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

Amaël Dupaix, Frédéric Ménard, 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 the 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 (247 words < 250)**

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

65

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

68

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91 **Introduction**

92 Many fish species are known to associate with floating objects (FOBs; Castro et al., 2002;
93 Fréon & Dagorn, 2000), with the first known descriptions of fishers exploiting these
94 associations dating from 200 AD in the Mediterranean Sea by the Roman author Oppian
95 (cited in Taquet, 2013). In particular, the use of FOBs to facilitate the capture of tropical
96 tunas (skipjack SKJ – *Katsuwonus pelamis*; yellowfin YFT – *Thunnus albacares*; and bigeye
97 BET – *T. obesus*), has undergone rapid expansion in recent decades, as a result of the
98 growing importance of these floating structures to the strategy and efficiency of tropical tuna
99 purse seine fleets (Dagorn et al., 2012; Fonteneau et al., 2000, 2013; Leroy et al., 2013;
100 Miyake et al., 2010). Since the onset of the tropical tuna purse seine fishery, fishers took
101 advantage of the associative behaviour of tunas with floating objects and actively searched
102 for natural floating objects (NLOGs) to improve their catches (Greenblatt, 1979 ; Hallier and
103 Parajua, 1999 ; Scott et al. 1999). Towards the end of the 1980s, fishers began to build and
104 deploy man-made drifting fish aggregating devices (DFADs), and to attach radio buoys to
105 locate them (Ariz et al., 1999 ; Hallier and Parajua, 1999 ; Hall et al. 1992 ; Scott et al. 1999 ;
106 Lopez et al., 2014; Marsac et al., 2014; Moreno et al., 2007; Morón, 2001; Stéquert &
107 Marsac, 1986). DFADs are commonly composed of a floating structure (such as a bamboo or
108 metal raft with buoyancy provided by corks, etc.) and a submerged structure (made of ropes,
109 old netting, canvas, weights, etc.). During the last two decades, radio buoys have been
110 replaced by GPS buoys communicating via satellite directly with fishing vessels. In the last
111 decade (2010-2020), most DFADs have been equipped with echo-sounder buoys, providing
112 estimates of aggregated biomass (Lopez et al., 2014). Some fleets also use supply vessels
113 to maintain their DFAD array and to inform the fishing vessels of tuna aggregations
114 (Arrizabalaga et al., 2001; Ramos et al., 2013). DFADs represent very efficient fishing tools
115 that increase the catchability of tunas, leading purse-seine fleets to target preferentially
116 associated schools and expanding their fishing grounds (Lopez et al. 2014, Fonteneau et al.
117 2015, Lennert-Cody et al. 2019).

118 Over time, given the growing contribution of purse seine fleets to world tuna catches and the
119 increasing importance of DFAD fishing in the strategy of purse seine fleets, managing

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

132 Other major DFAD-related measures concern the design of these objects, following the
133 discovery of sharks getting entangled in the netting composing the structure of DFADs
134 (Filmlalter et al. 2013). Limiting the pollution induced by DFADs in the ocean is also in front of
135 the agendas of tRFMOs, after realizing the large quantity of plastic used in DFADs and the
136 large numbers of DFAD beaching events in sensitive coastal ecosystems (Escalle et al.
137 2019, Imzilen et al. 2021, 2022). However, other impacts on tuna populations (unrelated to
138 fishery vulnerability) and ecosystems may be induced by the increased presence of DFADs
139 in their habitat (Marsac et al. 2000, Bromhead et al. 2003, Hallier & Gaertner 2008). Despite
140 the limits on operational buoys, DFADs number in the water has increased (Dagorn et al.
141 2013a, Maufroy et al. 2017, Imzilen et al. 2021, Dupaix et al. 2021). As such, while logs and
142 branches have always been components of the habitat of tropical tunas (originating from
143 rivers, mangroves or shorelines), the massive use of man-made DFADs has changed their
144 habitat, which could have numerous consequences on tropical tuna’s fitness, resulting in
145 population-level impacts.

146 Changing a habitat can positively or negatively impact the ecology of wild animals inhabiting
147 it. For example, artificial habitats could benefit some reef species (Lee et al. 2018).
148 Contrarily, alterations could also reduce habitat quality, e.g. by reducing the number of

149 shelters or nests for some species, or by decreasing their food resources (often through the
150 alteration of the habitat of these resources themselves, Mullu 2016). In some cases, animals
151 are misled by cues that were previously correlated with the habitat quality but no longer are,
152 due to anthropogenic influences (Sherley et al. 2017, Swearer et al. 2021). Such impacts
153 form the basis of the ecological trap theory and result in the preferential selection of low-
154 quality habitats by animals, when better alternatives exist (Battin, 2004; Schlaepfer et al.,
155 2002). It is worth noting that, depending on the definition, an ecological trap can occur
156 without any anthropogenic influence (Robertson & Hutto, 2006; Swearer et al., 2021; Teske
157 et al., 2021). In this paper, we will consider that ecological traps occur because of a sudden
158 anthropogenic change in the environment, i.e. in the case of tropical tuna, the modification of
159 their surface habitat by the increased deployment of DFADs (Gilroy & Sutherland, 2007;
160 Hallier & Gaertner, 2008; Schlaepfer et al., 2002). While this theory has been proposed
161 regularly in the face of anthropogenic environmental modifications and their impacts on
162 various species, few studies have empirically demonstrated the existence of such traps
163 (Battin, 2004; Swearer et al., 2021).

