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

Laurent Dagorn, Amaël Dupaix, John D Filmalter, Yannick Baidai, Nathalie Bodin, Manuela Capello, Emmanuel Chassot, Hervé Demarcq, Jean-Louis Deneubourg, Alain Fonteneau, et al.

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1 **Title 1: The challenge of assessing the effects of drifting fish aggregating devices on**
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 (236 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 scientific consensus exists regarding the effects of
51 DFADs on the large-scale movements and behaviour of tuna, mainly due to the difficulty of
52 disentangling the respective roles of DFADs and environmental factors. Some biological
53 indices show that tuna condition is lower when associated to a floating object than in a free-
54 swimming school. It is not possible, however, to elucidate whether this is the cause or result
55 of the association, or if it affects the fitness of individuals in the long term. Further scientific
56 progress would require (i) the collection of time series of indicators to monitor habitat change,
57 individual behaviour, individual fitness and population dynamics, and (ii) experimental studies
58 to identify the underlying behavioural and biological processes involved the associative
59 behaviour. The extent of the modification of the surface habitat by the massive deployment of
60 DFADs and the current uncertainty of the possible long-term consequences on the individual
61 fitness and dynamics of tuna populations argue for the need for increased awareness of this
62 issue by Regional Fisheries Management Organisations regulating tuna fishing.

63

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

66

67

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85 **Introduction**

86 Many fish species are known to associate with floating objects (Castro et al., 2002; Fréon &
87 Dagorn, 2000), with the first known descriptions of fishers exploiting these associations
88 dating from 200 AD in the Mediterranean Sea by the Roman author Oppian (cited in
89 Dempster & Taquet, 2004). In particular, the use of floating objects to facilitate the capture of
90 tropical tunas (skipjack – *Katsuwonus pelamis*; yellowfin – *Thunnus albacares*; and bigeye –
91 *T. obesus*), has undergone rapid expansion in recent decades, as a result of the growing
92 importance of these floating structures to the strategy and efficiency of tropical tuna purse
93 seine fleets (Dagorn et al., 2012; Fonteneau et al., 2000, 2013; Leroy et al., 2013; Miyake et
94 al., 2010). Since the onset of the tropical tuna purse seine fishery, fishers took advantage of
95 the associative behaviour of tunas with floating objects and actively searched for natural
96 floating objects to improve their catches (Greenblatt, 1979 ; Hallier and Parajua, 1999 ; Scott
97 et al. 1999). Towards the end of the 1980s, fishers began to build and deploy man-made
98 drifting fish aggregating devices (DFADs), and to attach radio buoys to locate them (Ariz et
99 al., 1999 ; Hallier and Parajua, 1999 ; Hall et al. 1992 ; Scott et al. 1999 ; Lopez et al., 2014;
100 Marsac et al., 2014; Moreno et al., 2007; Morón, 2001; Stéquert & Marsac, 1986). DFADs
101 are commonly composed of a floating structure (such as a bamboo or metal raft with

102 buoyancy provided by corks, etc.) and a submerged structure (made of ropes, old netting,
103 canvas, weights, etc.). During the last two decades, radio buoys have been replaced by GPS
104 buoys communicating via satellite directly with fishing vessels. In the last decade (2010-
105 2020), most DFADs have been equipped with echo-sounder buoys, providing estimates of
106 aggregated biomass (Lopez et al., 2014). Some fleets also use supply vessels to maintain
107 their DFAD array and to inform the fishing vessels of tuna aggregations, allowing these fleets
108 to manage much more efficiently their DFAD stock (Arrizabalaga et al., 2001; Ramos et al.,
109 2013). DFADs represent very efficient fishing tools that increase the catchability of tunas.
110 Over time, given the growing contribution of purse seine fleets to world tuna catches and the
111 increasing importance of DFAD fishing in the strategy of purse seine fleets, managing
112 DFADs has become a priority for all tuna Regional Fishery Management Organisations
113 (tRFMOs). In this paper we will use “operational” or “active” buoys to designate buoys
114 attached to a FOB that are tracked by one or several purse seine fishing vessel(s). Tuna
115 RFMOs set limits of the number of operational buoys (with the very first limit by the IOTC,
116 Indian Ocean Tuna Commission, in 2015) to mitigate the different risks induced by the
117 deployment and use of DFADs (most recent resolutions: IOTC Res 23/02, ICCAT Rec 22-01,
118 IATTC Res C-21-04, WCPFC CMM 2021-01). Other major DFAD-related measures
119 concerned the design of these objects, following the discovery of sharks getting entangled in
120 the netting composing the structure of DFADs (Filmlalter et al. 2013). Limiting the pollution
121 induced by DFADs in the ocean is also in front of the agendas of tRFMOs, after realizing the
122 large quantity of plastic used in DFADs and the large numbers of DFAD beaching events in
123 sensitive coastal ecosystems (Imzilen et al. 2021, 2022). However, other impacts on tuna
124 populations (unrelated to fishery vulnerability) and ecosystems may be induced by the
125 increased presence of DFADs in their habitat. Despite the limits on operational buoys,
126 DFADs number in the water has increased (Dagorn et al. 2013a, Maufroy et al. 2017, Imzilen
127 et al. 2021, Dupaix et al. 2021). As such, while logs and branches have always been
128 components of the habitat of tropical tunas (originating from rivers, mangroves or shorelines),
129 the massive use of man-made DFADs has changed their habitat.

