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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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2 **the behaviour and biology of tropical tuna**

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

5

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

7

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45 **Abstract (242 words < 250)**

46 Though fisheries have intensively used drifting fish aggregating devices (DFADs) over the  
47 last three decades to facilitate their catch of tropical tunas, assessing the consequences of  
48 the presence of DFADs at sea on tuna behaviour and biology is a challenge. The use of  
49 DFADs has resulted in a major increase in the number of floating objects, which are spatially  
50 heterogeneous at sea. To date, no **converging scientific results exist** regarding the **indirect**  
51 effects of DFADs **(unrelated with fishing mortality)** on the large-scale movements and  
52 behaviour of tuna, mainly due to the difficulty of disentangling the respective roles of DFADs  
53 and environmental factors. Some biological indices show that tuna condition is lower when  
54 associated to a floating object than in a free-swimming school. It is not possible, however, to  
55 elucidate whether this is the cause or result of the association, or if it affects the fitness of  
56 individuals in the long term. Further scientific progress would require (i) the collection of time  
57 series of indicators to monitor habitat change, individual behaviour, individual fitness and  
58 population dynamics, and (ii) experimental studies to identify the underlying behavioural and  
59 biological processes involved **in** associative behaviour. The extent of the modification of the  
60 surface habitat by the massive deployment of DFADs and the current uncertainty of the  
61 possible long-term consequences on the individual fitness and dynamics of tuna populations  
62 argue for the need for increased awareness of this issue by Regional Fisheries Management  
63 Organisations regulating tuna fishing.

64

65 **Keywords** (6 max): DFAD, ecological effects, ecological trap, fish behaviour, fisheries  
66 management, tuna

67

68

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## 90Introduction

91Many fish species are known to associate with floating objects (Castro et al., 2002; Fréon &  
92Dagorn, 2000), with the first known descriptions of fishers exploiting these associations  
93dating from 200 AD in the Mediterranean Sea by the Roman author Oppian (cited in Taquet,  
942013). In particular, the use of floating objects to facilitate the capture of tropical tunas  
95(skipjack SKJ – *Katsuwonus pelamis*; yellowfin YFT – *Thunnus albacares*; and bigeye BET –  
96*T. obesus*), has undergone rapid expansion in recent decades, as a result of the growing  
97importance of these floating structures to the strategy and efficiency of tropical tuna purse  
98seine fleets (Dagorn et al., 2012; Fonteneau et al., 2000, 2013; Leroy et al., 2013; Miyake et  
99al., 2010). Since the onset of the tropical tuna purse seine fishery, fishers took advantage of  
100the associative behaviour of tunas with floating objects and actively searched for natural  
101floating objects to improve their catches (Greenblatt, 1979 ; Hallier and Parajua, 1999 ; Scott  
102et al. 1999). Towards the end of the 1980s, fishers began to build and deploy man-made  
103drifting fish aggregating devices (DFADs), and to attach radio buoys to locate them (Ariz et  
104al., 1999 ; Hallier and Parajua, 1999 ; Hall et al. 1992 ; Scott et al. 1999 ; Lopez et al., 2014;  
105Marsac et al., 2014; Moreno et al., 2007; Morón, 2001; Stéquert & Marsac, 1986). DFADs  
106are commonly composed of a floating structure (such as a bamboo or metal raft with  
107buoyancy provided by corks, etc.) and a submerged structure (made of ropes, old netting,  
108canvas, weights, etc.). During the last two decades, radio buoys have been replaced by GPS  
109buoys communicating via satellite directly with fishing vessels. In the last decade (2010-  
1102020), most DFADs have been equipped with echo-sounder buoys, providing estimates of  
111aggregated biomass (Lopez et al., 2014). Some fleets also use supply vessels to maintain  
112their DFAD array and to inform the fishing vessels of tuna aggregations, allowing these fleets  
113to manage more efficiently their DFAD stock (Arrizabalaga et al., 2001; Ramos et al., 2013).  
114DFADs represent very efficient fishing tools that increased the catchability of tunas, leading  
115purse-seine fleets to target preferentially associated schools and expanding their fishing  
116grounds (Lopez et al. 2014, Fonteneau et al. 2015, Lennert-Cody et al. 2019).

117Over time, given the growing contribution of purse seine fleets to world tuna catches and the  
118increasing importance of DFAD fishing in the strategy of purse seine fleets, managing  
119DFADs has become a priority for all tuna Regional Fishery Management Organisations  
120(tRFMOs). In this paper we will use “operational” or “active” buoys to designate buoys  
121attached to a **floating object (FOB)** that are tracked by one or several purse seine fishing  
122vessel(s). Tuna RFMOs set limits of the number of operational buoys (with the very first limit  
123by the IOTC, Indian Ocean Tuna Commission, in 2015) to mitigate the different risks induced  
124by the deployment and use of DFADs (most recent resolutions: IOTC Res 23/02, ICCAT Rec  
12522-01, IATTC Res C-21-04, WCPFC CMM 2021-01). **Fishing at FOBs was demonstrated to**  
126**increase by-catch rates, compared to fishing on free-swimming schools (Amandé et al. 2012,**  
127**Escalle et al. 2018), and to increase the proportion of small BET and YFT (IOTC 2022).**  
128Other major DFAD-related measures concerned the design of these objects, following the  
129discovery of sharks getting entangled in the netting composing the structure of DFADs  
130(Filmlalter et al. 2013). Limiting the pollution induced by DFADs in the ocean is also in front of  
131the agendas of tRFMOs, after realizing the large quantity of plastic used in DFADs and the  
132large numbers of DFAD beaching events in sensitive coastal ecosystems (**Escalle et al.**  
133**2019,** Imzilen et al. 2021, 2022). However, other impacts on tuna populations (unrelated to  
134fishery vulnerability) and ecosystems may be induced by the increased presence of DFADs  
135in their habitat (**Marsac et al. 2000, Bromhead et al. 2003, Hallier & Gaertner 2008**). Despite  
136the limits on operational buoys, DFADs number in the water has increased (Dagorn et al.  
1372013a, Maufroy et al. 2017, Imzilen et al. 2021, Dupaix et al. 2021). As such, while logs and  
138branches have always been components of the habitat of tropical tunas (originating from  
139rivers, mangroves or shorelines), the massive use of man-made DFADs has changed their  
140habitat.

