADs (73 % of the total FOBs). In addition, increased numbers of DFADs also contribute to decreasing the distances between floating objects. In the IO, while estimated median distances between DFADs and between natural objects did not significantly differ in 2007-2008 (70 km and 74 km respectively), the distance between FADs was significantly smaller than the one between LOGs in 2014-2018 (37 km and 89 km, respectively) (Dupaix et al. 2021). Phillips et al. (2019), using data from 2016 and 2017 and Lagrangian simulations in the western Pacific Ocean, 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, to our knowledge, 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, but only the IOTC has limited the number of buoys purchased and in stock per year, per vessel (IOTC Res 23/02, 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. Moreover, as DFAD fishing is so efficient, many fleets worldwide have changed their fishing strategy from setting on free-swimming or dolphin-associated tuna schools, towards fishing with DFADs (Lennert-Cody et al., 2018). Thus, 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 anchored FADs were estimated by Scott & Lopez (2014)), although there may be regional exceptions, including few areas known to have 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 system as it has been recently adopted in the IO (Res 23/02). 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 and some DFADs may lack positional trackers and can drift for a long time, or can be (re)activated/deactivated, but it can be used as a proxy to illustrate the trend in numbers. Therefore, as the number of operational buoys does not limit efficiently 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. Moreover, if no characterisation of DFAD deployment trends is available at the global scale, 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 also increases.

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) they could cause tunas to relocate to new areas and (ii) they could increase residence times in some areas. 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 on DFAD numbers occurred (i.e. before or after the 1990's). To our knowledge, historical data to assess large-scale movement patterns before fishers started to massively deploy DFADs, necessary for this type of analysis, do not exist.

Effects on individual movement

Wang et al. (2014) found that the spatial dynamics of free-swimming school sets in the Western and Central Pacific Ocean (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. Catch data, however, reflect 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 populations.

Hallier & Gaertner (2008) analysed conventional tagging data of skipjack and yellowfin tuna 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 yellowfin and skipjack tuna caught in association with DFADs (13 and 15 nm/day, respectively) than those recaptured in free-swimming schools (3 and 4.5 nm/day, respectively). In addition, the directional pattern and the displacement rate of free-swimming schools differed significantly between both species but were not different for individuals caught with DFADs. The authors interpreted these results as indicating significant modifications of migratory patterns due to associations with DFADs, suggesting that the influence of DFAD association was strong enough to remove the normally observed difference in migratory direction between free-school skipjack and yellowfin tuna in the EOA. However, this study was the only one to assess differences of movement patterns between fish recaptured at DFADs and in free-swimming schools and, due to regional differences between oceans, more studies would be needed to interpret these results at a global scale.

Another way to investigate the potential of DFADs to modify large-scale movements of tunas is to observe such movements through archival tags and compare them with the general drift patterns of DFADs. In the equatorial Eastern Pacific Ocean (EPO), evaluation of archival tag data sets from 96 bigeye tuna (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 tracks of those bigeye were related to the general drift patterns of

DFADs in this area. This suggests that the large-scale spatial dynamics of bigeye tuna 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 bigeye tagged with conventional tags and archival tags was observed (Schaefer et al., 2015), in contrast to the results from bigeye tagging in the equatorial EPO (Schaefer et al., 2009; Schaefer & Fuller, 2010). The authors explain this result by the fact that in the equatorial EPO, where bigeye exhibit strong regional fidelity, it appears the high concentration of food is an important environmental factor leading to their residence and retention in that area. A plausible cause for the predominantly eastward dispersion of bigeye from releases in the equatorial CPO is the influence of the strong eastward-flowing North equatorial countercurrent, in combination with bigeye searching for higher concentrations of prey resources, so as to maximize foraging success in a more productive area.

In addition, the possibility of DFADs influencing the large-scale movements of tunas could be evaluated through the measure of the time tunas spend associated with DFADs and the time they spend unassociated (or between two DFAD associations). It could be considered that the longer tunas spend 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 bigeye tuna or sometimes yellowfin tuna) have been used by scientists to measure these parameters (Table 2). Passive acoustic tagging studies conducted on DFADs in the Indian and Pacific oceans revealed that the majority of residence times of tunas were a few days. Mean values of DFAD residence times (i.e. continuous periods of time spent associated with a given DFAD) ranged from 0.2 to 4.6 days for skipjack tuna (Dagorn et al., 2007; Govinden et al., 2021; Matsumoto et al., 2014, 2016), and from 1.0 to 6.6 days for yellowfin tuna and 1.4 to 7.6 days for bigeye tuna (Dagorn et al., 2007; Govinden et al., 2021; Matsumoto et al., 2016). Long associations, however, have been observed on rare occasions – *e.g.* 27 and 28 days for yellowfin tuna, in the IO (Govinden et al., 2021) and WCPO (Phillips et al., 2017), respectively. A recent study in the EAO (Tolotti et al., 2020) reported significantly larger mean residence times for the three tuna species, from 9 days (skipjack tuna) to 19 days (yellowfin tuna) and 25 days (bigeye tuna), with record values of 55 days and 600 km travelled associated to a DFAD for both bigeye and yellowfin tuna.