130 Changing a habitat can positively or negatively impact the ecology of wild animals inhabiting
131 it. For example, artificial habitats could benefit some reef species (Lee et al. 2018).
132 Contrarily, alterations could also reduce habitat quality, e.g. by reducing the number of
133 shelters or nests for some species, or by decreasing their food resources (often through the
134 alteration of the habitat of these resources themselves, Mullu 2016). In some cases, animals
135 may be misled by cues that were previously correlated with the habitat quality but no longer
136 are, due to anthropogenic influences. Such impacts form the basis of the ecological trap
137 theory and result in the preferential selection of low-quality habitats by animals, when better
138 alternatives exist (Battin, 2004; Schlaepfer et al., 2002). It is worth noting that, depending on
139 the definition, it is also considered that an ecological trap can occur without any
140 anthropogenic influence (Robertson & Hutto, 2006; Swearer et al., 2021; Teske et al., 2021).
141 In this paper, we will consider that ecological traps occur because of a sudden anthropogenic
142 change in the environment, i.e. in the case of tropical tuna, the modification of their surface
143 habitat by the increased deployment of DFADs (Gilroy & Sutherland, 2007; Hallier &
144 Gaertner, 2008; Schlaepfer et al., 2002). While this theory has been proposed regularly in
145 the face of anthropogenic environmental modifications and their impacts on various species,
146 few studies have empirically demonstrated the existence of such traps (Battin, 2004;
147 Swearer et al., 2021).

148 Noting the increasing number of floating objects being deployed by fishers during the 1990s,
149 scientists hypothesized that the increase in the number of DFADs could lead to an ecological
150 trap, altering the ecological value of floating objects for tropical tunas associated to DFADs
151 (Marsac et al., 2000). It is hypothesized that large numbers of DFADs may alter certain
152 biological characteristics of epipelagic populations associated with them: migration, schooling
153 behaviour, growth, fish condition and bioenergetics, predation and natural mortality (Figures
154 1 & 2). TRFMOs primarily focus on developing management schemes to address the known
155 effects of DFADs on catches (particularly of small yellowfin and bigeye tunas, as well as
156 sharks) or their stranding on coasts. However, there is also a need to assess whether
157 DFADs, through their presence on the ocean, can alter the biology and behaviour of tunas,
158 so as to manage the number of DFADs deployed at sea if negative impacts are suspected or

159 demonstrated. The objective of this paper is to review the current knowledge on the effects of
160 DFADs on the behaviour and biology of tropical tunas, identify knowledge gaps, and propose
161 future research priorities. This paper is structured around four major questions:

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

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

164 iii) Do DFADs modify the biology of tropical tunas?

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

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

167 Natural floating objects have always occurred in the habitats occupied by tunas. Such natural
168 objects are primarily tree trunks or branches that were washed down rivers into the ocean.
169 Human activities (logging, coastal development, shipping, etc.) also modified the number of
170 floating objects encountered by tunas, in some cases even before modern purse-seine tuna
171 fishing began (Caddy & Majkowski, 1996; Thiel & Gutow, 2005). Some of these trends may
172 have been consistently positive (coastal development, shipping), whereas others, such as
173 logging, may have varied due to increased global trade and subsequent deforestation of
174 some areas (Caddy & Majkowski, 1996). In addition, environmental changes also affect the
175 production and movement of floating objects (e.g. floods, El Niño events, tsunamis), with
176 global warming supposed to increase the frequency of extreme events. It should be noted
177 that the current largest tuna purse seine fishery in the world was first developed in the
178 western Pacific by Japanese exploratory fishing cruises that perfected methods for seining
179 tuna schools found in association with natural floating logs that later evolved into DFAD
180 based effort in all oceans (Watanabe 1988). In recent years, the large and persistent
181 increase in the number of DFADs deployed by fishers raised the question of the impacts of
182 this practice on the tropical tuna habitat. It is therefore essential to assess the extent to which
183 DFADs have changed the habitat of tunas, in comparison to the historic pristine state when
184 only natural floating objects existed.

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

195 Habitat changes due to DFADs can be assessed by estimating and comparing densities of
196 objects (with information on their nature: LOGs or DFADs) and distance between objects
197 (nearest neighbour), with both parameters being closely related. These parameters depend
198 upon the rates at which DFADs are added or removed from the ocean (by sinking, beaching
199 or retrieved by humans), as well as their drift. For every oceanic spatio-temporal unit (e.g.
200 region and season), comparing these parameters with those of natural floating objects (e.g.
201 logs, whether equipped or not with buoys, operational or not) and for all types together
202 (natural and artificial) is challenging. The primary concern here is to identify the origin of the
203 floating object, which could either be man-made (DFADs), natural (NLOG) or artificial discard
204 (ALOG).

205 The number of DFADs have regularly increased (Maufroy et al. 2017), but it is necessary to
206 put this in perspective with respect to all floating objects. Using data from observers onboard
207 tuna purse seine vessels in the Indian Ocean, Dupaix et al. (2021) highlighted a drastic
208 increase in the total number of floating objects in the western IO, from 2006 to 2018, with
209 multiplication factors greater than 2 in every region and reaching as high as 60 in some
210 areas (e.g. Somali area). The whole western IO is impacted, with DFADs representing more
211 than 85% of the overall FOBs. Since 2014, even the Mozambique Channel, an area known
212 to have a large number of natural objects (Dagorn et al., 2013a), is impacted showing a
213 higher number of DFADs (73 % of the total FOBs). In addition, increased numbers of DFADs

214 also contribute to decreasing the distances between floating objects. In the IO, while
215 estimated median distances between DFADs and between natural objects did not
216 significantly differ in 2007-2008 (70 km and 74 km respectively), the distance between FADs
217 was significantly smaller than the one between LOGs in 2014-2018 (37 km and 89 km,
218 respectively) (Dupaix et al. 2021). Phillips et al. (2019), using data from 2016 and 2017 and
219 Lagrangian simulations in the western Pacific Ocean, also showed an increase in FOB
220 densities induced by DFAD deployments, and observed a shift of the area with the highest
221 FOB densities, from the North-Eastern area of the Bismark Sea to the Tuvalu archipelago.