141Changing a habitat can positively or negatively impact the ecology of wild animals inhabiting  
142it. For example, artificial habitats could benefit some reef species (Lee et al. 2018).  
143Contrarily, alterations could also reduce habitat quality, e.g. by reducing the number of  
144shelters or nests for some species, or by decreasing their food resources (often through the  
145alteration of the habitat of these resources themselves, Mullu 2016). In some cases, animals

146are misled by cues that were previously correlated with the habitat quality but no longer are,  
147due to anthropogenic influences (Sherley et al. 2017, Swearer et al. 2021). Such impacts  
148form the basis of the ecological trap theory and result in the preferential selection of low-  
149quality habitats by animals, when better alternatives exist (Battin, 2004; Schlaepfer et al.,  
1502002). It is worth noting that, depending on the definition, an ecological trap can occur  
151without any anthropogenic influence (Robertson & Hutto, 2006; Swearer et al., 2021; Teske  
152et al., 2021). In this paper, we will consider that ecological traps occur because of a sudden  
153anthropogenic change in the environment, i.e. in the case of tropical tuna, the modification of  
154their surface habitat by the increased deployment of DFADs (Gilroy & Sutherland, 2007;  
155Hallier & Gaertner, 2008; Schlaepfer et al., 2002). While this theory has been proposed  
156regularly in the face of anthropogenic environmental modifications and their impacts on  
157various species, few studies have empirically demonstrated the existence of such traps  
158(Battin, 2004; Swearer et al., 2021).

159Noting the increasing number of floating objects being deployed by fishers during the 1990s,  
160some scientists hypothesized that the increase in the number of DFADs could lead to an  
161ecological trap, altering the ecological value of floating objects for tropical tunas associated  
162to DFADs (Marsac et al., 2000). It is hypothesized that large numbers of DFADs may alter  
163certain biological characteristics of epipelagic populations associated with them: migration,  
164schooling behaviour, growth, fish condition and bioenergetics, predation and natural mortality  
165(Figures 1 & 2). TRFMOs primarily focus on developing management schemes to address  
166the known effects of DFADs on catches (particularly of small YFT and BET, as well as  
167sharks) or their stranding on coasts. However, there is also a need to assess whether  
168DFADs, through their presence on the ocean, can alter the life history parameters and  
169behaviour of tunas, so as to manage the number of DFADs deployed at sea if negative  
170impacts are suspected or demonstrated.

171Almost 20 years ago, Dempster & Taquet (2004) made a systematic review of the published  
172literature on FADs and concluded that further research should assess the use of DFADs by  
173pelagic species, the mechanisms underlying their associative behaviour and the ecological  
174consequences of the presence of DFADs at sea on pelagic fish stocks. Since then, several



175 papers reviewed existing evidence and/or proposed future research directions to address the  
176 impacts of DFADs on tropical tuna (Dagorn et al. 2013b, Evans et al. 2015, Davies et al.  
177 2014, Fonteneau et al. 2015, Leroy et al. 2013, Taquet 2013). Yet, most of these papers,  
178 except Taquet (2013), addressed these impacts at a regional scale and all were mainly  
179 focussing on the direct impacts of DFADs (induced by an increase of fishing mortality), even  
180 though they mentioned potential indirect impacts (not related to fishing mortality increase).  
181 The objective and originality of this paper is to review the current knowledge on the impacts  
182 of DFADs on the ecology and life history traits of tropical tuna, focussing only on the indirect  
183 effects (consequences of fishing on DFADs are not addressed here). The reason for this is  
184 that this particular question has generated a global scientific debate for years, precluding  
185 management bodies from having a complete and synthetic view of the current knowledge. An  
186 in-depth literature review provides an overview of the state of the art in this area, identifies  
187 knowledge gaps, and proposes future research priorities. This paper is structured around  
188 four major questions:

189i) How much do DFADs change the habitat of tropical tunas?

190ii) Do DFADs modify the migration and the schooling behaviour of tropical tunas?

191iii) Do DFADs modify the life history parameters of tropical tunas?

192iv) What are the scientific challenges to fill the knowledge gaps?

### 193 **How much do DFADs change the habitat of tropical tunas?**

194 Natural floating objects, primarily tree trunks or branches carried by rivers, have always been  
195 a component of tuna habitat. It should be noted that the current largest tuna purse seine  
196 fishery in the world was first developed in the Western and Central Pacific Ocean (WCPO) by  
197 Japanese exploratory fishing cruises that perfected methods for seining tuna schools found  
198 in association with natural floating logs that later evolved into DFAD fisheries in all oceans  
199 (Watanabe 1988). Human activities (logging, coastal development, shipping, etc.) modified  
200 the number of floating objects at sea, in some cases even before modern purse-seine tuna  
201 fishing began (Caddy & Majkowski, 1996; Thiel & Gutow, 2005). Some of these activities

202 may have consistently increased (coastal development, shipping), whereas others, such as  
203 logging, may have varied due to increased global trade and subsequent deforestation of  
204 some areas (Caddy & Majkowski, 1996). In addition, environmental changes also affect the  
205 production and movement of floating objects (e.g. floods, El Niño events, tsunamis), with  
206 global warming supposed to increase the frequency of extreme events. In recent years, the  
207 increase in the number of DFADs deployed by fishers raised the question of the impacts of  
208 this practice on tropical tuna habitat. It is therefore essential to assess the extent to which  
209 DFADs have changed the habitat of tunas, in comparison to the historical pristine state when  
210 only natural floating objects existed.

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

221 Habitat changes due to DFADs can be assessed by estimating and comparing densities of  
222 objects (with information on their nature: LOGs or DFADs) and distance between objects  
223 (nearest neighbour), with both parameters being closely related. These parameters depend  
224 upon the rates at which DFADs are added or removed from the ocean (by sinking, beaching  
225 or retrieved by humans), as well as their drift. For every oceanic spatio-temporal unit (e.g.  
226 region and season), comparing these parameters with those of natural floating objects and  
227 for all types together (natural and artificial) is challenging, the primary concern being to  
228 identify the origin of the floating object.

229The number of DFADs have regularly increased (Maufroy et al. 2017), but it is necessary to  
230put this in perspective with respect to all floating objects. Using data from observers onboard  
231tuna purse seine vessels in the Indian Ocean (IO), noting all FOBs encountered when the  
232vessel cruises, Dupaix et al. (2021) highlighted a drastic increase in the total number of  
233floating objects in the western IO, from 2006 to 2018, with multiplication factors greater than  
2342 in every region and reaching as high as 60 in some areas (e.g. Somali area). The entire  
235western IO is affected, with DFADs comprising over 85% of the total FOBs and DFADs  
236contributing to reduce the distances between floating objects (mean distances between  
237DFADs and between NLOGs of 37 km and 89 km, respectively, in 2014-2018). The impact of  
238DFADs on tuna habitat reducing the distance between FOBs was observed in the study both  
239when considering all DFADs or only randomly encountered DFADs (objects which do not  
240belong to the vessel or its fishing company), to account for a potential sampling bias. Phillips  
241et al. (2019a), using data from 2016 and 2017 and Lagrangian simulations in the Western  
242and Central Pacific Ocean (WCPO), also showed an increase in FOB densities induced by  
243DFAD deployments, and observed a shift of the area with the highest FOB densities, from  
244the North-Eastern area of the Bismark Sea to the Tuvalu archipelago. Unfortunately, to our  
245knowledge, no similar detailed study has been conducted in the other oceans, precluding  
246from estimating the extent of the change of the habitat of tunas due to the addition of new  
247floating objects globally.

