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

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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 (248 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 impacts on tuna natural  
49 mortality and reproductive potential and assessing the consequences of their presence at  
50 sea on tuna populations is a challenge. The use of DFADs results in a major increase in the  
51 number of floating objects, which are spatially heterogeneous at sea. To date, no converging  
52 scientific results exist regarding the 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

69

70	<b>Table of contents</b>	
71		
72	<b>Introduction.....</b>	<b>4</b>
73	<b>Theoretical background.....</b>	<b>6</b>
74	<b>How much do DFADs change the habitat of tropical tunas?.....</b>	<b>11</b>
75	<b>Do DFADs modify the migration and the schooling behaviour of tropical tunas? .....</b>	<b>15</b>
76	<i>Effects on individual large-scale movements.....</i>	<i>16</i>
77	<i>Effects on individual fine-scale movements .....</i>	<i>17</i>
78	<i>Effects on schooling behaviour.....</i>	<i>20</i>
79	<b>Do DFADs modify the life-history parameters of tropical tunas?.....</b>	<b>21</b>
80	<i>Effects on feeding.....</i>	<i>21</i>
81	<i>Effects on body condition.....</i>	<i>23</i>
82	<i>Effects on reproduction and growth.....</i>	<i>25</i>
83	<b>What are the scientific challenges to fill the knowledge gaps? .....</b>	<b>26</b>
84	<b>Conclusion .....</b>	<b>31</b>
85	<b>Acknowledgements.....</b>	<b>32</b>
86	<b>Data availability statement .....</b>	<b>32</b>
87	<b>References.....</b>	<b>33</b>
88	<b>Tables.....</b>	<b>45</b>
89	<b>Figures .....</b>	<b>2</b>

90

## 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 (Filmalter 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. TRFMOs primarily focus on developing management schemes to  
146 address the known effects of DFADs on catches (particularly of small YFT and BET, as well  
147 as bycatch) or their stranding on coasts. Through the increase of FOB density they induce,  
148 DFADs could also impact tropical tuna natural mortality and reproductive potential, hence,  
149 altering their individual fitness which could have population-level consequences. Despite the  
150 high level of uncertainty on these impacts, assessing them is central as they could act as  
151 compounding factors and worsen the increase of fishing mortality induced by DFADs. Hence,  
152 there is a need to assess whether DFADs can alter the life history parameters and behaviour  
153 of tunas. This will help to determine the magnitude of DFADs impacts on natural mortality  
154 relative to those on fishing mortality and to manage the number of DFADs deployed at sea if  
155 negative impacts on natural mortality are suspected or demonstrated.

## 156 **Theoretical background**

157 Fisheries management, as practiced since the 1940s, was based on the ecosystem theory  
158 but focused mainly on fishing activity and target fish resources (Garcia et al. 2003). In the  
159 early 2000s, following an abundant documentation of the relative failure of conventional

160 fisheries management (Garcia & Grainger 1997; Pauly et al. 2002; Sutinen & Soboi 2003),  
161 the need for other frameworks emerged, among which the Ecosystem Approach to Fisheries  
162 (EAF; FAO 2003; Garcia et al. 2003). The EAF stresses the need to recognize “more  
163 explicitly the interdependence between human well-being and ecosystem health and the  
164 need to maintain ecosystems productivity for present and future generations” (Ward et al.  
165 2002). As opposed to conventional fisheries management, EAF calls for the consideration of  
166 human activities other than fisheries and the generation of knowledge on ecosystem  
167 processes to understand the consequences of human activities (Figure 1, Pikitch et al.  
168 2004). When considering the impact of a fishery on a target species, conventional fisheries  
169 management only considered the increase of fishing mortality induced by the removal of  
170 individuals, and the impact of such removals on the reproduction (Figure 1). However,  
171 fisheries can also modify the habitat of the target species, ultimately impacting their natural  
172 mortality and their reproductive potential. For example, habitat modifications induced by  
173 fisheries can impact benthic community composition and sensitivity (Neumann et al., 2016),  
174 and could also affect fish recruitment (Macura et al., 2019). The EAF framework stresses the  
175 need to determine and assess the extent of fisheries impacts not only on the fishing mortality  
176 (as done by conventional fisheries management), but also on species habitat and the  
177 induced impacts on natural mortality and reproductive potential.