222 Unfortunately, to our knowledge, no similar detailed study has been conducted in the other
223 oceans, precluding from estimating the extent of the change of the habitat of tunas due to the
224 addition of new floating objects globally. Most of the management effort by tRFMOs is
225 focused on the monitoring and control of satellite-tracked buoys attached to floating objects
226 (either to DFADs or to LOGs), emitting positions (and other variables) to vessels and
227 qualified as operational buoys, as this variable is strongly related to fishing effort. This also
228 explains why most scientific studies prioritized the estimate of operational buoys rather than
229 the number of DFADs in the ocean (Table 1). Currently, all tRFMOs have implemented a limit
230 on the instantaneous number of operational satellite buoys per vessel, but only the IOTC has
231 limited the number of buoys purchased and in stock per year, per vessel (IOTC Res 23/02,
232 ICCAT Rec 22-01, IATTC Res C-21-04, WCPFC CMM 2021-01). This clearly reflects a lack
233 of concerted action worldwide to limit the number of new floating objects deployed in the
234 oceans. Moreover, as DFAD fishing is so efficient, many fleets worldwide have changed their
235 fishing strategy from setting on free-swimming or dolphin-associated tuna schools, towards
236 fishing with DFADs (Lennert-Cody et al., 2018). Thus, even under the limit of active DFADs
237 at sea per vessel, the actual total numbers of DFADs in the ocean could have increased. So
238 far, few studies have produced estimates of the total number of DFADs deployed annually,
239 with estimations providing a range of 81,000 to 121,000 deployments worldwide, but these
240 global estimates were made a decade ago (Baske et al., 2012; Gershman et al., 2015; Scott
241 & Lopez, 2014). As a comparison, AFADs seem to be less numerous worldwide (13,000
242 anchored FADs were estimated by Scott & Lopez (2014)), although there may be regional

243 exceptions, including few areas known to have very high densities of AFADs, such as
244 Indonesia (5,000-10,000, Proctor et al. 2019), the Philippines or Papua New Guinea.

245 In practice, despite efforts by tRFMOs to require the submission of DFAD data, accurately
246 determining a simple indicator such as the total number of DFADs that are drifting in the
247 world's oceans is a major challenge. The easiest way would be to monitor the number of
248 deployments through logbooks or onboard observers or set up a FAD register system as it
249 has been recently adopted in the IO (Res 23/02). The number of operational buoys does not
250 correspond to the number of DFADs in the water (and/or deployed) as some buoys can be
251 attached to LOGs and some DFADs may lack positional trackers and can drift for a long
252 time, or can be (re)activated/deactivated, but it can be used as a proxy to illustrate the trend
253 in numbers. Therefore, as the number of operational buoys does not limit efficiently DFAD
254 deployments, the number of DFADs in the water and/or deployments could be larger than the
255 limits adopted by the tRFMOs. Under the assumption that the number of natural floating
256 objects remains relatively constant, the increasing number of electronic buoys used reflects
257 an increase of the number of FOBs. Moreover, if no characterisation of DFAD deployment
258 trends is available at the global scale, the clear trend in the number of DFAD sets or DFAD
259 catches (Floch et al., 2019; FIRMS Global Tuna Atlas cited in IOTC, 2021; Restrepo et al.,
260 2017) suggests that DFAD deployment also increases.

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

262 DFADs may affect both the movements of tunas and their schooling behaviour. Large-scale
263 movements of tunas can be impacted in the following two ways: (i) they could cause tunas to
264 relocate to new areas and (ii) they could increase residence times in some areas. Ideally, the
265 best approach for investigating such potential effects would be to compare the large-scale
266 movement patterns of tunas before and after the period in which the increase on DFAD
267 numbers occurred (i.e. before or after the 1990's). To our knowledge, historical data to
268 assess large-scale movement patterns before fishers started to massively deploy DFADs,
269 necessary for this type of analysis, do not exist.

270 *Effects on individual movement*

271 Wang et al. (2014) found that the spatial dynamics of free-swimming school sets in the
272 Western and Central Pacific Ocean (WCPO) were influenced by the onset of El Niño
273 Southern Oscillation (ENSO) events, while these events had no effects on the location of
274 floating-object-associated school sets. Catch data, however, reflect the movements of the
275 available catchable portion of the stocks and the catchability of different set types (e.g. DFAD
276 sets catching smaller individuals than the free-school sets), and not the true movements of
277 populations.