164 Noting the increasing number of floating objects being deployed by fishers during the 1990s,
165 some scientists hypothesized that the increase in the number of DFADs could lead to an
166 ecological trap, altering the ecological value of floating objects for tropical tunas associated
167 to DFADs (Marsac et al., 2000). This hypothesis is not the only potential indirect impact of
168 DFADs and it is hypothesized that large numbers of DFADs may alter certain biological
169 characteristics of epipelagic populations associated with them: migration, schooling
170 behaviour, growth, fish condition and bioenergetics, predation and natural mortality (Figures
171 1 & 2). TRFMOs primarily focus on developing management schemes to address the known
172 effects of DFADs on catches (particularly of small YFT and BET, as well as bycatch) or their
173 stranding on coasts. Through the increase of FOB density they induce, DFADs could also
174 impact tropical tuna natural mortality and reproductive potential, hence, altering their
175 individual fitness which could have population-level consequences. These indirect impacts
176 could act as compounding factors and worsen the increase of fishing mortality induced by
177 DFADs. Hence, there is a need to assess whether DFADs can alter the life history

178 parameters and behaviour of tunas. This will help to determine the magnitude of indirect
179 impacts relative to direct ones and to manage the number of DFADs deployed at sea if
180 negative indirect impacts are suspected or demonstrated.

181 Almost 20 years ago, Dempster & Taquet (2004) made a systematic review of the published
182 literature on FADs and concluded that further research should assess the use of DFADs by
183 pelagic species, the mechanisms underlying their associative behaviour and the ecological
184 consequences of the presence of DFADs at sea on pelagic fish stocks. Since then, several
185 papers reviewed existing evidence and/or proposed future research directions to address the
186 impacts of DFADs on tropical tuna (Dagorn et al. 2013b, Evans et al. 2015, Davies et al.
187 2014, Fonteneau et al. 2015, Leroy et al. 2013, Taquet 2013). Yet, most of these papers,
188 except Taquet (2013), addressed these impacts at a regional scale and all were mainly
189 focussing on the direct impacts of DFADs (induced by an increase of fishing mortality), even
190 though they mentioned potential indirect impacts (not related to fishing mortality increase).
191 The objective and originality of this paper is to review the current knowledge on the impacts
192 of DFADs on the ecology and life history traits of tropical tuna, focussing only on the indirect
193 effects (consequences of fishing on DFADs are not addressed here). This particular question
194 has generated a global scientific debate for years, precluding management bodies from
195 having a complete and synthetic view of the current knowledge. The extent of these indirect
196 impacts is unknown and determining if they act as compounding factors on the increase of
197 fishing mortality induced by DFADs is urgent. An in-depth literature review provides an
198 overview of the state of the art in this area, identifies knowledge gaps, and proposes future
199 research priorities. This paper is structured around four major questions:

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

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

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

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

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

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

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

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

254 The number of DFADs have regularly increased (Maufroy et al. 2017), but it is necessary to
255 put this in perspective with respect to all floating objects. Using data from observers onboard
256 tuna purse seine vessels in the Indian Ocean (IO), noting all FOBs encountered when the
257 vessel cruises, Dupaix et al. (2021) highlighted a drastic increase in the total number of
258 floating objects in the western IO, from 2006 to 2018, with multiplication factors greater than
259 2 in every region and reaching as high as 60 in some areas (e.g. Somali area). The entire
260 western IO is affected, with DFADs comprising over 85% of the total FOBs and DFADs
261 contributing to reduce the distances between floating objects (mean distances between

262 DFADs and between NLOGs of 37 km and 89 km, respectively, in 2014-2018). The impact of
263 DFADs on tuna habitat reducing the distance between FOBs was observed in the study both
264 when considering all DFADs or only randomly encountered DFADs (objects which do not
265 belong to the vessel or its fishing company), to account for a potential sampling bias. Phillips
266 et al. (2019a), using data from 2016 and 2017 and Lagrangian simulations in the Western
267 and Central Pacific Ocean (WCPO), also showed an increase in FOB densities induced by
268 DFAD deployments, and observed a shift of the area with the highest FOB densities, from
269 the North-Eastern area of the Bismark Sea to the Tuvalu archipelago. Unfortunately, to our
270 knowledge, no similar detailed study has been conducted in the other oceans, precluding
271 from estimating the extent of the change of the habitat of tunas due to the addition of new
272 floating objects globally.

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

290 densities of AFADs, such as Indonesia (5,000-10,000, Proctor et al. 2019), the Philippines or
291 Papua New Guinea.