178 Noting the increasing number of floating objects being deployed by fishers since the 1990s,  
179 some scientists hypothesized that this modifies tropical tuna habitat, leading to an ecological  
180 trap and to an increase of their natural mortality (Marsac et al., 2000). An ecological trap  
181 occurs when animals are misled by cues that were previously correlated with the habitat  
182 quality but no longer are, due to anthropogenic influences (Sherley et al. 2017, Swearer et al.  
183 2021). Such impacts form the basis of the ecological trap theory and result in the preferential  
184 selection of low-quality habitats by animals, when better alternatives exist (Battin, 2004;  
185 Schlaepfer et al., 2002). It is worth noting that, depending on the definition, an ecological trap  
186 can occur without any anthropogenic influence (Robertson & Hutto, 2006; Swearer et al.,  
187 2021; Teske et al., 2021). In this paper, we will consider that ecological traps occur because  
188 of a sudden anthropogenic change in the environment, i.e. in the case of tropical tuna, the



189 modification of their surface habitat by the increased deployment of DFADs (Gilroy &  
190 Sutherland, 2007; Hallier & Gaertner, 2008; Schlaepfer et al., 2002). The ecological trap  
191 concept has been proposed regularly in the face of human-induced environmental changes  
192 and offers an important framework to assess the impact of human induced habitat changes  
193 on species fitness (Hale & Swearer 2016; Swearer et al. 2021).

194 Although fish associative behaviour with FOBs has been known for almost two millennia  
195 (Oppian, 200 AD), the reasons underlying it are still largely unknown, complicating the  
196 assessment of DFADs impacts on tuna natural mortality and reproductive potential. To date,  
197 two main hypotheses have been retained to explain the associative behaviour of tropical  
198 tuna: the *indicator-log* and the *meeting-point* hypotheses (Hall 1992, Dagorn 1995). Based  
199 on these two hypotheses, the impacts of DFADs on tropical tuna would differ. The indicator-  
200 log hypothesis posits that tuna would associate with FOBs to find rich areas (Hall 1992;  
201 Castro et al. 2002). NLOGs are mainly parts of trees and they would indicate rich areas  
202 because they originate from rivers and can accumulate in rich frontal zones (Castro et al.  
203 2002; Hallier & Gaertner 2008). The associative behaviour would then result from an  
204 evolutionary process where tuna use FOBs to stay in rich waters. Under this behavioural  
205 hypothesis, by modifying the distribution and density of FOBs, DFADs could act as ecological  
206 traps and retain and/or attract tuna in areas that are detrimental to them, inducing an  
207 increase of their natural mortality (Figure 2).

208 The meeting-point hypothesis states that pelagic species would associate with FOBs to  
209 facilitate school formation (Fréon & Dagorn 2000). Provided that tuna can detect floating  
210 objects from further away than they can detect other schools, associating with floating  
211 objects could increase the probability to encounter other conspecifics. Schooling behaviour  
212 can be seen as a trade-off between, on the one hand, increasing protection against  
213 predators, encounters of reproduction partners, foraging and swimming efficiency and, on the  
214 other hand, increasing detection by predators and inter-individual competition (Rubenstein  
215 1978; Ioannou 2017; Maury 2017). Considering the meeting-point hypothesis, DFADs, by  
216 increasing the density of FOBs, could provoke the dispersion of tuna, disturbing schooling  
217 behaviour and ultimately impacting their natural mortality (Figure 3, Fréon & Dagorn 2000). It

218 is important to note here that this potential impact on tuna natural mortality does not  
219 constitute an ecological trap: by associating with FOBs, tuna try to meet with conspecifics  
220 and do not use FOBs as cues to select a habitat. Hence, in the framework of the EAF and to  
221 consider all the potential impacts of DFAD fishing on tropical tuna, we need to characterize  
222 the extent to which DFADs change the density and distribution of FOBs. We also need to  
223 determine if this modification impacts tropical tuna natural mortality and reproductive  
224 potential, impact which is behaviourally mediated.