248Most of the management effort by tRFMOs is focused on the monitoring and control of  
249satellite-tracked buoys attached to floating objects (either to DFADs or to LOGs), emitting  
250positions (and other variables) to vessels and qualified as operational buoys, as this variable  
251is strongly related to fishing effort. This also explains why most scientific studies prioritized  
252the estimate of operational buoys rather than the number of DFADs in the ocean (Table 1).  
253Currently, all tRFMOs have implemented a limit on the instantaneous number of operational  
254satellite buoys per vessel, and, except in the Atlantic Ocean (AO), limited the re-activation of  
255buoys while at sea, but only the IOTC has limited the number of buoys purchased and in  
256stock per year, per vessel (IOTC Res 23/02, ICCAT Rec 22-01, IATTC Res C-21-04,  
257WCPFC CMM 2021-01). This clearly reflects a lack of concerted action worldwide to limit the

258number of new floating objects deployed in the oceans. Even under the limit of active DFADs  
259at sea per vessel, the actual total numbers of DFADs in the ocean could have increased. So  
260far, few studies have produced estimates of the total number of DFADs deployed annually,  
261with estimations providing a range of 81,000 to 121,000 deployments worldwide, but these  
262global estimates were made a decade ago (Baske et al., 2012; Gershman et al., 2015; Scott  
263& Lopez, 2014). As a comparison, AFADs seem to be less numerous worldwide (13,000  
264AFADs estimated in Scott & Lopez 2014), although there may be few areas with very high  
265densities of AFADs, such as Indonesia (5,000-10,000, Proctor et al. 2019), the Philippines or  
266Papua New Guinea.

267In practice, despite efforts by tRFMOs to require the submission of DFAD data, accurately  
268determining a simple indicator such as the total number of DFADs that are drifting in the  
269world's oceans is a major challenge. The easiest way would be to monitor the number of  
270deployments through logbooks or onboard observers or set up a FAD register (see Res  
27123/02 of the IOTC). The number of operational buoys does not correspond to the number of  
272DFADs in the water (and/or deployed) as some buoys can be attached to LOGs, can be  
273deactivated, and some DFADs may lack positional trackers, but it can be used as a proxy to  
274illustrate the trend in numbers. Therefore, as the number of operational buoys does not  
275effectively limit DFAD deployments, the number of DFADs in the water and/or deployments  
276could be larger than the limits adopted by the tRFMOs. Under the assumption that the  
277number of natural floating objects remains relatively constant, the increasing number of  
278electronic buoys used reflects an increase of the number of FOBs. In recent years, DFAD  
279deployments were stable in the WCPO (2011-2019; Escalle et al. 2020), decreased in the IO  
280(2016-2021; IOTC, 2022), increased in the Eastern Pacific Ocean (EPO, 2015-2020; Lopez  
281et al. 2021) and buoy deployments increased in the AO (2007-2013; Maufroy et al. 2017).  
282Hence, a characterisation of DFAD deployment trends at the global scale is needed.  
283However, the clear trend in the number of DFAD sets or DFAD catches (Floch et al., 2019;  
284FIRMS Global Tuna Atlas cited in IOTC, 2021; Restrepo et al., 2017) suggests that DFAD  
285deployment has also increased.

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

287 DFADs may affect both the movements of tunas and their schooling behaviour. Large-scale  
288 movements of tunas can be impacted in the following two ways: (i) DFADs could cause tunas  
289 to relocate to new areas and (ii) they could increase residence times in some areas. Ideally,  
290 the best approach for investigating such potential effects would be to compare the large-  
291 scale movement patterns of tunas before and after the period in which the increase of DFAD  
292 numbers occurred (i.e. before or after the 1990's). To our knowledge, historical data to  
293 assess large-scale movement patterns before fishers started to massively deploy DFADs,  
294 necessary for this type of analysis, exist only in the WCPO (Kim 2015) and in the EAO  
295 (Cayré et al. 1986) and we do not know of any long-term study that compared movement  
296 patterns before and after DFAD use increased.

### 297 *Effects on individual large-scale movements*

298 Wang et al. (2014) found that the spatial dynamics of free-swimming school sets in the  
299 WCPO were influenced by the onset of El Niño Southern Oscillation (ENSO) events, while  
300 these events had no effects on the location of floating-object-associated school sets. Catch  
301 data, however, reflect the movements of the available catchable portion of the stocks and the  
302 catchability of different set types (e.g. DFAD sets catching smaller individuals than the free-  
303 school sets), and not the true movements of populations.

304 Hallier & Gaertner (2008) analysed conventional tagging data of SKJ and YFT in the Eastern  
305 Atlantic Ocean (EAO). Different migratory directional patterns and displacement rates were  
306 observed between fish recaptures associated with DFADs and those in free-swimming  
307 schools. Displacement rates were significantly larger for both YFT and SKJ recaptured in  
308 association with DFADs (13 and 15 nm/day, respectively) than those recaptured in free-  
309 swimming schools (3 and 4.5 nm/day, respectively), which suggests that DFADs could  
310 relocate tunas to new areas. In the IO, Stehfest and Dagorn (2010) found similar results for  
311 SKJ, YFT and BET, but with lower displacement rates differences than in the AO. Hallier and  
312 Gaertner (2008) interpreted these results as indicating significant modifications of migratory  
313 patterns due to associations with DFADs, suggesting an influence of DFAD association

314 strong-enough to disturb tropical tuna migratory patterns. However, Stehfest and Dagorn  
315 (2010) argue that it could only reflect an artefact of the non-uniform distribution of DFAD  
316 fishing. Also, authors of both studies agree that school type at recapture might not be  
317 representative of the associative history of individuals before their recapture. Using an  
318 advection-diffusion model, Kim (2015) also showed that including a DFAD attraction  
319 component to the model better fitted SKJ tagging data in the WCPO, suggesting an effect of  
320 DFADs on SKJ migratory patterns. Comparing DFAD induced movements in the 2000s with  
321 those in the 1990s, they showed that the rising DFAD density increased this modification of  
322 migration patterns. These studies were the only ones to assess differences of movement  
323 patterns induced by DFADs and, due to species and ocean differences, more studies would  
324 be needed to interpret these results at a global scale.