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

293 Another way to investigate the potential of DFADs to modify large-scale movements of tunas
294 is to observe such movements through archival tags and compare them with the general drift
295 patterns of DFADs. In the equatorial Eastern Pacific Ocean (EPO), evaluation of archival tag
296 data sets from 96 bigeye tuna (54-159 cm in length, 1-5.5 years of age) tagged between
297 2000 – 2005 (Schaefer et al., 2009; Schaefer & Fuller, 2010) did not support the hypothesis
298 that the most probable tracks of those bigeye were related to the general drift patterns of

299 DFADs in this area. This suggests that the large-scale spatial dynamics of bigeye tuna are
300 not strongly influenced by DFADs at the densities and conditions found in the EPO.
301 However, in the Central Pacific Ocean (CPO), a predominantly eastward extensive
302 dispersion of bigeye tagged with conventional tags and archival tags was observed
303 (Schaefer et al., 2015), in contrast to the results from bigeye tagging in the equatorial EPO
304 (Schaefer et al., 2009; Schaefer & Fuller, 2010). The authors explain this result by the fact
305 that in the equatorial EPO, where bigeye exhibit strong regional fidelity, it appears the high
306 concentration of food is an important environmental factor leading to their residence and
307 retention in that area. A plausible cause for the predominantly eastward dispersion of bigeye
308 from releases in the equatorial CPO is the influence of the strong eastward-flowing North
309 equatorial countercurrent, in combination with bigeye searching for higher concentrations of
310 prey resources, so as to maximize foraging success in a more productive area.

311 In addition, the possibility of DFADs influencing the large-scale movements of tunas could be
312 evaluated through the measure of the time tunas spend associated with DFADs and the time
313 they spend unassociated (or between two DFAD associations). It could be considered that
314 the longer tunas spend associated with DFADs, the larger the influence DFADs could have
315 on their large-scale movements. Acoustic tags and archival tags (only when a species
316 exhibits a distinct vertical behaviour when associating with a floating object, as observed for
317 bigeye tuna or sometimes yellowfin tuna) have been used by scientists to measure these
318 parameters (Table 2). Passive acoustic tagging studies conducted on DFADs in the Indian
319 and Pacific oceans revealed that the majority of residence times of tunas were a few days.
320 Mean values of DFAD residence times (i.e. continuous periods of time spent associated with
321 a given DFAD) ranged from 0.2 to 4.6 days for skipjack tuna (Dagorn et al., 2007; Govinden
322 et al., 2021; Matsumoto et al., 2014, 2016), and from 1.0 to 6.6 days for yellowfin tuna and
323 1.4 to 7.6 days for bigeye tuna (Dagorn et al., 2007; Govinden et al., 2021; Matsumoto et al.,
324 2016). Long associations, however, have been observed on rare occasions – e.g. 27 and 28
325 days for yellowfin tuna, in the IO (Govinden et al., 2021) and WCPO (Phillips et al., 2017),
326 respectively. A recent study in the EAO (Tolotti et al., 2020) reported significantly larger
327 mean residence times for the three tuna species, from 9 days (skipjack tuna) to 19 days

328 (yellowfin tuna) and 25 days (bigeye tuna), with record values of 55 days and 600 km
329 travelled associated to a DFAD for both bigeye and yellowfin tuna.

330 These studies suggest that residence times at a single DFAD could vary between oceanic
331 regions. Without more studies in other oceanic regions, it is difficult to assess whether the
332 long DFAD associations observed off the coast of Guinea (about 10°N in the EAO) are
333 restricted to this area (and the time period of the observations), or if they can also be
334 observed in other regions. In fact, even short DFAD residence times as those observed in
335 the Indian and Pacific oceans do not prove that DFADs cannot influence large-scale
336 movements. The short residence times clearly suggest that a single DFAD does not
337 significantly impact the behaviour of tunas for long enough to influence their large-scale
338 movements. However, in an array of DFADs, a tuna can “switch” from one DFAD to a
339 neighbouring one, which could retain it in the array. It is therefore important to also measure
340 the time tunas spend between two associations (or unassociated), or in other words, the total
341 percentage of time a tuna spends in the associative mode over long periods. This variable is
342 likely to depend on the density of all floating objects in the area. A small percentage of time
343 associated with floating objects would indicate no or little influence of DFADs, while a high
344 percentage could indicate a significant influence of DFADs on large-scale movements. So
345 far, very few durations between two DFAD associations have been measured using acoustic
346 tags because it is difficult to locate and exhaustively instrument with acoustic receivers all
347 DFADs in an area, as it has previously been done with AFADs (Dagorn et al., 2007; Pérez et
348 al., 2020; Robert et al., 2013a; Rodriguez-Tress et al., 2017).

349 In the WCPO, 13 yellowfin tuna and 12 bigeye tuna displayed “homing” behaviour by
350 returning to the same DFAD with absences superior to a day (Forget, unpublished data). The
351 average duration of these absences were about 1.5 days for yellowfin tuna and three days
352 for bigeye tuna (Forget, unpublished data). By contrast, in the other tropical oceans, few
353 tunas were observed performing such homing behaviour: one bigeye tuna in the AO (out of
354 23 tagged fish, Tolotti et al., 2020), one yellowfin tuna and two skipjack tuna in the IO (out of
355 31 and 17 tagged fish respectively, Govinden et al., 2021), and these absences lasted less
356 than two days. Because bigeye tuna and sometimes yellowfin tuna exhibit different vertical

357 behaviour patterns when associated or non-associated with floating objects, archival tags
358 have been used to assess residence times at and between floating objects, and therefore
359 percentage of days associated with floating objects, without the need to instrument all
360 objects with acoustic receivers. Using satellite archival tagging data where individual bigeye
361 tracks could be recorded over several months or even years, the percentage of time
362 associated with floating objects was estimated to be between 4 % and 17 % depending on
363 the size of the fish and the oceanic region (Fuller et al., 2015; Phillips et al., 2017; Schaefer
364 & Fuller, 2010). Associative and non-associative behaviours with floating objects have also
365 been described with archival tags for yellowfin tuna (Phillips et al., 2017; Schaefer et al.,
366 2009; Schaefer & Fuller, 2013), with estimates of the percentage of time spent associated
367 with floating objects between 10% and 23%.