292 In practice, despite efforts by tRFMOs to require the submission of DFAD data, accurately
293 determining a simple indicator such as the total number of DFADs that are drifting in the
294 world's oceans is a major challenge. The easiest way would be to monitor the number of
295 deployments through logbooks or onboard observers or set up a FAD register (see Res
296 23/02 of the IOTC). The number of operational buoys does not correspond to the number of
297 DFADs in the water (and/or deployed) as some buoys can be attached to LOGs, can be
298 deactivated, and some DFADs may lack positional trackers, but it can be used as a proxy to
299 illustrate the trend in numbers. Therefore, as the number of operational buoys does not
300 effectively limit DFAD deployments, the number of DFADs in the water and/or deployments
301 could be larger than the limits adopted by the tRFMOs. Under the assumption that the
302 number of natural floating objects remains relatively constant, the increasing number of
303 electronic buoys used reflects an increase of the number of FOBs. In recent years, DFAD
304 deployments were stable in the WCPO (2011-2019; Escalle et al. 2020), decreased in the IO
305 (2016-2021; IOTC, 2022), increased in the Eastern Pacific Ocean (EPO, 2015-2020; Lopez
306 et al. 2021) and buoy deployments increased in the AO (2007-2013; Maufroy et al. 2017).
307 Hence, a characterisation of DFAD deployment trends at the global scale is needed.
308 However, the clear trend in the number of DFAD sets or DFAD catches (Floch et al., 2019;
309 FIRMS Global Tuna Atlas cited in IOTC, 2021; Restrepo et al., 2017) suggests that DFAD
310 deployment has also increased.

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

312 DFADs may affect both the movements of tunas and their schooling behaviour. Large-scale
313 movements of tunas can be impacted in the following two ways: (i) DFADs could cause tunas
314 to relocate to new areas and (ii) they could increase residence times in some areas. If
315 DFADs were to have an impact on tuna's large-scale movements, it could increase their
316 natural mortality by retaining or relocating them in unsuitable areas or disturbing their
317 migration (Marsac et al. 2000). Although we are currently not able to quantify, and even

318 demonstrate, such impacts, they could result in population-scale effects. Ideally, the best
319 approach for investigating such potential effects would be to compare the large-scale
320 movement patterns of tunas before and after the period in which the increase of DFAD
321 numbers occurred (i.e. before or after the 1990's). To our knowledge, historical data to
322 assess large-scale movement patterns before fishers started to massively deploy DFADs,
323 necessary for this type of analysis, exist only in the WCPO (Kim 2015) and in the EAO
324 (Cayré et al. 1986) and we do not know of any long-term study that compared movement
325 patterns before and after DFAD use increased.

326 *Effects on individual large-scale movements*

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

334 Hallier & Gaertner (2008) analysed conventional tagging data of SKJ and YFT in the Eastern
335 Atlantic Ocean (EAO). Different migratory directional patterns and displacement rates were
336 observed between fish recaptures associated with DFADs and those in free-swimming
337 schools. Displacement rates were significantly larger for both YFT and SKJ recaptured in
338 association with DFADs (13 and 15 nm/day, respectively) than those recaptured in free-
339 swimming schools (3 and 4.5 nm/day, respectively), which suggests that DFADs could
340 relocate tunas to new areas. In the IO, Stehfest and Dagorn (2010) found similar results for
341 SKJ, YFT and BET, but with lower displacement rates differences than in the AO. Hallier and
342 Gaertner (2008) interpreted these results as indicating significant modifications of migratory
343 patterns due to associations with DFADs, suggesting an influence of DFAD association
344 strong-enough to disturb tropical tuna migratory patterns. However, Stehfest and Dagorn
345 (2010) argue that it could only reflect an artefact of the non-uniform distribution of DFAD

346 fishing. Also, authors of both studies agree that school type at recapture might not be
347 representative of the associative history of individuals before their recapture. Using an
348 advection-diffusion model, Kim (2015) also showed that including a DFAD attraction
349 component to the model better fitted SKJ tagging data in the WCPO, suggesting an effect of
350 DFADs on SKJ migratory patterns. Comparing DFAD induced movements in the 2000s with
351 those in the 1990s, they showed that the rising DFAD density increased this modification of
352 migration patterns. These studies were the only ones to assess differences of movement
353 patterns induced by DFADs and, due to species and ocean differences, more studies would
354 be needed to interpret these results at a global scale.

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

368 *Effects on individual fine-scale movements*

369 The possibility of DFADs influencing tuna movements could be evaluated by determining the
370 impact of DFADs on tuna's fine-scale movements. First, if DFADs increase the percentage of
371 the time tuna spend associated with floating objects, it will increase their availability to
372 fishers. It can therefore have a direct impact by increasing catchability and fishing mortality.
373 In addition, a modification of fine-scale tuna movements could also result in indirect

374 population-scale impacts by inducing larger-scale movement changes. In this section, we
375 focus on the modifications of tuna fine-scale movements induced by DFADs and on how
376 these changes could result in large-scale movement modifications. Fine-scale movements
377 can be assessed through the measurement of the time tuna spend associated with DFADs
378 and the time they spend unassociated (or between two DFAD associations). It could be
379 considered that the longer tunas remain associated with DFADs, the larger the influence
380 DFADs could have on their large-scale movements.