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

### 338 *Effects on individual fine-scale movements*

339 In addition, the possibility of DFADs influencing the large-scale movements of tunas could be  
340 evaluated through the measure of the time tunas spend associated with DFADs and the time  
341 they spend unassociated (or between two DFAD associations). It could be considered that

342the longer tunas remain associated with DFADs, the larger the influence DFADs could have  
343on their large-scale movements. Acoustic tags and archival tags (only when a species  
344exhibits a distinct vertical behaviour when associating with a floating object, as observed for  
345BET or sometimes YFT) have been used by scientists to measure these parameters (Table  
3462). Passive acoustic tagging studies on DFADs revealed that the majority of residence times  
347of tunas (i.e. continuous periods of time spent associated with a given DFAD) were of a few  
348days. Mean values ranged from 0.2 to 4.6 days for SKJ (Dagorn et al., 2007; Govinden et al.,  
3492021; Matsumoto et al., 2014, 2016), from 1.0 to 6.6 days for YFT and 1.4 to 10 days for  
350BET (Dagorn et al., 2007; Govinden et al., 2021; Matsumoto et al., 2016, Phillips et al.  
3512019b). Long associations, however, have been observed on rare occasions – e.g. 27 days  
352for YFT in the IO (Govinden et al., 2021) and up to 18, 50 and 30 days for SKJ, YFT and  
353BET respectively, in the WCPO (Phillips et al. 2017, Phillips et al. 2019b). A recent study in  
354the EAO (Tolotti et al., 2020) reported significantly larger mean residence times for the three  
355tuna species, from 9 days (SKJ) to 19 days (YFT) and 25 days (BET), with record values of  
35655 days and 600 km travelled associated to a DFAD for both BET and YFT.

357These studies suggest that residence times at a single DFAD vary between oceanic regions  
358and species. Without more studies, it is difficult to assess whether the long DFAD  
359associations observed are restricted to specific areas and time periods, or if they can often  
360occur. In fact, even short DFAD residence times as those observed in the Indian and Pacific  
361oceans do not prove that DFADs cannot influence large-scale movements. The short  
362residence times suggest that a single DFAD does not significantly impact the behaviour of  
363tunas for long enough to influence their large-scale movements. However, in an array of  
364DFADs, a tuna can “switch” from one DFAD to a neighbouring one, which could retain it in  
365the array. It is therefore important to also measure the time tunas spend between two  
366associations (or unassociated), or in other words, the total percentage of time a tuna spends  
367associated over long periods. This variable is likely to depend on the density of all floating  
368objects in the area. So far, very few durations between two DFAD associations have been  
369measured using acoustic tags because it is difficult to locate and exhaustively instrument  
370with acoustic receivers all DFADs in an area.

371In the WCPO, 25 BET, 6 YFT and 2 SKJ displayed "homing" behaviour by returning to the  
372same DFAD with absences greater than a day (Phillips et al. 2019b). Most of these absences  
373were short for BET (median: 3.2 days) and longer for YFT (median: 10.5 days) but with a low  
374sample size not allowing to be conclusive. In the other tropical oceans, even fewer tunas  
375were observed performing such homing behaviour: one BET in the AO (out of 23 tagged fish,  
376Tolotti et al., 2020), one YFT and two SKJ in the IO (out of 31 and 17 tagged fish  
377respectively, Govinden et al., 2021), and these absences lasted less than two days.

378Because BET and sometimes YFT exhibit different vertical behaviour patterns when  
379associated or non-associated with floating objects (Holland and Brill 1990, Abascal et al.  
3802018), archival tags have been used to assess residence times at and between floating  
381objects, and therefore percentage of days associated with floating objects, without the need  
382to instrument all objects with acoustic receivers. Using satellite archival tagging data where  
383individual BET tracks could be recorded over several months or even years, the percentage  
384of time associated with floating objects was estimated to be between 4 % and 17 %  
385depending on the size of the fish and the oceanic region (Fuller et al., 2015; Phillips et al.,  
3862017; Schaefer & Fuller, 2010, Leroy et al. 2013, Schaefer & Fuller 2002). Associative and  
387non-associative behaviour with floating objects have also been described with archival tags  
388for YFT (Phillips et al., 2017; Schaefer et al., 2009; Schaefer & Fuller, 2013, Leroy et al.  
3892013), with estimates of the percentage of time spent associated with floating objects  
390between 10% and 23%. These percentages are much lower than those estimated from  
391acoustic telemetry data (e.g. 75 % for small BET based on the measurements in Phillips, et  
392al. 2019b).

393This inconsistency between studies using different tagging methods could result from the  
394size of tagged individuals or the way the percentage of time spent by tuna associated and  
395non-associated is calculated. Individuals monitored with archival tags were generally larger  
396(fork length: 50-146 cm YFT and 46-102 cm BET in Phillips et al. 2017, 51-134 cm BET in  
397Fuller et al. 2015, 88-134 cm BET in Schaefer & Fuller 2002, 54-159 cm BET in Schaefer &  
398Fuller 2010) than those marked with passive acoustic tags (38-90 cm BET in Phillips et al.  
3992019), even though size ranges largely overlap. This suggests that small BET spend a higher



400 proportion of their time associated with FOBs than large individuals. This agrees with  
401 observed size distributions of DFAD catches, where smaller individuals are caught, and with  
402 the negative correlation between BET individual length and percentage of time associated  
403 found by Schaefer & Fuller (2002). However, Schaefer et al. (2009) found lower association  
404 percentages with archival tags on small tunas (10.4 and 15.9 % of the time associated for  
405 51-60 cm FL YFT and 65-99 cm FL BET respectively) than the work of Phillips et al. (2019)  
406 with acoustic tagging. This could suggest a potential bias of the different methodologies that  
407 should be further investigated, as a small percentage of time associated with floating objects  
408 would indicate no or little influence of DFADs, while a high percentage could indicate a  
409 potentially significant influence of DFADs on large-scale movements, which could result in an  
410 ecological trap.

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

#### 418 *Effects on schooling behaviour*

419 DFADs could also affect schooling behaviour, which can have a wide range of consequences  
420 on the **life-history parameters** and the movements of tunas. Dagorn & Fréon (1999) and  
421 Fréon & Dagorn (2000) suggested that tunas could associate with floating objects for social  
422 advantages such as facilitating schooling behaviour. To date no result has been obtained **on**  
423 **tropical tuna** from DFADs regarding this question. If floating objects facilitate the schooling  
424 behaviour of tunas, then the deployment of large numbers of DFADs may have effects on  
425 school size, either by facilitating the formation of large (but less) schools or decreasing  
426 school size with DFADs offering too many aggregation sites (**Figure 2**, Dagorn et al., 2010).  
427 DFADs could also modify the size structure of tuna schools, allowing the formation of large

428 aggregations composed of several unassociated schools of different size structures (Wang et  
429 al. 2012). Sempo et al. (2013) modelled the impact of the increasing deployment of DFADs  
430 on the distribution of social fish species such as tunas. They demonstrated that for social  
431 species, increasing the number of DFADs does not necessarily lead to an increase in the  
432 total amount of tuna associated with DFADs, a non-intuitive result. Capello et al. (2022) also  
433 showed that the number of DFADs with associated schools and the size of associated  
434 schools were not linearly related to the total number of DFADs and that this relationship  
435 varied according to the considered social scenario.