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

377 *Effects on schooling behaviour*

378 DFADs could also affect schooling behaviour, which can have a wide range of consequences
379 on the biology and the movements of tunas. Dagorn & Fréon (1999) and Fréon & Dagorn
380 (2000) suggested that tunas could associate with floating objects for social advantages such
381 as facilitating schooling behaviour. To date no result has been obtained from DFADs
382 regarding this question. If floating objects facilitate the schooling behaviour of tunas, then the
383 deployment of large numbers of DFADs may have effects on school size, either by facilitating
384 the formation of large (but less) schools or decreasing school size with DFADs offering too

385 many aggregation sites (Dagorn et al., 2010). DFADs could also modify the size structure of
386 tuna schools, allowing the formation of large aggregations composed of several
387 unassociated schools of different size structures (Wang et al. 2012). Sempo et al. (2013)
388 modelled the impact of the increasing deployment of DFADs on the distribution of social fish
389 species such as tunas. They demonstrated that for social species, increasing the number of
390 DFADs does not necessarily lead to an increase in the total amount of tuna associated with
391 DFADs, a non-intuitive result. Capello et al. (2022), also demonstrated, using a model, that
392 the number of DFADs with associated schools and the size of associated schools were not
393 linearly related to the total number of DFADs and that this relationship varied according to
394 the considered social scenario.

395 **Do DFADs modify the biology of tropical tunas?**

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

399 *Effects on feeding*

400 Trophic studies on tropical tunas, based on stomach content analyses have shown that
401 small-sized tunas may not feed while associated with DFADs in the Atlantic (Hallier &
402 Gaertner, 2008; Ménard et al., 2000), Indian (Grande et al., 2013; Jaquemet et al., 2011;
403 Zudaire et al., 2015) and Western and Central Pacific (Machful et al., 2021) oceans. Indeed,
404 the fraction of empty stomachs was higher among DFAD-associated skipjack and small
405 yellowfin tuna than those captured in free swimming schools. Lower stomach fullness or daily
406 food rates were estimated for tunas associated with DFADs compared to tunas from free
407 swimming schools in the EAO (Hallier & Gaertner, 2008; Ménard et al., 2000). Similarly,
408 lower prey weights were found for tunas associated to DFADs than for tunas from free
409 swimming schools in the IO (Grande et al., 2013; Zudaire et al., 2015). These results support
410 the fact that the quantity of prey present in DFAD assemblages is not sufficient to sustain the
411 dietary requirements of large aggregations of small-sized tunas commonly found at DFADs

412 (several tens of tons) (Fréon & Dagorn, 2000). However, the influence of the sampling time
413 of tunas on the stomach content has to be taken into account as purse seine vessels mainly
414 fish tunas on DFADs at dawn (Forget et al., 2015) and during daytime in free-swimming
415 schools. First, feeding activities are believed to often take place in the early evening on
416 organisms performing diel vertical migration between the deep scattering layer and the
417 surface (Schaefer & Fuller, 2002), resulting in prey being fully digested by the time the fish
418 are caught and sampled, at dawn. Second, free-swimming schools of tunas are almost
419 exclusively caught when actively feeding at the sea surface, hence higher levels of stomach
420 fullness are to be expected. In addition, the association of tunas with DFADs could affect the
421 composition and quality of their diet, as shown for yellowfin tuna in the WIO (Zudaire et al.
422 2015). The largest difference of diet composition observed for this species was indeed due to
423 their aggregative behaviour, with DFAD-associated individuals' stomach contents
424 characterised by the absence of *Cubiceps pauciradiatus* (i.e. driftfish from the Scombriforme
425 order), which constituted by far the main fish prey of free-swimming yellowfin tunas in the
426 WIO.

427 Independently of the trophic role of DFADs, the deployment and the drift trajectories of
428 DFADs could create new zones of high floating object densities, which may be unfavourable
429 for the foraging success of tunas. Jaquemet et al. (2011) partitioned their samples in "rich"
430 (i.e., no limiting food) versus "poor" forage areas in the Indian Ocean, in relation to an
431 exceptional demographic outburst of a pelagic stomatopod (Crustacea), which composed the
432 bulk of tuna diet in this region (Potier et al., 2004, 2007). These authors found that in "rich"
433 forage areas, DFADs have no impact on the feeding pattern of tunas, whereas in "poor"
434 forage areas, tunas associated with DFADs had lower stomach fullness compared to DFAD-
435 associated tunas in rich areas and to tunas in free-swimming schools. Jaquemet et al. (2011)
436 suggested that the impact of DFADs on feeding success could be location-dependent. This
437 led the authors to emphasize the possible detrimental effect on the condition of tuna
438 associated with DFADs if associated tunas drift towards areas with poor forage resources. In
439 such cases, food competition could be enhanced as local abundance of tuna would be higher
440 than what limited forage resources could sustain.

441 In the Pacific Ocean, Hunsicker et al. (2012) observed that predation on skipjack and
442 yellowfin tunas by large pelagic fishes sampled from DFAD sets was greater than for those
443 captured via other fishing methods (e.g. free-swimming schools). These authors concluded
444 that by aggregating small-sized skipjack, yellowfin, and bigeye tunas, DFADs enhance their
445 vulnerability to predators such as sharks and billfishes, and thus increase natural mortality of
446 small sized tunas. To our knowledge, this is the only study assessing the impact of DFADs
447 on tuna vulnerability to predators, hence additional data from other regions would be needed
448 for further testing these assumptions.