225 Almost 20 years ago, Dempster & Taquet (2004) made a systematic review of the published  
226 literature on FADs and concluded that further research should assess the use of DFADs by  
227 pelagic species, the mechanisms underlying their associative behaviour and the ecological  
228 consequences of the presence of DFADs at sea on pelagic fish stocks. Since then, several  
229 papers reviewed existing evidence and/or proposed future research directions to address the  
230 impacts of DFADs on tropical tuna (Dagorn et al. 2013b, Evans et al. 2015, Davies et al.  
231 2014, Fonteneau et al. 2015, Leroy et al. 2013, Taquet 2013, Pons et al. 2023). Yet, most of  
232 these papers, except those by Taquet (2013) and Pons et al. (2023), addressed these  
233 impacts at a regional scale and all were mainly focussing on the impacts of DFADs on fishing  
234 mortality, even though they mentioned potential impacts on natural mortality. A recent review  
235 by Pons et al. (2023) assessed the advantages and drawbacks of fishing with DFADs at the  
236 global scale. They identified seven sources of concern for FAD fishing, including habitat  
237 perturbation generated by DFADs and the risk of DFADs acting as ecological traps. On this  
238 question, they highlighted the difficulty of testing the ecological trap hypothesis. The objective  
239 and originality of our review paper is not to look at the impacts of fishing at DFADs but to  
240 examine in depth if the presence of DFADs in the ocean could impact the natural mortality  
241 and reproductive potential of tropical tuna. This particular question has never been fully  
242 addressed, precluding management bodies from having a complete view of the current  
243 knowledge. To examine the sustainability of DFAD fisheries, in line with the EAF framework,  
244 it is therefore essential not only to examine the impact of DFADs on fishing mortality, but also  
245 on natural mortality and reproductive potential. The effects induced by DFADs on tuna  
246 behaviour and biology could thus act as compounding factors to the already known effects

247 on increasing fishing mortality. An in-depth literature review provides an overview of the state  
248 of the art in this area, identifies knowledge gaps, and proposes future research priorities.  
249 Following the ecological trap hypothesis framework and the consideration that these impacts  
250 are necessarily behaviourally mediated, this paper is structured around four major questions:

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

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

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

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

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

256 Tropical tuna are circumtropical pelagic fish, preferring relatively warm and stratified waters,  
257 with larvae preferring waters above 24°C (Artetxe-Arrate et al., 2021). SKJ, YFT and BET are  
258 considered epipelagic species which also exploit the mesopelagic zone, especially during the  
259 day when searching for deep scattering prey organisms (Schaefer et al. 2009). Whereas  
260 small and large BET are capable of spending long periods of time in the mesopelagic zone,  
261 due to their thermal physiology, SKJ and YFT are only able to remain for brief periods of time  
262 when exhibiting repetitive bounce diving behaviour. Hence, tropical tuna have distinct  
263 ecological niches at different stages of their life-history (Artetxe-Arrate et al., 2021). Tuna  
264 habitat can be defined as the surface and sub-surface ocean waters, with all the abiotic  
265 (temperature, dissolved oxygen, etc.) and biotic (prey, competitors, etc.) parameters  
266 important for their biological functions. Among the components of tuna habitats, floating  
267 objects represent very peculiar features. They represent physical discontinuities that tuna are  
268 known to associate with, at least at given stages of their life-history (mainly adult SKJ, small  
269 YFT and BET). Human activities (logging, coastal development, shipping, etc.) modified the  
270 number of floating objects at sea, in some cases even before modern purse-seine tuna  
271 fishing began (Caddy & Majkowski, 1996; Thiel & Gutow, 2005). Some of these activities  
272 may have consistently increased (coastal development, shipping), whereas others, such as  
273 logging, may have varied due to increased global trade and subsequent deforestation of