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

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

#### 440 *Effects on feeding*

441 In his review on DFAD impacts on tropical tunas, Taquet (2013) recommended comparative  
442 analyses of stomach contents on tropical tunas. Such analyses have shown that small-sized  
443 tunas may not feed while associated with DFADs in the Atlantic (Hallier & Gaertner, 2008;  
444 Ménard et al., 2000), Indian (Grande et al., 2013; Jaquemet et al., 2011; Zudaire et al., 2015,  
445 Malone et al. 2011, Hallier & Gaertner, 2008) and Western and Central Pacific (Machful et  
446 al., 2021) oceans. Small YFT and SKJ captured in DFAD-associated schools had a higher  
447 fraction of empty stomachs, lower stomach fullness or daily food rates (in the EAO; Hallier &  
448 Gaertner 2008, Ménard et al. 2000; and in the IO, Hallier & Gaertner 2008), and lower prey  
449 weight (in the IO; Grande et al. 2013, Zudaire et al. 2015) than those captured in free-  
450 swimming schools. These results support the hypothesis that the quantity of prey present in  
451 DFAD assemblages is not sufficient to sustain the dietary requirements of large aggregations  
452 of small-sized tunas commonly found at DFADs (several tens of tons) (Fréon & Dagorn,  
453 2000). However, except in Hallier & Gaertner (2008), the influence of the sampling time of  
454 tunas on the stomach content was not taken into account. Purse seine vessels mainly fish on

455 DFADs at dawn (Forget et al., 2015) and on free-swimming schools during daytime. First,  
456 feeding activities are believed to often take place in the early evening on organisms  
457 performing diel vertical migration between the deep scattering layer and the surface  
458 (Schaefer & Fuller, 2002), resulting in prey being fully digested by the time the fish are  
459 caught and sampled, at dawn. Second, free-swimming schools of tunas are almost  
460 exclusively caught when actively feeding at the sea surface, hence higher levels of stomach  
461 fullness are to be expected. Nevertheless, the association of tunas with DFADs could also  
462 affect the composition and quality of their diet, as shown for YFT in the Western IO (WIO)  
463 and WCPO and for SKJ in the WCPO (Zudaire et al. 2015, Allain et al. 2010). Differences of  
464 diet composition were observed for these species, that may be due to their associative  
465 behaviour despite the above-mentioned sampling bias, with associated tuna in the WCPO  
466 feeding on shallower prey than free-swimming tunas (Allain et al. 2010), which is in  
467 agreement with YFT staying closer to the surface when associated (Holland and Brill, 1990,  
468 Schaefer et al. 2009).

469 Independently of the trophic role of DFADs, the deployment and the drift trajectories of  
470 DFADs could create new zones of high floating object densities, which may be unfavourable  
471 for the foraging success of tunas (Marsac et al. 2000). Jaquemet et al. (2011) partitioned  
472 their samples in “rich” (i.e., no limiting food) versus “poor” forage areas in the Indian Ocean,  
473 in relation to an exceptional demographic outburst of a pelagic stomatopod (Crustacea),  
474 which composed the bulk of tuna diet in this region (Potier et al., 2004, 2007). These authors  
475 found that in “rich” forage areas, DFADs have no impact on the feeding pattern of tunas,  
476 whereas in “poor” forage areas, tunas associated with DFADs had lower stomach fullness  
477 compared to tunas in free-swimming schools. Jaquemet et al. (2011) suggested that the  
478 impact of DFADs on feeding success could be location-dependent. This led the authors to  
479 emphasize the possible detrimental effect on the condition of tuna associated with DFADs if  
480 associated tunas drift towards areas with poor forage resources. However, such an effect  
481 relies on the assumption that a tuna’s probability to depart from a DFAD is independent of  
482 their local environment which seems in disagreement with behavioral studies (Fuller et al.  
483 2015, Nootboom et al. 2023).

484In the Pacific Ocean, Hunsicker et al. (2012) observed that predation on SKJ and YFT by  
485large pelagic fishes sampled from DFAD sets was greater than for those captured via other  
486fishing methods (e.g. free-swimming schools). These authors concluded that by aggregating  
487small-sized SKJ, YFT, and BET, DFADs enhance their vulnerability to predators such as  
488sharks and billfishes, and thus increase natural mortality of small sized tunas. To our  
489knowledge, this is the only study assessing the impact of DFADs on tuna vulnerability to  
490predators, hence additional data from other regions would be needed for further testing these  
491assumptions.

#### 492 *Effects on body condition*

493Tuna condition has been investigated using different methods: biometric condition factors  
494(e.g. plumpness), and biochemical indices (e.g., fat and water contents, lipid class  
495composition). Gaertner et al. (1999) in a preliminary investigation did not find evidence of a  
496morphometric difference between free-swimming school or DFAD-caught tunas in the EAO.  
497But Marsac et al. (2000) in the EAO and Hallier & Gaertner (2008) in the WIO found that  
498individuals associated with DFADs were in lower condition than those in free-swimming  
499schools, using morphometric indicators (thorax width or girth, plumpness of fish) as fish  
500health indicators. Robert et al. (2014) measured the condition of SKJ using BIA (Bioelectrical  
501Impedance Analysis), a non-invasive field tool that estimates body water content (inversely  
502correlated with body fat content), and determines total lipid and main lipid class  
503concentrations. They confirmed the lower condition of SKJ associated with floating objects  
504compared to those in free-swimming schools. Because the studied area (Mozambique  
505Channel, WIO) is naturally rich with NLOGs and had undergone little habitat modifications  
506due to DFADs at the time of the study (Dagorn et al., 2013a, Dupaix et al. 2021), the authors  
507concluded that before the use of DFADs, tunas associated with logs could have also been in  
508lower condition than tunas in free-swimming schools. These results can mean that (1) a  
509lower measured condition could reflect normal variations and does not necessarily imply  
510detrimental physiological consequences, or (2) some specific areas where NLOGs have

511always been in high numbers could also have negatively impacted the condition of tunas that  
512passed through and stayed in these areas.

513As a lower condition measured at DFADs does not necessarily imply longer-term detrimental  
514consequences for tuna, there is a need to monitor tuna condition and other biological  
515parameters on a longer term and determine if they are influenced by the density of DFADs in  
516the area. Dupaix et al. (2023), using length-weight data from 1987 to 2018 in the WIO, found  
517no decreasing trend of YFT condition over the studied period, during which the number of  
518DFADs has increased. Hence, this study, using one morphometric indicator as a proxy for  
519condition (Le Cren's relative condition factor), suggests the absence of a long-term impact of  
520DFADs on YFT condition, under the conditions encountered in the WIO in the last three  
521decades. Nevertheless, it should be noted that other factors could also have counteracted  
522potential negative effects of DFADs on tuna condition.