449 *Effects on body condition*

450 Tuna condition has been investigated using different methods: biometric condition factors
451 (e.g. plumpness), and biochemical indices (e.g., fat and water contents, lipid class
452 composition). Gaertner et al. (1999) in a preliminary investigation did not find evidence of a
453 morphometric difference between free-swimming school or DFAD-caught tunas in the EAO.
454 But Marsac et al. (2000) and Hallier & Gaertner (2008) in the EAO, and Robert et al. (2014)
455 in the Mozambique Channel (WIO) all found that individuals associated with DFADs were in
456 lower condition than those in free-swimming schools, assuming that thorax width or girth or
457 plumpness of fish are good fish health indicators. However, Sardenne et al. (2016), when
458 comparing biometric and biochemical indicators concluded that biometric indicators
459 measured on whole tuna should be interpreted with caution as they may not always reflect
460 the energetic condition measured in the tissues of the fish. Robert et al. (2014) measured the
461 condition of skipjack tunas using BIA (Bioelectrical Impedance Analysis), a non-invasive field
462 tool that estimates body water content (inversely correlated with body fat content), and
463 determines total lipid and main lipid class concentrations. They confirmed the lower condition
464 of skipjack tuna associated with floating objects compared to those in free-swimming
465 schools. Taking into account the particularity of the studied area (i.e. Mozambique Channel –
466 naturally rich with NLOGs) and assuming that the Mozambique Channel, at the time of
467 sampling, had undergone very little habitat modification due to DFADs (Dagorn et al.,
468 2013a), the authors concluded that before the use of DFADs, tunas associated with logs

469 could have also been in lower condition than tunas in free-swimming schools. These results
470 can therefore be interpreted in two different ways. First, a lower measured condition does not
471 necessarily imply detrimental physiological consequences. The difference in conditions
472 between associated and unassociated fish could reflect normal variations in their condition.
473 The other explanation is that some specific areas where NLOGs have always been in high
474 numbers, such as the Mozambique Channel, could also have negatively impacted the
475 condition of tunas that passed through and stayed in these areas. Hence, only a few studies
476 have investigated tuna condition and assessed the potential impact of DFADs. These studies
477 mainly suggest that the condition of associated tuna is lower than that of free-swimming tuna.
478 These results are reinforced by the example of the preparation of katsuobushi (shaved dried
479 skipjack) in Japan. Indeed the Japanese tuna industry prefers skipjack tuna caught on
480 DFADs as they have less fat than those from free-swimming schools (Nishida, pers. comm.).
481 However, experimental validation of the condition factors used is still needed to determine
482 the potential impacts and the underlying mechanisms of this difference in tuna condition.

483 *Effects on reproduction and growth*

484 In the WIO, Zudaire et al. (2014, 2015) examined the patterns of energy acquisition and
485 allocation to gonadal development and egg production in yellowfin tuna through the
486 combined analyses of female trophic ecology (diet) and distribution of related high-energy
487 lipid compounds in their reproductive and somatic tissues. The studies revealed (i) a
488 significantly higher proportion of energy-rich fish prey in the diet (stomach contents; Zudaire
489 et al., 2015), as well as (ii) significantly higher total lipid concentrations and triacylglycerol to
490 sterol (TAG:ST) ratio, indicators of energetic condition, in the gonads of females caught in
491 free-swimming schools compared to females associated with DFADs (Zudaire et al., 2014).
492 This can be interpreted as simply reflecting differences in prey availability and feeding activity
493 and thus differential lipid incorporation to tissues between DFAD-associated and non-
494 associated tunas. It could also highlight higher energetic investment to reproduction in free-
495 swimming yellowfin tuna due to a higher condition (i.e., better health). However, the study
496 failed to demonstrate a direct effect on the fecundity, most likely due to the low number of

497 actively spawning females analysed and the high intra-species variability of fecundity
498 observed in yellowfin tuna (Pecoraro et al., 2017).

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

513 Using tagging data collected in the EAO, Hallier & Gaertner (2008) estimated and compared
514 the growth rates of skipjack and yellowfin tunas associated with DFADs versus free-
515 swimming schools. Released and recaptured skipjack tunas associated with DFADs had a
516 significantly lower growth rate than those in free-swimming schools, but the difference was
517 not significant for yellowfin tuna (though it was lower, as for skipjack). However, the history
518 experienced by individual fish between release and recapture was unknown. The
519 “experimental” design could not be controlled as the time one specimen spent associated
520 with DFADs and in free-swimming schools is not available. In addition, the authors were only
521 able to process a small sample of yellowfin tuna.

522 Available results indicate that differences in feeding patterns between tunas in free-
523 swimming schools and associated with drifting FOBs have been observed, and that tunas
524 associated with DFADs are generally in lower condition than those from free-swimming

525 schools. Although tunas also show differences in energy allocation for reproduction between
526 DFAD-associated and free-swimming schools, it does not seem to induce a difference in
527 fecundity.