381 Acoustic tags and archival tags (only when a species exhibits a distinct vertical behaviour
382 when associating with a floating object, as observed for BET or sometimes YFT) have been
383 used by scientists to measure these parameters (Table 2). Passive acoustic tagging studies
384 on DFADs revealed that the majority of residence times of tunas (i.e. continuous periods of
385 time spent associated with a given DFAD) were of a few days. Mean values ranged from 0.2
386 to 4.6 days for SKJ (Dagorn et al., 2007; Govinden et al., 2021; Matsumoto et al., 2014,
387 2016), from 1.0 to 6.6 days for YFT and 1.4 to 10 days for BET (Dagorn et al., 2007;
388 Govinden et al., 2021; Matsumoto et al., 2016, Phillips et al. 2019b). Long associations,
389 however, have been observed on rare occasions – e.g. 27 days for YFT in the IO (Govinden
390 et al., 2021) and up to 18, 50 and 30 days for SKJ, YFT and BET respectively, in the WCPO
391 (Phillips et al. 2017, Phillips et al. 2019b). A recent study in the EAO (Tolotti et al., 2020)
392 reported significantly larger mean residence times for the three tuna species, from 9 days
393 (SKJ) to 19 days (YFT) and 25 days (BET), with record values of 55 days and 600 km
394 travelled associated to a DFAD for both BET and YFT.

395 These studies suggest that residence times at a single DFAD vary between oceanic regions
396 and species. Without more studies, it is difficult to assess whether the long DFAD
397 associations observed are restricted to specific areas and time periods, or if they can often
398 occur. In fact, even short residence times at single DFADs as those observed in the Indian
399 and Pacific oceans do not prove that arrays of DFADs cannot influence large-scale
400 movements. In an array of DFADs, a tuna can “switch” from one DFAD to a neighbouring
401 one, which could retain it in the array. It is therefore important to also measure the time tunas
402 spend between two associations (or unassociated), or in other words, the total percentage of

403 time a tuna spends associated over long periods. This variable is likely to depend on the
404 density of all floating objects in the area. So far, very few durations between two DFAD
405 associations have been measured using acoustic tags because it is difficult to locate and
406 exhaustively instrument with acoustic receivers all DFADs in an area.

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

414 Because BET and sometimes YFT exhibit different vertical behaviour patterns when
415 associated or non-associated with floating objects (Holland and Brill 1990, Abascal et al.
416 2018), archival tags have been used to assess residence times at and between floating
417 objects, and therefore percentage of days associated with floating objects, without the need
418 to instrument all objects with acoustic receivers. Using satellite archival tagging data where
419 individual BET tracks could be recorded over several months or even years, the percentage
420 of time associated with floating objects was estimated to be between 4 % and 17 %
421 depending on the size of the fish and the oceanic region (Fuller et al., 2015; Phillips et al.,
422 2017; Schaefer & Fuller, 2010, Leroy et al. 2013, Schaefer & Fuller 2002). Associative and
423 non-associative behaviour with floating objects have also been described with archival tags
424 for YFT (Phillips et al., 2017; Schaefer et al., 2009; Schaefer & Fuller, 2013, Leroy et al.
425 2013), with estimates of the percentage of time spent associated with floating objects
426 between 10% and 23%. These percentages are much lower than those estimated from
427 acoustic telemetry data (e.g. 75 % for small BET based on the measurements in Phillips, et
428 al. 2019b).

429 This inconsistency between studies using different tagging methods could result from the
430 size of tagged individuals or the way the percentage of time spent by tuna associated and

431 non-associated is calculated. Individuals monitored with archival tags were generally larger
432 (fork length: 50-146 cm YFT and 46-102 cm BET in Phillips et al. 2017, 51-134 cm BET in
433 Fuller et al. 2015, 88-134 cm BET in Schaefer & Fuller 2002, 54-159 cm BET in Schaefer &
434 Fuller 2010) than those marked with passive acoustic tags (38-90 cm BET in Phillips et al.
435 2019), even though size ranges largely overlap. This suggests that small BET spend a higher
436 proportion of their time associated with FOBs than large individuals. This agrees with
437 observed size distributions of DFAD catches, where smaller individuals are caught, and with
438 the negative correlation between BET individual length and percentage of time associated
439 found by Schaefer & Fuller (2002). However, Schaefer et al. (2009) found lower association
440 percentages with archival tags on small tunas (10.4 and 15.9 % of the time associated for
441 51-60 cm FL YFT and 65-99 cm FL BET respectively) than the work of Phillips et al. (2019)
442 with acoustic tagging. This could suggest a potential bias in the different methodologies that
443 need to be further investigated. A small percentage of time associated with floating objects
444 would indicate no or little influence of DFADs, while a high percentage could indicate a
445 potentially significant influence of DFADs which could result in impacts on large-scale
446 movements.

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

454 *Effects on schooling behaviour*

455 DFADs could also affect schooling behaviour, which can have a wide range of consequences
456 on the life-history parameters and the movements of tunas. Dagorn & Fréon (1999) and
457 Fréon & Dagorn (2000) suggested that tuna could associate with floating objects for social
458 advantages such as facilitating the formation of larger schools. Tuna associative behaviour