523Studies that investigated potential DFAD impacts on tuna condition mainly suggest that the  
524condition of associated tuna is lower than that of free-swimming tuna. These results are  
525reinforced by the example of the preparation of katsuobushi (shaved dried SKJ) in Japan.  
526Indeed the Japanese tuna industry prefers SKJ caught on DFADs as they have less fat than  
527those from free-swimming schools (Nishida, pers. comm.). However, Sardenne et al. (2016),  
528when comparing biometric and biochemical indicators found inconsistencies due to a high  
529variability of biometric indicators with season and ontogeny. They concluded that biometric  
530indicators measured on whole tuna (e.g. thorax girth, fish plumpness, Le Cren's  $K_n$ ) should  
531be interpreted with caution as they may not always reflect the energetic condition measured  
532in the tissues of the fish. Experimental validation of the condition factors used is needed to  
533determine the potential impacts and the underlying mechanisms of the difference in tuna  
534condition. For example, condition factors could be calibrated and validated by monitoring  
535them during fasting experiments on captive tuna, although measuring some of them regularly  
536in experimental conditions could represent a methodological challenge.

537 *Effects on reproduction and growth*

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

551 Similarly, Ashida et al. (2017) investigated the difference in reproductive traits of female SKJ,  
552 of similar size distribution, between school types in the WCPO, highlighting a significant  
553 higher proportion of mature females in free swimming schools, characterised by higher  
554 relative condition factor, than associated with DFADs. However, as for YFT in the IO (Zudaire  
555 et al. 2014), no significant effect of the school type was observed on the WCPO SKJ  
556 fecundity, which corroborates previous results observed for WIO SKJ (Grande, 2013; Grande  
557 et al. 2014). The lack of relationship between condition and fecundity of SKJ could be related  
558 to their energy allocation and reproductive strategies. SKJ tuna females fuel their gametes  
559 with energy gained concomitantly during reproduction (i.e., income breeding strategy,  
560 Grande et al. 2016). However, YFT females can store additional energy reserves prior to  
561 spawning, which define them as income-capital breeder (Zudaire et al., 2014) unlike SKJ.  
562 Therefore, as SKJ females exhibit better condition when free swimming, it can be assumed  
563 that their reproductive efficiency is lower when associated with DFADs, but the same  
564 conclusion cannot be made for YFT.

565 Using tagging data collected in the EAO, Hallier & Gaertner (2008) estimated and compared  
566 the growth rates of SKJ and YFT associated with DFADs versus free-swimming schools.  
567 Released and recaptured SKJ associated with DFADs had a significantly lower growth rate  
568 than those in free-swimming schools, but the difference was not significant for YFT (though it  
569 was lower, as for SKJ). However, the history experienced by individual fish between release  
570 and recapture was unknown. The “experimental” design could not be controlled as the time  
571 one specimen spent associated with DFADs and in free-swimming schools is not available.  
572 In addition, the authors were only able to process a small sample of free-swimming YFT (n =  
573 10).

#### 574 **What are the scientific challenges to fill the knowledge gaps?**

575 DFADs have been representing one of the key management priorities and challenges of  
576 RFMOs over the last decade. Since fishers started using them, DFADs numbers  
577 continuously increased until first management measures limiting the number of operational  
578 buoys were adopted in the mid-2010s (Song & Shen 2022). The massive use of DFADs in all  
579 oceans has been generating major concerns on the sustainability of this fishing mode.  
580 DFADs increase the catchability of tropical tunas leading to large catches of small BET and  
581 YFT (Dagorn et al., 2013b; Fonteneau et al., 2013), generate more bycatch, including  
582 vulnerable species such as some shark species, silky (*Carcharhinus falciformis*) and oceanic  
583 whitetip (*Carcharhinus longimanus*) sharks (Dagorn et al., 2013b; Fonteneau et al., 2013;  
584 Leroy et al., 2013), and can strand on coastal areas causing damage to marine habitats  
585 (Imzilen et al., 2021; Maufroy et al., 2015, Escalle et al. 2019). Although there is increasing  
586 knowledge and literature on DFADs, the issue of their indirect impacts (not related to fishing  
587 mortality) on tropical tuna remains a scientific debate. All knowledge collected and reviewed  
588 on the behaviour and life-history parameters of tunas at DFADs clearly reveals a lack of  
589 converging scientific results on the long term consequences on tuna (at the individual or  
590 population levels) of increased numbers of floating objects. Therefore, if DFADs seem to  
591 affect the short-term condition of tropical tunas, we are not currently able to conclude  
592 whether DFADs affect the movements and/or other life-history parameters of tunas in a way

593that could significantly affect the fitness of individuals and the demography of their  
594populations. As such, there is a need to improve the observation and understand this  
595associative phenomenon to provide scientific advice on the effects of DFADs on the life-  
596history parameters and behaviour of tropical tunas and other associated species.

597A major gap in tuna and DFAD science is the lack of time series of key parameters such as  
598the numbers of DFADs and natural floating objects, residence and absence times at DFADs  
599as well as large movements between oceanic regions, school sizes, condition and  
600reproduction indices. The first research priority in this context is to initiate or continue time  
601series of such indicators (Capello et al. 2023). Setting long-term monitoring programs in  
602every ocean appears to be a priority, as effects of DFADs could vary depending on the  
603species, the characteristics of each ecosystem and on the density of floating objects.  
604Moreover, it would facilitate comparative analyses between oceans to better understand the  
605drivers of tuna associative behaviour. The collection of some parameters will require  
606dedicated scientific surveys (e.g. electronic tagging, biological sampling) while others (e.g.  
607numbers of DFADs and natural objects, biological condition factors) have started to be  
608routinely collected by tRFMOs through FAD-specific data requirements included in  
609conservation and management measures (Grande et al. 2018, Báez et al. 2022, Song &  
610Shen 2022) as well as government and industry initiatives (e.g., routine fishery monitoring  
611and at-sea observer programs).

612Another research priority is to develop experimental studies to identify the biological and  
613behavioural processes involved in the associative behaviour. The only scientific consensus is  
614the fact that in a given area, conditions of tunas associated with floating objects seem to  
615often be lower than those of fish in free-swimming schools. However, the different indicators  
616used to assess tuna condition are not always well correlated (Sardenne et al. 2016), and  
617experimental studies are needed to validate them against proper benchmarks, allowing to  
618determine how representative they are of individuals' health. Then, understanding how fast  
619these indicators change with the fish's associative behaviour appears essential. This could  
620also be achieved through studies on captive tropical tunas (e.g., Estess et al. 2017), but non  
621lethal observations should be promoted (e.g. BIA) in order to track changes throughout the



622fish lifespan. No evidence exists suggesting whether the lower condition at DFADs is the  
623consequence or the cause of their association with DFADs. Often the robustness of the  
624findings of **investigation on the life-history parameters** of tunas was hampered by the lack of  
625knowledge of the time spent associated with a DFAD or in an array of DFADs by each  
626specimen analysed. The history of each individual tuna is a hidden variable that must be  
627taken into account in statistical analyses, which is a challenge. Studies combining  
628behavioural observations (tagging) and condition of the individuals (e.g. BIA or biochemical  
629analyses of biopsies made at the time of tagging) should then be encouraged. Ideally, tags  
630equipped with physiological sensors would clearly help understanding the interplay between  
631associative behaviour and tuna physiology. Such tags, however, are **only starting** to be  
632developed.