528 **What are the scientific challenges to fill the knowledge gaps?**

529 DFADs have been representing one of the key management priorities and challenges of
530 tRFMOs over the last decade. Since fishers started using them, DFADs numbers
531 continuously increased until first management measures limiting the number of operational
532 buoys were adopted in the mid-2010s (Song & Shen 2022). The massive use of DFADs in all
533 oceans has been generating major concerns on the sustainability of this fishing mode.
534 DFADs increase the catchability of tropical tunas leading to large catches of small bigeye
535 and yellowfin tuna (Dagorn et al., 2013b; Fonteneau et al., 2013). In addition, DFADs have
536 ecological impacts that must be mitigated as DFAD sets usually generate more bycatch,
537 including vulnerable species such as some shark species, silky (*Carcharhinus falciformis*)
538 and oceanic whitetip (*Carcharhinus longimanus*) sharks (Dagorn et al., 2013b; Fonteneau et
539 al., 2013; Leroy et al., 2013), and DFADs can strand on sensitive coastal areas causing
540 damage to marine habitats (Imzilen et al., 2021; Maufroy et al., 2015). Although there is
541 increasing knowledge and literature on DFADs, the issue of the ecological trap remains a
542 scientific debate. All knowledge collected and reviewed, on the associative behaviour and
543 biology of tunas at DFADs clearly reveals a lack of scientific consensus on the long term
544 consequences on tuna (at the individual or population levels) of increased numbers of
545 floating objects. Therefore, we are not currently able to conclude whether DFADs affect the
546 movements and/or biology of tunas in a way that could significantly affect the fitness of
547 individuals and the demography of their populations. As such, there is a need to improve the
548 observation and understand this associative phenomenon to provide scientific advice on the
549 effects of DFADs on the biology and behaviour of tropical tunas and other associated
550 species.

551 A major gap in tuna and DFAD science is the lack of time series of key parameters such as
552 the numbers of DFADs and natural floating objects, residence and absence times at DFADs

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

565 Another research priority is to develop experimental studies to identify the biological and
566 behavioural processes involved in the associative behaviour. The only scientific consensus is
567 the fact that in a given area, conditions of tunas associated with floating objects seem to
568 often be lower than those of fish in free-swimming schools. However, the different indicators
569 used to assess tuna condition are not always well correlated (Sardenne et al. 2016), and
570 experimental studies are needed to validate them against proper benchmarks, allowing to
571 determine how representative they are of individuals' health. Then, understanding how fast
572 these indicators change with the fish's associative behaviour appears essential. This could
573 also be achieved through studies on captive tropical tunas (e.g., Estess et al. 2017), but non
574 lethal observations should be promoted (e.g. BIA) in order to track changes throughout the
575 fish lifespan. No evidence exists suggesting whether the lower condition at DFADs is the
576 consequence or the cause of their association with DFADs. Often the robustness of the
577 findings of these investigations on the biology of tunas was hampered by the lack of
578 knowledge of the time spent associated with a DFAD or in an array of DFADs by each
579 specimen analysed. The history of each individual tuna is a hidden variable that must be
580 taken into account in statistical analyses, which is a challenge. Studies combining
581 behavioural observations (tagging) and condition of the individuals (e.g. BIA or biochemical

582 analyses of biopsies made at the time of tagging) should then be encouraged. Ideally, tags
583 equipped with physiological sensors would clearly help understanding the interplay between
584 associative behaviour and tuna physiology. Such tags, however, are yet to be developed.

585 Studies on AFADs could provide insights to the questions addressed in this manuscript: as
586 argued by Dagorn et al. (2010), AFADs also alter the natural environment (by adding floating
587 objects to the ocean). However, it remains questionable if they are comparable due to the
588 fact that AFADs are generally located nearshore, with corresponding particular
589 oceanographic conditions, and they do not move with water masses. Papua New Guinea, the
590 Philippines and Indonesia are examples of areas with very high numbers of AFADs (Proctor
591 et al. 2019) and as such, these dense arrays of AFADs could generate the same concerns
592 on tuna biology and behaviour that those expressed for DFADs. Understanding the
593 behaviour of tunas around AFADs can also improve our general understanding of tunas
594 around all types of floating objects and help design new, well focused studies for DFADs.
595 More studies have been performed on the behaviour of tuna at AFADs (e.g. Dagorn et al.,
596 2007; Govinden et al., 2013; Holland et al., 1990; Ohta & Kakuma, 2005; Rodriguez-Tress et
597 al., 2017) than at DFADs mainly due to easier access. It is also easier to exhaustively
598 instrument AFADs within an array, providing estimates of residence times between two
599 AFAD associations and therefore the percentage of time spent associated to AFADs (e.g.
600 Pérez et al., 2020; Robert et al., 2013b; Rodriguez-Tress et al., 2017), one of the key
601 variables to characterize the behaviour of tunas inside FAD arrays. For example, Pérez et al.
602 (2020) used acoustic tagging data on AFAD arrays to demonstrate that when inter-AFAD
603 distance decreases, tuna visit more AFADs, spend less time travelling between AFADs and
604 more time associated with them. Concerning DFADs, as actual densities of drifting floating
605 objects are difficult to obtain, studies using a modelling approach based on experimental
606 data should be promoted (Pérez et al. 2022). These studies should investigate the
607 consequences of changes in floating object density on tuna school sizes and associative
608 behaviour. These modelling studies could be complemented and/or calibrated by studies
609 which use data from echosounder buoys deployed by fishers on floating objects. Recent
610 methodological advances allowed the prediction of tuna presence or absence under FOBs

611 (Baidai et al., 2020; Orue et al., 2020). These new methodological developments, in
612 combination with tagging data both conventional and electronic, and modelling approaches
613 offer promising perspectives for the study of the behaviour of tuna aggregations under FOBs.