These studies suggest that residence times at a single DFAD could vary between oceanic regions. Without more studies in other oceanic regions, it is difficult to assess whether the long DFAD associations observed off the coast of Guinea (about 10°N in the EAO) are restricted to this area (and the time period of the observations), or if they can also be observed in other regions. In fact, even short DFAD residence times as those observed in the Indian and Pacific oceans do not prove that DFADs cannot influence large-scale movements. The short residence times clearly suggest that a single DFAD does not significantly impact the behaviour of tunas for long enough to influence their large-scale movements. However, 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 in the associative mode over long periods. This variable is likely to depend on the density of all floating objects in the area. A small percentage of time associated with floating objects would indicate no or little influence of DFADs, while a high percentage could indicate a significant influence of DFADs on large-scale movements. 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, as it has previously been done with AFADs (Dagorn et al., 2007; Pérez et al., 2020; Robert et al., 2013a; Rodriguez-Tress et al., 2017).

In the WCPO, 13 yellowfin tuna and 12 bigeye tuna displayed “homing” behaviour by returning to the same DFAD with absences superior to a day (Forget, unpublished data). The average duration of these absences were about 1.5 days for yellowfin tuna and three days for bigeye tuna (Forget, unpublished data). By contrast, in the other tropical oceans, few tunas were observed performing such homing behaviour: one bigeye tuna in the AO (out of 23 tagged fish, Tolotti et al., 2020), one yellowfin tuna and two skipjack tuna in the IO (out of 31 and 17 tagged fish respectively, Govinden et al., 2021), and these absences lasted less than two days. Because bigeye tuna and sometimes yellowfin tuna exhibit different vertical behaviour patterns when associated or non-associated with floating objects, 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 bigeye 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). Associative and non-associative behaviours with floating objects have also been described with archival tags for yellowfin tuna (Phillips et al., 2017; Schaefer et al., 2009; Schaefer & Fuller, 2013), with estimates of the percentage of time spent associated with floating objects between 10% and 23%.

Except in the EAO (Tolotti et al., 2020), all other electronic tagging data did not show that bigeye or yellowfin tuna spend the majority of their time associated with floating objects, which questions the possible influence of floating objects on large-scale movements of these species. However, we are far from understanding the effects of different densities of floating objects on tuna movements and more data are clearly needed, in particular on skipjack tuna, the main tuna species targetted by tropical tuna purse seine fisheries found at floating objects. In particular, the link between the response of tuna to an increased DFAD density and to other external signals (e.g. quality of the environment, prey density) needs to be assessed.

Effects on schooling behaviour

DFADs could also affect schooling behaviour, which can have a wide range of consequences on the biology and the movements of tunas. Dagorn & Fréon (1999) and Fréon & Dagorn (2000) suggested that tunas could associate with floating objects for social advantages such as facilitating schooling behaviour. To date no result has been obtained 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 (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 demonstrated, using a model, 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 biology 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

Trophic studies on tropical tunas, based on stomach content 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) and Western and Central Pacific (Machful et al., 2021) oceans. Indeed, the fraction of empty stomachs was higher among DFAD-associated skipjack and small yellowfin tuna than those captured in free swimming schools. Lower stomach fullness or daily food rates were estimated for tunas associated with DFADs compared to tunas from free swimming schools in the EAO (Hallier & Gaertner, 2008; Ménard et al., 2000). Similarly, lower prey weights were found for tunas associated to DFADs than for tunas from free swimming schools in the IO (Grande et al., 2013; Zudaire et al., 2015). These results support the fact that the quantity of prey present in DFAD assemblages is not sufficient to sustain the dietary requirements of large aggregations of small-sized tunas commonly found at DFADs (several tens of tons) (Fréon & Dagorn, 2000). However, the influence of the sampling time of tunas on the stomach content has to be taken into account as purse seine vessels mainly fish tunas on DFADs at dawn (Forget et al., 2015) and during daytime in free-swimming schools. 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. In addition, the association of tunas with DFADs could affect the composition and quality of their diet, as shown for yellowfin tuna in the WIO (Zudaire et al. 2015). The largest difference of diet composition observed for this species was indeed due to their aggregative behaviour, with DFAD-associated individuals' stomach contents characterised by the absence of *Cubiceps pauciradiatus* (i.e. driftfish from the Scombriforme order), which constituted by far the main fish prey of free-swimming yellowfin tunas in the WIO.