459 would have been selected because schooling behaviour provides several evolutionary
460 advantages. It can be seen as an evolutionary trade-off between (i) increasing protection
461 against predators, swimming and foraging efficiency, mating, and (ii) increasing detection by
462 predators and intra- and inter-specific competition (Rubenstein 1978; Ioannou 2017; Maury
463 2017). Hence, if tuna use FOBs for social behaviour, the number of FOBs could affect the
464 size of schools and therefore reduce their evolutionary advantages, which could impact both
465 tuna survival and reproduction, resulting in population-scale impacts. To date no result has
466 been obtained on tropical tuna from DFADs regarding this question. If floating objects
467 facilitate the schooling behaviour of tunas, then the deployment of large numbers of DFADs
468 may have effects on school size, either by facilitating the formation of large (but less) schools
469 or decreasing school size with DFADs offering too many aggregation sites (Figure 2, Dagorn
470 et al., 2010). DFADs could also modify the size structure of tuna schools, allowing the
471 formation of large aggregations composed of several unassociated schools of different size
472 structures (Wang et al. 2012). Sempo et al. (2013) modelled the impact of the increasing
473 deployment of DFADs on the distribution of social fish species such as tunas. They
474 demonstrated that for social species, increasing the number of DFADs does not necessarily
475 lead to an increase in the total amount of tuna associated with DFADs, a non-intuitive result.
476 Capello et al. (2022) also showed that the number of DFADs with associated schools and the
477 size of associated schools were not linearly related to the total number of DFADs and that
478 this relationship varied according to the considered social scenario.

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

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

483 *Effects on feeding*

484 In his review on DFAD impacts on tropical tunas, Taquet (2013) recommended comparative
485 analyses of stomach contents on tropical tunas. Such analyses have shown that small-sized

486 tunas may not feed while associated with DFADs in the Atlantic (Hallier & Gaertner, 2008;
487 Ménard et al., 2000), Indian (Grande et al., 2013; Jaquemet et al., 2011; Zudaire et al., 2015,
488 Malone et al. 2011, Hallier & Gaertner, 2008) and Western and Central Pacific (Machful et
489 al., 2021) oceans. Small YFT and SKJ captured in DFAD-associated schools had a higher
490 fraction of empty stomachs, lower stomach fullness or daily food rates (in the EAO; Hallier &
491 Gaertner 2008, Ménard et al. 2000; and in the IO, Hallier & Gaertner 2008), and lower prey
492 weight (in the IO; Grande et al. 2013, Zudaire et al. 2015) than those captured in free-
493 swimming schools. These results support the hypothesis that the quantity of prey present in
494 DFAD assemblages is not sufficient to sustain the dietary requirements of large aggregations
495 of small-sized tuna commonly found at DFADs (several tens of tons) (Fréon & Dagorn,
496 2000). Hence, if tuna were to spend more time associated with FOBs, due to the increase in
497 the number of FOBs induced by the deployment of DFADs, it could impact their feeding
498 behaviour, potentially resulting in an increase in their natural mortality. However, evidence is
499 still too scarce to allow the determination and quantification of this potential increase of
500 natural mortality. Also, except in Hallier & Gaertner (2008), the influence of the sampling time
501 of tunas on the stomach content was not taken into account. Purse seine vessels mainly fish
502 on DFADs at dawn (Forget et al., 2015) and on free-swimming schools during daytime. First,
503 feeding activities are believed to often take place in the early evening on organisms
504 performing diel vertical migration between the deep scattering layer and the surface
505 (Schaefer & Fuller, 2002), resulting in prey being fully digested by the time the fish are
506 caught and sampled, at dawn. Second, free-swimming schools of tunas are almost
507 exclusively caught when actively feeding at the sea surface, hence higher levels of stomach
508 fullness are to be expected. Nevertheless, the association of tunas with DFADs could also
509 affect the composition and quality of their diet, as shown for YFT in the Western IO (WIO)
510 and WCPO and for SKJ in the WCPO (Zudaire et al. 2015, Allain et al. 2010). Differences of
511 diet composition were observed for these species, that may be due to their associative
512 behaviour despite the above-mentioned sampling bias, with associated tuna in the WCPO
513 feeding on shallower prey than free-swimming tunas (Allain et al. 2010), which is in

514 agreement with YFT staying closer to the surface when associated (Holland and Brill, 1990,
515 Schaefer et al. 2009).

516 Independently of the trophic role of DFADs, the deployment and the drift trajectories of
517 DFADs could create new zones of high floating object densities, which may be unfavourable
518 for the foraging success of tunas, resulting in an increase of natural mortality (Marsac et al.
519 2000). In the Western Indian Ocean, Jaquemet et al. (2011) found that in “rich” forage areas,
520 DFADs have no impact on the feeding pattern of tunas, whereas in “poor” forage areas,
521 tunas associated with DFADs had lower stomach fullness compared to tunas in free-
522 swimming schools. The authors suggested that the impact of DFADs on feeding success
523 could be location-dependent, leading them to emphasize the possible detrimental effect on
524 the condition of tuna associated with DFADs if associated tunas drift towards areas with poor
525 forage resources. However, such an effect relies on the assumption that a tuna’s probability
526 to depart from a DFAD is independent of their local environment which seems in
527 disagreement with behavioural studies (Fuller et al. 2015, Nooteboom et al. 2023).