614 Tuna RFMOs set limits on the number of operational buoys (IATTC: up to 340 depending on
615 the vessel size, Res C-21-04; ICCAT: 300 in Rec 22-01; IOTC: 250 in Res 23/02; WCPFC:
616 350 in CMM 2021-01). These limits are essentially set to control the fishing effort and the
617 catches of tunas and non-target species, but how such limits also limit the number of
618 deployed DFADs is not known. In theory, all purse seine vessels could use the same amount
619 of DFADs than the maximum number of operational buoys authorized in each of the regions.
620 Multiplying this maximum number of operational buoys authorized per vessel by the number
621 of purse seine vessels in each ocean provides a global authorized limit of about 233,000
622 operational buoys (Supplementary Materials 1). This number is about twice higher than the
623 estimate of the global number of DFADs deployments made by Gershman et al. (2015),
624 based on data from 2013. Hence, it would mean that the global purse seine fishery could
625 have increased the number of DFADs in the ocean while still respecting the current limits on
626 the number of active buoys. Estimations of DFAD deployment are still scarce as, until
627 recently, there was no requirement for fishers within tRFMOs to report the number of DFAD
628 deployments. However, now most tRFMOs require that DFAD identification, characteristics,
629 deployment date and deployment location are reported (e.g. ICCAT Rec 22-01; IOTC Res.
630 23/02; IATTC C-21-04). Some studies evidenced an increase of DFAD deployments (Floch
631 et al., 2019; Maufroy et al., 2017), but no study assessed this trend on a global scale after
632 2013 (Gershman et al., 2015). Tuna RFMOs should collect and make fine-scale DFAD data
633 available to scientists to allow regular estimations of the extent of the habitat modifications
634 generated by DFADs.

635 Finally, although no consensus exists on the indirect impacts of DFADs on tropical tuna, it
636 should be underlined that not only the direct effects of DFADs on catches (target and non-
637 target species) should be addressed but also the other possible impacts such as marine
638 debris, stranding events, and density dependent effects on the behaviour and biology of
639 tunas. The current lack of scientific consensus justifies a major and urgent scientific effort, in

640 terms of data collection, experimental research and modelling to tackle definitively whether
641 the increased use of DFADs could lead to indirect impacts on tropical tuna species.

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649 document and will be applied to all subsequent versions up to the Author Accepted
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651 **Data availability statement**

652 Data used in the supplementary material were obtained from Justel-Rubio et al. (2022) and
653 the following website: <https://www.iattc.org/en-US/Management/Vessel-register> (accessed
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656 **Tables**

657 **Table 1: Summary of main findings from previous studies on the numbers of**
 658 **monitored floating objects or the number of DFADs used in large-scale tropical tuna**
 659 **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 buoys	active 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)
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)

660 **Table 2: Summary of main findings from previous studies on tuna individual CRT and CAT assessed under anchored and drifting FADs.**
 661 CRT: Continuous Residence Time – continuous bouts of time spent at the same FAD without any absence longer than 24h. CAT: Continuous Absence
 662 Time – 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
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)

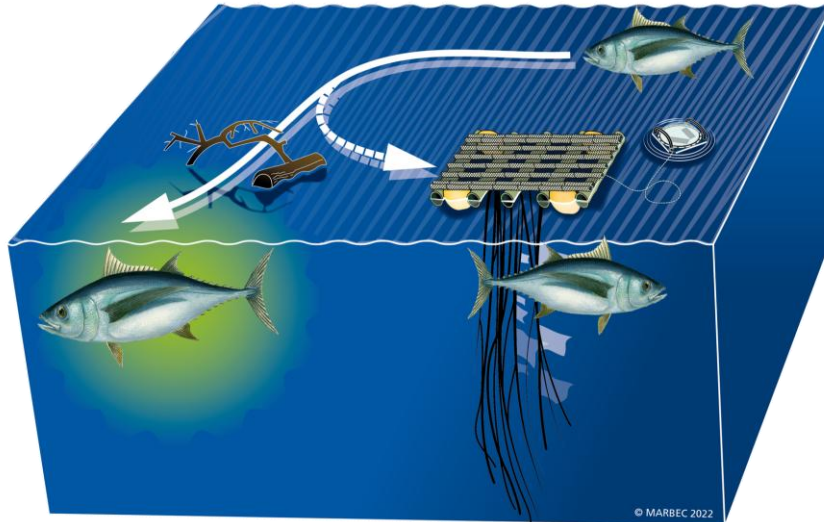
- Short association: 2.9 days
- Two long association modes : 13.8 and 23.2 days

CAT 2 behavioural modes:

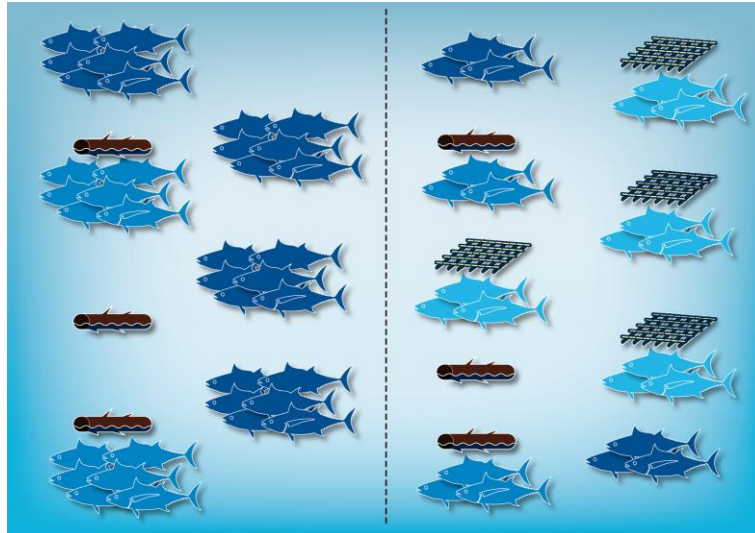
- Short: 2.8 days
- Long: infinite

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)

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



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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.