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. Jaquemet et al. (2011) partitioned their samples in “rich” (i.e., no limiting food) versus “poor” forage areas in the Indian Ocean, in relation to an exceptional demographic outburst of a pelagic stomatopod (Crustacea), which composed the bulk of tuna diet in this region (Potier et al., 2004, 2007). These authors 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 DFAD-associated tunas in rich areas and to tunas in free-swimming schools. Jaquemet et al. (2011) suggested that the impact of DFADs on feeding success could be location-dependent. This led the authors to emphasize the possible detrimental effect on the condition of tuna associated with DFADs if associated tunas drift towards areas with poor forage resources. In such cases, food competition could be enhanced as local abundance of tuna would be higher than what limited forage resources could sustain.

In the Pacific Ocean, Hunsicker et al. (2012) observed that predation on skipjack and yellowfin tunas 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 skipjack, yellowfin, and bigeye tunas, DFADs enhance their vulnerability to predators such as sharks and billfishes, and thus increase natural mortality of small sized tunas. To our knowledge, this 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

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) and Hallier & Gaertner (2008) in the EAO, and Robert et al. (2014) in the Mozambique Channel (WIO) all found that individuals associated with DFADs were in lower condition than those in free-swimming schools, assuming that thorax width or girth or plumpness of fish are good fish health indicators. However, Sardenne et al. (2016), when comparing biometric and biochemical indicators concluded that biometric indicators measured on whole tuna should be interpreted with caution as they may not always reflect the energetic condition measured in the tissues of the fish. Robert et al. (2014) measured the condition of skipjack tunas 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 skipjack tuna associated with floating objects compared to those in free-swimming schools. Taking into account the particularity of the studied area (i.e. Mozambique Channel – naturally rich with NLOGs) and assuming that the Mozambique Channel, at the time of sampling, had undergone very little habitat modification due to DFADs (Dagorn et al., 2013a), 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 therefore be interpreted in two different ways. First, a lower measured condition does not necessarily imply detrimental physiological consequences. The difference in conditions between associated and unassociated fish could reflect normal variations in their condition. The other explanation is that some specific areas where NLOGs have always been in high numbers, such as the Mozambique Channel, could also have negatively impacted the condition of tunas that passed through and stayed in these areas. Hence, only a few studies have investigated tuna condition and assessed the potential impact of DFADs. These studies 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 skipjack) in Japan. Indeed the Japanese tuna industry prefers skipjack tuna caught on DFADs as they have less fat than those from free-swimming schools (Nishida, pers. comm.). However, experimental validation of the condition factors used is still needed to determine the potential impacts and the underlying mechanisms of this difference in tuna condition.

Effects on reproduction and growth

In the WIO, Zudaire et al. (2014, 2015) examined the patterns of energy acquisition and allocation to gonadal development and egg production in yellowfin tuna through the combined analyses of female trophic ecology (diet) and distribution of related high-energy lipid compounds in their reproductive and somatic tissues. The studies revealed (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 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 yellowfin tuna due to a higher condition (i.e., better health). 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 intra-species variability of fecundity observed in yellowfin tuna (Pecoraro et al., 2017).

Similarly, Ashida et al. (2017) investigated the difference in reproductive traits of female skipjack tuna between schools in the WCPO, highlighting a significant higher proportion of mature females found in free swimming schools than associated with DFADs and characterised by higher relative condition factor. As for yellowfin tuna in the IO, however, no significant effect of the school type was observed on the WCPO skipjack fecundity, which corroborates previous results observed for WIO skipjack (Grande, 2013; Grande et al. 2014). The lack of relationship between condition and fecundity of tropical tunas could be related to their energy allocation and reproductive strategies. Skipjack and yellowfin tuna females fuel their gametes with energy gained concomitantly during reproduction (i.e., income breeding strategy) (Grande et al., 2016; Zudaire et al., 2014). However, yellowfin tuna females can store additional energy reserves prior to spawning, which define yellowfin tuna as an income-capital breeder (Zudaire et al., 2014) unlike skipjack tuna. Therefore, as skipjack females exhibit better condition when free swimming, it can be assumed that reproductive efficiency is lower when associated with DFADs.