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

536 *Effects on body condition*

537 Individual condition can be seen as a proxy of individual’s fitness, as it can impact both the
538 individual survival and reproduction (Lloret et al. 2014). Tuna condition has been investigated
539 using different methods: biometric condition factors (e.g. plumpness), and biochemical
540 indices (e.g., fat and water contents, lipid class composition). Gaertner et al. (1999) in a
541 preliminary investigation did not find evidence of a morphometric difference between free-

542 swimming school or DFAD-caught tunas in the EAO. But Marsac et al. (2000) in the EAO
543 and Hallier & Gaertner (2008) in the WIO found that individuals associated with DFADs were
544 in lower condition than those in free-swimming schools, using morphometric indicators
545 (thorax width or girth, plumpness of fish) as fish health indicators. This result suggests that
546 DFADs, by reducing individual condition, could increase tuna natural mortality and/or impact
547 their reproduction (specifically for SKJ who also associate to DFADs when they are mature).
548 Robert et al. (2014) measured the condition of SKJ using BIA (Bioelectrical Impedance
549 Analysis), a non-invasive field tool that estimates body water content (inversely correlated
550 with body fat content), and determines total lipid and main lipid class concentrations. They
551 confirmed the lower condition of SKJ associated with floating objects compared to those in
552 free-swimming schools. Because the studied area (Mozambique Channel, WIO) is naturally
553 rich with NLOGs and had undergone little habitat modifications due to DFADs at the time of
554 the study (Dagorn et al., 2013a, Dupaix et al. 2021), the authors concluded that before the
555 use of DFADs, tunas associated with logs could have also been in lower condition than tunas
556 in free-swimming schools. These results can mean that (1) a lower measured condition could
557 reflect normal variations and does not necessarily imply detrimental physiological
558 consequences, or (2) some specific areas where NLOGs have always been in high numbers
559 could also have negatively impacted the condition of tunas that passed through and stayed in
560 these areas.

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

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

585 *Effects on reproduction and growth*

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

598 fecundity, most likely due to the low number of actively spawning females analysed and the
599 high inter-individual fecundity variability observed in YFT (Pecoraro et al., 2017).

600 Similarly, Ashida et al. (2017) investigated the difference in reproductive traits of female SKJ,
601 of similar size distribution, between school types in the WCPO, highlighting a significant
602 higher proportion of mature females in free swimming schools, characterised by higher
603 relative condition factor, than associated with DFADs. However, as for YFT in the IO (Zudaire
604 et al. 2014), no significant effect of the school type was observed on the WCPO SKJ
605 fecundity, which corroborates previous results observed for WIO SKJ (Grande, 2013; Grande
606 et al. 2014). Also, an investigation of the reproductive dynamics of SKJ in the EPO based on
607 the histological evaluations of ovaries from 3732 females indicated spawning was observed
608 for fish captured in both unassociated and floating object sets (Schaefer and Fuller 2019).
609 The lack of relationship between condition and fecundity of SKJ could be related to their
610 energy allocation and reproductive strategies. SKJ tuna females fuel their gametes with
611 energy gained concomitantly during reproduction (i.e., income breeding strategy, Grande et
612 al. 2016). However, YFT females can store additional energy reserves prior to spawning,
613 which define them as income-capital breeder (Zudaire et al., 2014) unlike SKJ. Therefore, as
614 SKJ females exhibit better condition when free swimming, it can be assumed that their
615 reproductive efficiency is lower when associated with DFADs, but the same conclusion
616 cannot be made for YFT.

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

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

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

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

668 Another research priority is to develop experimental studies to identify the biological and
669 behavioural processes involved in tuna associative behaviour. The only scientific consensus
670 is the fact that in a given area, conditions of tunas associated with floating objects often
671 seem to be lower than those of fish in free-swimming schools. However, the different
672 indicators used to assess tuna condition are not always well correlated (Sardenne et al.
673 2016), and experimental studies are needed to validate them against proper benchmarks,
674 allowing to determine how representative they are of individuals' health. Then, understanding
675 how fast these indicators change with the fish's associative behaviour appears essential.
676 This could also be achieved through studies on captive tropical tunas (e.g., Estess et al.
677 2017), but non-lethal observations should be promoted (e.g. BIA) in order to track changes
678 throughout the fish lifespan. No evidence exists suggesting whether the lower condition at
679 DFADs is the consequence or the cause of their association with DFADs. Often the
680 robustness of the findings of investigation on the life-history parameters of tunas is hampered
681 by the lack of knowledge of the time spent associated with a DFAD or in an array of DFADs

682 by each specimen analysed. The history of each individual tuna is a hidden variable that
683 must be taken into account in statistical analyses, which is a challenge. Studies combining
684 behavioural observations (tagging) and condition of the individuals (e.g. BIA or biochemical
685 analyses of biopsies made at the time of tagging) should then be encouraged. Ideally, tags
686 equipped with physiological sensors would clearly help understanding the interplay between
687 associative behaviour and tuna physiology. Such tags, however, are only starting to be
688 developed.