633Studies on AFADs could provide insights to the questions addressed in this manuscript: as  
634argued by Dagorn et al. (2010), AFADs also alter the natural environment (by adding floating  
635objects to the ocean). However, it remains questionable if they are comparable due to the  
636fact that AFADs are generally located nearshore, with corresponding particular  
637oceanographic conditions, and they do not move with water masses. Papua New Guinea, the  
638Philippines and Indonesia are examples of areas with very high numbers of AFADs (Proctor  
639et al. 2019) and as such, these dense arrays of AFADs could generate the same concerns  
640on tuna **life-history parameters** and behaviour that those expressed for DFADs.  
641Understanding the behaviour of tunas around AFADs can also improve our general  
642understanding of tunas around all types of floating objects and help design new, well focused  
643studies for DFADs. **For practical reasons, more** studies have been performed on the  
644behaviour of tuna at AFADs **than at DFADs** (e.g. Dagorn et al., 2007; Govinden et al., 2013;  
645Holland et al., 1990; Ohta & Kakuma, 2005; Rodriguez-Tress et al., 2017). **They provided**  
646estimates of residence times between two AFAD associations and therefore **of** the  
647percentage of time spent associated to AFADs (e.g. Pérez et al., 2020; Robert et al., 2013b;  
648Rodriguez-Tress et al., 2017), **which still needs to be further explored at DFADs**. For  
649example, Pérez et al. (2020) used acoustic tagging data on AFAD arrays to demonstrate that  
650when inter-AFAD distance decreases, tuna visit more AFADs, spend less time travelling

651between AFADs and more time associated with them. Concerning DFADs, as actual  
652densities of drifting floating objects are difficult to obtain, studies using a modelling approach  
653based on experimental data should be promoted (Pérez et al. 2022, Capello et al. 2023).  
654These studies should investigate the consequences of changes in floating object density on  
655tuna school sizes and associative behaviour. These modelling studies could be  
656complemented and/or calibrated by studies which use data from echosounder buoys  
657deployed by fishers on floating objects. Recent methodological advances allowed the  
658prediction of tuna presence or absence under FOBs (Baidai et al., 2020; Orue et al., 2020).  
659Using an extensive dataset from echosounder buoys in the WCPO (more than 3.8 million  
660transmissions), Escalle et al. (2021c) determined different profiles of acoustic signals related  
661to different types of aggregations. Other studies also show that multi-frequency echosounder  
662buoys could allow the discrimination of tropical tuna species under DFADs (Moreno et al.  
6632019, Sobradillo et al. 2023). These new methodological developments, in combination with  
664tagging data both conventional and electronic, and modelling approaches offer promising  
665perspectives for the study of tuna aggregation behaviour under FOBs and the potential  
666impact of DFAD density on tuna schooling behaviour.

667Tuna RFMOs set limits on the number of operational buoys (IATTC: up to 340 depending on  
668the vessel size, Res C-21-04; ICCAT: 300 in Rec 22-01; IOTC: 250 in Res 23/02; WCPFC:  
669350 in CMM 2021-01). These limits are essentially set to control the fishing effort and the  
670catches of tunas and non-target species, but how such limits also limit the number of  
671deployed DFADs is not known. In theory, all purse seine vessels could use at least the same  
672amount of DFADs than the maximum number of operational buoys authorized in each of the  
673regions. Multiplying this maximum number of operational buoys authorized per vessel by the  
674number of purse seine vessels in each ocean provides a global authorized limit of about  
675233,000 operational buoys (Supplementary Materials 1). This number is about twice higher  
676than the estimate of the global number of DFADs deployments made by Gershman et al.  
677(2015), based on data from 2013. Hence, it would mean that the global purse seine fishery  
678could have increased the number of DFADs in the ocean while still respecting the current  
679limits on the number of active buoys. Most tRFMOs now require that DFAD identification,

680 characteristics, deployment date and deployment location are reported (e.g. ICCAT Rec 22-  
681 01; IOTC Res. 23/02; IATTC C-21-04). Some studies evidenced different regional trends of  
682 DFAD deployments (IOTC, 2022, Escalle et al. 2020, Lopez et al. 2021, Floch et al., 2019;  
683 Maufroy et al., 2017), but no study assessed this trend on a global scale after 2013  
684 (Gershman et al., 2015). Tuna RFMOs should continue to collect and make fine-scale DFAD  
685 data available to scientists to allow regular estimations of the extent of the habitat  
686 modifications generated by DFADs, which should be addressed at a global scale.

## 687 **Conclusion**

688 To summarize the questions formulated in this study:

689 (1) although the deployment of DFADs has undoubtedly modified the habitat of tropical  
690 tunas, the extent of this modification still needs to be better characterized in some regions.

691 This characterization can be achieved through the continued monitoring of indicators (e.g.  
692 spatialized DFAD and NLOG densities, DFAD/NLOG ratio) collected by tRFMOs.

693 (2) studies assessing the impacts of DFADs on tuna large-scale movements show  
694 contradictory results. Strong ocean and species specific variability is observed for the  
695 proportion of time spent associated with FOBs. However, the effect of the methodology used  
696 (archival tagging vs acoustic tagging) should be investigated. To date, besides theoretical  
697 studies, no evidence has been shown on the impact of DFADs on associative and schooling  
698 behaviour.

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

703 (4) The main conclusion of this work is the lack of clear converging scientific results on the  
704 indirect impacts of DFADs on the behaviour and life-history parameters of tropical tuna. It  
705 should therefore be underlined that scientific efforts should not only focus on the direct  
706 effects of DFADs on catches (target and non-target species) but should also address other

707possible impacts, such as density dependent effects on the behaviour and **life-history**  
708**parameters** of tunas. This **current lack of converging results** justifies a major and urgent  
709scientific effort, in terms of data collection, experimental research and modelling to tackle  
710definitively whether the increased **deployment** of DFADs could lead to indirect impacts on  
711tropical tuna **populations**.