Using tagging data collected in the EAO, Hallier & Gaertner (2008) estimated and compared the growth rates of skipjack and yellowfin tunas associated with DFADs versus free-swimming schools. Released and recaptured skipjack tunas associated with DFADs had a significantly lower growth rate than those in free-swimming schools, but the difference was not significant for yellowfin tuna (though it was lower, as for skipjack). 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. In addition, the authors were only able to process a small sample of yellowfin tuna.

Available results indicate that differences in feeding patterns between tunas in free-swimming schools and associated with drifting FOBs have been observed, and that tunas associated with DFADs are generally in lower condition than those from free-swimming schools. Although tunas also show differences in energy allocation for reproduction between DFAD-associated and free-swimming schools, it does not seem to induce a difference in fecundity.

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 bigeye and yellowfin tuna (Dagorn et al., 2013b; Fonteneau et al., 2013). In addition, DFADs have ecological impacts that must be mitigated as DFAD sets usually 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 DFADs can strand on sensitive coastal areas causing damage to marine habitats (Imzilen et al., 2021; Maufroy et al., 2015). Although there is increasing knowledge and literature on DFADs, the issue of the ecological trap remains a scientific debate. All knowledge collected and reviewed, on the associative behaviour and biology of tunas at DFADs clearly reveals a lack of scientific consensus on the long term consequences on tuna (at the individual or population levels) of increased numbers of floating objects. Therefore, we are not currently able to conclude whether DFADs affect the movements and/or biology 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 the observation and understand this associative phenomenon to provide scientific advice on the effects of DFADs on the biology and behaviour of tropical tunas and other associated species.

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, and condition indices. The first research priority in this context is to initiate or continue time series of such indicators. Setting long-term monitoring programs in every ocean appears to be a priority, as effects of DFADs could vary depending on 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 most 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 the associative behaviour. The only scientific consensus is the fact that in a given area, conditions of tunas associated with floating objects seem to often 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 these investigations on the biology of tunas was 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 yet 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 biology and behaviour that those expressed 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. More studies have been performed on the behaviour of tuna at AFADs (e.g. Dagorn et al., 2007; Govinden et al., 2013; Holland et al., 1990; Ohta & Kakuma, 2005; Rodriguez-Tress et al., 2017) than at DFADs mainly due to easier access. It is also easier to exhaustively instrument AFADs within an array, providing estimates of residence times between two AFAD associations and therefore the percentage of time spent associated to AFADs (e.g. Pérez et al., 2020; Robert et al., 2013b; Rodriguez-Tress et al., 2017), one of the key variables to characterize the behaviour of tunas inside FAD arrays. 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). 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). These new methodological developments, in combination with tagging data both conventional and electronic, and modelling approaches offer promising perspectives for the study of the behaviour of tuna aggregations under FOBs.

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: 250 in Res 23/02; 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, but how such limits also limit the number of deployed DFADs is not known. In theory, all purse seine vessels could use 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 purse seine vessels in each ocean provides a global authorized limit of about 233,000 operational buoys (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. Estimations of DFAD deployment are still scarce as, until recently, there was no requirement for fishers within tRFMOs to report the number of DFAD deployments. However, now most tRFMOs require that DFAD identification, characteristics, deployment date and deployment location are reported (e.g. ICCAT Rec 22-01; IOTC Res. 23/02; IATTC C-21-04). Some studies evidenced an increase of DFAD deployments (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 collect and make fine-scale DFAD data available to scientists to allow regular estimations of the extent of the habitat modifications generated by DFADs.

Finally, although no consensus exits on the indirect impacts of DFADs on tropical tuna, it should be underlined that not only the direct effects of DFADs on catches (target and non-target species) should be addressed but also the other possible impacts such as marine debris, stranding events, and density dependent effects on the behaviour and biology of tunas. The current lack of scientific consensus justifies a major and urgent scientific effort, in terms of data collection, experimental research and modelling to tackle definitively whether the increased use of DFADs could lead to indirect impacts on tropical tuna species.

Acknowledgements

The initial impetus for this work was a workshop funded by the International Seafood Sustainability Foundation (ISSF, 2014). The research was conducted independently by the authors and its results, professional opinions and conclusions are solely the work of the authors. There are no contractual obligations between ISSF and the authors that might influence the results, professional opinions and conclusions. For the purpose of Open Access, a CC-BY public copyright licence has been applied by the authors to the present document and will be applied to all subsequent versions up to the Author Accepted Manuscript arising from this submission.