689 Studies on AFADs could provide insights to the questions addressed in this manuscript: as
690 argued by Dagorn et al. (2010), AFADs also alter the natural environment (by adding floating
691 objects to the ocean). However, it remains questionable if they are comparable due to the
692 fact that AFADs are generally located nearshore, with corresponding particular
693 oceanographic conditions, and they do not move with water masses. Papua New Guinea, the
694 Philippines and Indonesia are examples of areas with very high numbers of AFADs (Proctor
695 et al. 2019) and as such, these dense arrays of AFADs could generate the same concerns
696 on tuna life-history parameters and behaviour that those described for DFADs.
697 Understanding the behaviour of tunas around AFADs can also improve our general
698 understanding of tunas around all types of floating objects and help design new, well focused
699 studies for DFADs. For practical reasons, more studies have been performed on the
700 behaviour of tuna at AFADs than at DFADs (e.g. Dagorn et al., 2007; Govinden et al., 2013;
701 Holland et al., 1990; Ohta & Kakuma, 2005; Rodriguez-Tress et al., 2017). They provided
702 estimates of residence times between two AFAD associations and therefore of the
703 percentage of time spent associated to AFADs (e.g. Pérez et al., 2020; Robert et al., 2013b;
704 Rodriguez-Tress et al., 2017), which still needs to be further explored at DFADs. For
705 example, Pérez et al. (2020) used acoustic tagging data on AFAD arrays to demonstrate that
706 when inter-AFAD distance decreases, tuna visit more AFADs, spend less time travelling
707 between AFADs and more time associated with them. Concerning DFADs, as actual
708 densities of drifting floating objects are difficult to obtain, studies using a modelling approach
709 based on experimental data should be promoted (Pérez et al. 2022, Capello et al. 2023).
710 These studies should investigate the consequences of changes in floating object density on

711 tuna school sizes and associative behaviour. These modelling studies could be
712 complemented and/or calibrated by studies which use data from echosounder buoys
713 deployed by fishers on floating objects. Recent methodological advances allowed the
714 prediction of tuna presence or absence under FOBs (Baidai et al., 2020; Orue et al., 2020).
715 Using an extensive dataset from echosounder buoys in the WCPO (more than 3.8 million
716 transmissions), Escalle et al. (2021c) determined different profiles of acoustic signals related
717 to different types of aggregations. Other studies also show that multi-frequency echosounder
718 buoys could allow the discrimination of tropical tuna species under DFADs (Moreno et al.
719 2019, Sobradillo et al. 2023). These new methodological developments, in combination with
720 tagging data, both conventional and electronic, and modelling approaches offer promising
721 perspectives for the study of tuna aggregation behaviour under FOBs and the potential
722 impact of DFAD density on tuna schooling behaviour.

723 Tuna RFMOs set limits on the number of operational buoys (IATTC: up to 340 depending on
724 the vessel size, Res C-21-04; ICCAT: 300 in Rec 22-01; IOTC: 300 in Res 19/02; WCPFC:
725 350 in CMM 2021-01). These limits are essentially set to control the fishing effort and the
726 catches of tunas and non-target species, hence to control fishing mortality. How such limits
727 also act on the number of deployed DFADs and the potential impacts of DFADs on tuna's
728 natural mortality, is unknown. In theory, all purse seine vessels could use at least the same
729 amount of DFADs than the maximum number of operational buoys authorized in each of the
730 regions. Multiplying this maximum number of operational buoys authorized per vessel by the
731 number of large-scale purse seine vessels in each ocean provides a global authorized limit of
732 about 238,000 operational buoys (details of the calculation in Supplementary Materials 1).
733 This number is about twice higher than the estimate of the global number of DFADs
734 deployments made by Gershman et al. (2015), based on data from 2013. Hence, it would
735 mean that the global purse seine fishery could have increased the number of DFADs in the
736 ocean while still respecting the current limits on the number of active buoys. Most tRFMOs
737 now require that DFAD identification, characteristics, deployment date and deployment
738 location are reported (e.g. ICCAT Rec 22-01; IOTC Res. 19/02; IATTC C-21-04). Some
739 studies evidenced different regional trends of DFAD deployments (IOTC, 2022, Escalle et al.

740 2020, Lopez et al. 2021, Floch et al., 2019; Maufroy et al., 2017), but no study assessed this
741 trend on a global scale after 2013 (Gershman et al., 2015). Tuna RFMOs should continue to
742 collect and make fine-scale DFAD data available to scientists to allow regular estimations of
743 the extent of the habitat modifications generated by DFADs, which should be addressed at a
744 global scale.

745 **Conclusion**

746 This study reviews the current state of knowledge on the indirect impacts of DFADs on
747 tropical tuna, i.e. how DFADs could also impact natural mortality and reproduction
748 additionally to their impact on fishing mortality. To summarize the questions formulated:

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

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

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

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

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

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

782 Data used in the supplementary material were obtained from Justel-Rubio et al. (2023) and
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1324 **Tables**

1325 **Table 1: Summary of main findings from previous studies on the numbers of**
 1326 **monitored floating objects or the number of DFADs used in large-scale tropical tuna**
 1327 **purse seine fisheries.**