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718Access, a CC-BY public copyright licence has been applied by the authors to the present  
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## 721**Data availability statement**

722Data used in the supplementary material were obtained from Justel-Rubio et al. (2022) and  
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1222**Tables**

1223**Table 1: Summary of main findings from previous studies on the numbers of**  
 1224**monitored floating objects or the number of DFADs used in large-scale tropical tuna**  
 1225**purse seine fisheries.**

<b>Area</b>	<b>Period</b>	<b>Indicator</b>	<b>Associated number of vessels</b>	<b>Estimation</b>	<b>Reference</b>
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		From 2,679	Maufroy et al.



		active buoys		(2007)	to (2017)	
				10,929 (2013)		
	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)
	<b>2016-2021</b>	<b>DFADs deployed yearly</b>	<b>Whole ocean</b>	<b>10,514</b>	<b>to</b>	<b>IOTC (2022)</b>
				<b>24,550</b>		
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. (2020, 2021a)
			<b>(whole WCPO)</b>			
	<b>2016-2019</b>	<b>Buoys deployed yearly</b>	<b>Whole WCPO</b>	<b>31,000</b>	<b>to</b>	<b>Escalle et al. (2020)</b>
				<b>39,500</b>		
	<b>2016-2020</b>	<b>Buoys deployed</b>	<b>187 to 235 vessels</b>	<b>16,000</b>	<b>to</b>	<b>Escalle et al. (2021b)</b>
				<b>22,000</b>		

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		yearly						
Eastern Pacific Ocean	2018-2020	Daily active buoys	100 to 140	8,000-11,000				Lopez et al. (2021)
	2015-2020	DFADs deployed yearly	100 to 140	20,000 to 40,000				Lopez et al. (2021)

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1226**Table 2: Summary of main findings from previous studies on tuna individual CRT and CAT assessed under anchored and drifting FADs.**

1227CRT: Continuous Residence Time – continuous bouts of time spent at the same FAD without any absence longer than 24h. CAT: Continuous Absence

1228Time – the time between two associations with a FAD. FL: fork length, YFT: *Thunnus albacares*, SKJ: *Katsuwonus pelamis*, BET: *Thunnus obesus*).

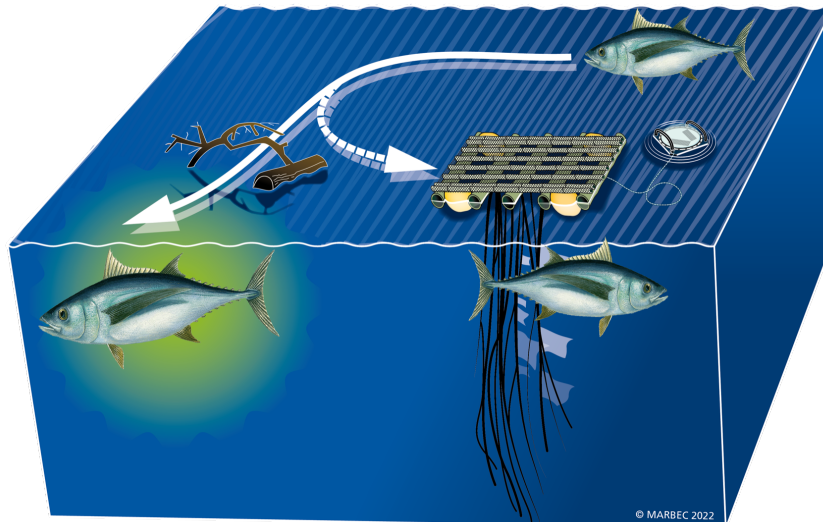
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FAD type	Study location	Metric	Findings	Reference
	Eastern Atlantic Ocean	CRT	YFT (34-82 cm FL): average of 19.15 days (maximum value of 55 days) SKJ (39-61 cm FL): average of 9.19 days (maximum value of 15 days) BET (45-61 cm FL): average of 25.31 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)
Drifting	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)	

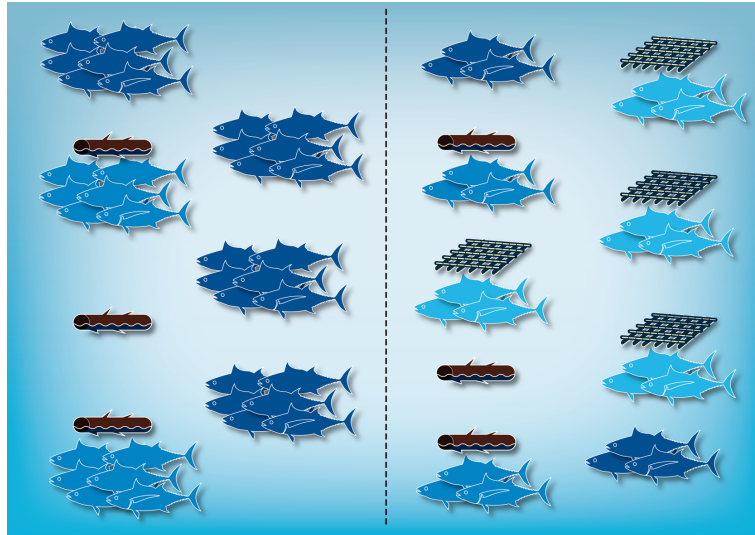
		Large YFT (63-68 cm FL): 9.44 days	
	CAT	4 days for small YFT and 1.65 days for large YFT	
(Pacific Ocean)	CRT	4 behavioural modes reported for YFT (54 to 95 cm FL) : - Brief association : 13.1 minutes - Short association: 2.9 days - Two long association modes : 13.8 and 23.2 days	Robert et al. (2013a)
	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)

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## 1235 Figures



1237 **Figure 1: Schematic representation of the ecological trap hypothesis applied to**  
1238 **Drifting Fish Aggregating Devices (DFADs), as originally formulated.** Under this  
1239 hypothesis, before DFADs introduction, when only natural floating objects (NLOGs) were  
1240 present, floating objects were indicators of productive areas. Hence, by associating with  
1241 floating objects, tuna selected high quality habitats. DFAD massive deployment modified  
1242 the distribution of floating objects (FOBs), which are not representative of rich areas  
1243 anymore. By associating with FOBs, tunas can be attracted to or retained in habitats of  
1244 lesser quality.



1246 **Figure 2: Schematic representation of potential effects of Drifting Fish Aggregating Devices**  
 1247 **(DFADs) on tuna schooling behaviour. The left side represents an ocean with natural**  
 1248 **floating objects (NLOGs) only (no DFAD), while the right side represents an ocean with**  
 1249 **both NLOGs and DFADs, i.e. more floating objects (FOBs).** Dark blue represents tuna in free-  
 1250 swimming schools, intermediate blue tuna associated with NLOGs and light blue tuna associated  
 1251 with DFADs. An increase in FOB density (right panel) could lead both to (i) more tuna associated  
 1252 to FOBs and less free-swimming schools, (ii) more numerous but smaller FOB-associated  
 1253 schools.