Data availability statement

Data used in the supplementary material were obtained from Justel-Rubio et al. (2022) and the following website: https://www.iattc.org/en-US/Management/Vessel-register (accessed 2023/03/14)

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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)
	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		From 2,679	Maufroy et al.

		active buoys		(2007) to 10,929 (2013)	(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)
Western and Central Pacific Ocean	2011-2019	Daily active buoys	Per vessel	45-75	Escalle et al. (2021)
	2011-2019	DFADs deployed yearly	268 to 322 vessels	20,000-40,000	Escalle et al. (2021)
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 to of 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)
	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)
	Equatorial Central Pacific Ocean	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 (Pacific Ocean)	CRT	Small YFT (30-39 cm FL) : 13.58 days Large YFT (63-68 cm FL): 9.44 days	Robert et al. (2012)
		CAT	4 days for small YFT and 1.65 days for large YFT	
	Hawaii islands (Pacific Ocean)	CRT	4 behavioural modes reported for YFT (54 to 95 cm FL) : - Brief association : 13.1 minutes	Robert et al. (2013a)

			- Short association: 2.9 days - Two long association modes : 13.8 and 23.2 days	
		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

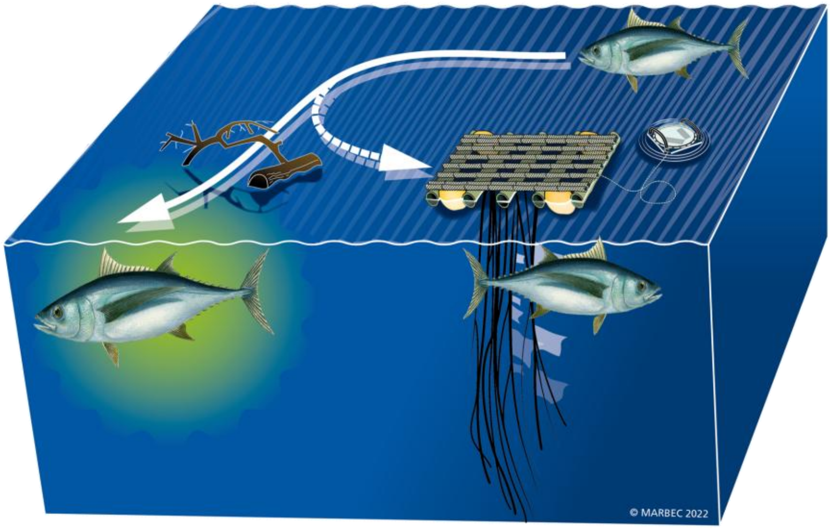

Figure 1: Schematic representation of the ecological trap hypothesis applied to Drifting Fish Aggregating Devices (DFADs), as originally formulated. Under this hypothesis, before DFADs introduction, when only natural floating objects (NLOGs) were present, floating objects were indicators of productive 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.

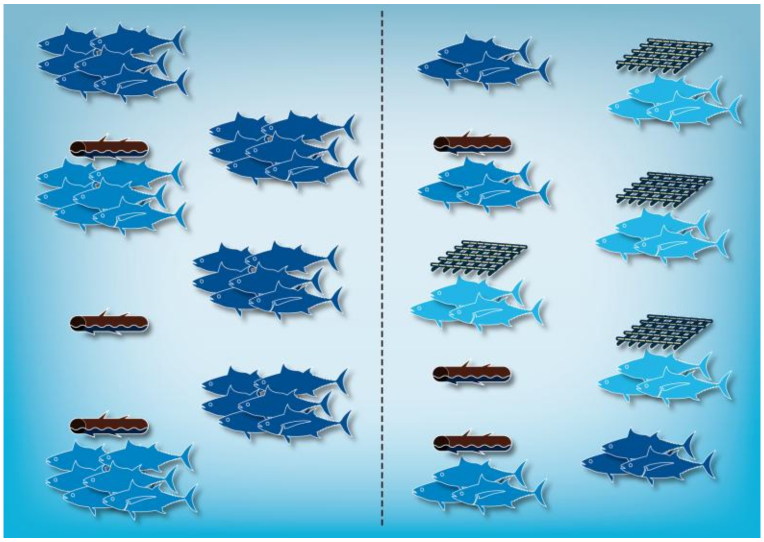

Figure 2: Schematic representation of potential effects of Drifting Fish Aggregating Devices (DFADs) on tuna schooling behaviour. The left side represents an ocean with natural floating objects (NLOGs) only (no DFAD), while the right side represents an ocean with both NLOGs and DFADs, i.e. more floating 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.