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

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

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

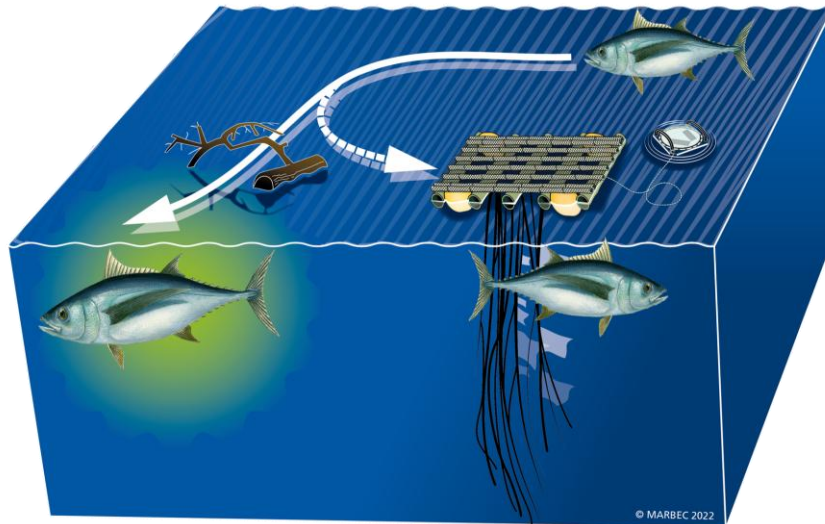
1328 **Table 2: Summary of main findings from previous studies on tuna individual CRT and CAT assessed under anchored and drifting FADs.**
 1329 CRT: Continuous Residence Time – continuous bouts of time spent at the same FAD without any absence longer than 24h. CAT: Continuous Absence
 1330 Time – the 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 of 15 days) BET (45-61 cm FL): average of 25.31 days (maximum value of 55 days) | Tolotti et al. (2020) | |
| | Mozambique Chanel (Western Indian Ocean) | CRT | YFT (29-60 cm FL): between 0.00-26.72 days with median at 9.98 days SKJ (47-57 cm FL): between 0.09-18.33 days with median at 4.47days BET (54-56 cm FL): between 0.00-6.56 days with median at 3.89 days | Govinden et al. (2010) | |
| | Western and Central Pacific Ocean | CRT | SKJ (46-60 cm FL): median of 1 day (maximum value of 18 days) YFT (36-98 cm FL): median of 2 days (maximum value of 50 days) BET (38-90 cm FL): median of 10 days (maximum value of 30 days) | Phillips et al. (2019b) | |
| | | CAT | BET (38-90 cm FL): median of 3.2 days (maximum value of 48.2 days) | | |
| | Equatorial Central Pacific Ocean | CRT | SKJ (36-65 cm FL) : from 0.0 to 6.4 days (with average value at 2.3 days) | Matsumoto et al. (2014) | |
| | | CRT | SKJ (34.5–65.0 cm FL): less than 7 days YFT (31.6–93.5 cm FL): less than 7 days BET (33.5–85.5 cm FL): less than 7 days | Matsumoto et al. (2016) | |
| | Anchored | Philippines (Indian Ocean) | CRT | Juvenile YFT (19–31 cm FL) : between 1 and 6 days | Mitsunaga et al., (2012) |
| | | Maldives Islands (Indian Ocean) | CRT | SKJ (37–54 cm FL) : 0.20-3.75 days YFT (35–53 cm FL) : 0.61-0.70 days | Govinden et al. (2013) |
| | | Mauritius islands (Indian Ocean) | CRT | SKJ (41 -59 cm FL) : 2.5 days YFT (46 -81cm FL) : 9.6 days BET (48 - 60 cm FL) : 5.2 days | Rodriguez-Tress et al. (2017) |
| CAT | | | SKJ (41 -59 cm FL) : 2.9 days YFT (46 -81cm FL) : 1.4 days BET (48 - 60 cm FL) : 0.8 days | | |
| Hawaii islands | | CRT | Small YFT (30-39 cm FL) : 13.58 days | Robert et al. (2012) | |

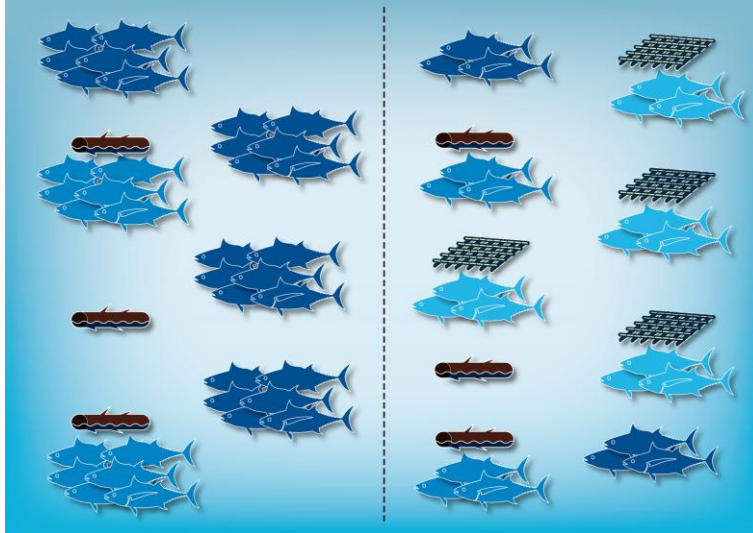
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|--|-----|---|-------------------------|
| (Pacific Ocean) | | Large YFT (63-68 cm FL): 9.44 days | |
| | CAT | 4 days for small YFT and 1.65 days for large YFT | |
| | CRT | 4 behavioural modes reported for YFT (54 to 95 cm FL) : - Brief association : 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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Figure 1: Schematic representation of the ecological trap hypothesis applied to Drifting Fish Aggregating Devices (DFADs), as originally formulated. Under this hypothesis, before DFADs introduction, when only natural floating objects (NLOGs) were present, floating objects were indicators of productive areas. Hence, by associating with floating objects, tuna selected high quality habitats. DFAD massive deployment modified the distribution of floating objects (FOBs), which are not representative of rich areas anymore. By associating with FOBs, tunas can be attracted to or retained in habitats of lesser quality.



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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.