274 some areas (Caddy & Majkowski, 1996). In addition, environmental changes also affect the  
275 production and movement of floating objects (e.g. floods, El Niño events, tsunamis), with  
276 global warming supposed to increase the frequency of extreme events. In recent years, the  
277 increasing use of DFADs by fishers raised several questions about the sustainability of this  
278 practice. The primary concern is the increase in fishing efficiency and mortality induced by  
279 DFAD fishing (Dagorn et al. 2013b, IOTC 2022, Pons et al. 2023). However, the increase of  
280 the number of floating objects could also induce impacts on tuna behaviour and life history  
281 parameters, which are more challenging to address. In the current framework of the  
282 ecosystem approach to fisheries (Pikitch et al. 2004), the assessment and management of  
283 these impacts is fundamental.

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

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

303 natural floating objects and for all types together (natural and artificial) is challenging, the  
304 primary concern being to identify the origin of the floating object.

305 The number of DFADs have regularly increased (Maufroy et al. 2017), but it is necessary to  
306 put this in perspective with respect to all floating objects. Using data from observers onboard  
307 tuna purse seine vessels in the Indian Ocean (IO), noting all FOBs encountered when the  
308 vessel cruises, Dupaix et al. (2021) highlighted a drastic increase in the total number of  
309 floating objects in the western IO, from 2006 to 2018, with multiplication factors greater than  
310 2 in every region and reaching as high as 60 in some areas (e.g. Somali area). The entire  
311 western IO is affected, with DFADs comprising over 85% of the total FOBs and DFADs  
312 contributing to reduce the distances between floating objects (mean distances between  
313 DFADs and between NLOGs of 37 km and 89 km, respectively, in 2014-2018). The impact of  
314 DFADs on tuna habitat reducing the distance between FOBs was observed in the study both  
315 when considering all DFADs or only randomly encountered DFADs (objects which do not  
316 belong to the vessel or its fishing company), to account for a potential sampling bias. Phillips  
317 et al. (2019a), using data from 2016 and 2017 and Lagrangian simulations in the Western  
318 and Central Pacific Ocean (WCPO), also showed an increase in FOB densities induced by  
319 DFAD deployments, and observed a shift of the area with the highest FOB densities, from  
320 the North-Eastern area of the Bismark Sea to the Tuvalu archipelago. Unfortunately no  
321 similar detailed study has been conducted in the other oceans, precluding from estimating  
322 the extent of the change of the habitat of tunas due to the addition of new floating objects  
323 globally.

324 Most of the management effort by tRFMOs is focused on the monitoring and control of  
325 satellite-tracked buoys attached to floating objects (either to DFADs or to LOGs), emitting  
326 positions (and other variables) to vessels and qualified as operational buoys, as this variable  
327 is strongly related to fishing effort. This also explains why most scientific studies prioritized  
328 the estimate of operational buoys rather than the number of DFADs in the ocean (Table 1).  
329 Currently, all tRFMOs have implemented a limit on the instantaneous number of operational  
330 satellite buoys per vessel, and, except in the Atlantic Ocean (AO), limited the re-activation of  
331 buoys while at sea, but only the IOTC has limited the number of buoys purchased and in

332 stock per year, per vessel (IOTC Res 19/02, ICCAT Rec 22-01, IATTC Res C-21-04,  
333 WCPFC CMM 2021-01). This clearly reflects a lack of concerted action worldwide to limit the  
334 number of new floating objects deployed in the oceans. Even under the limit of active DFADs  
335 at sea per vessel, the actual total numbers of DFADs in the ocean could have increased. So  
336 far, few studies have produced estimates of the total number of DFADs deployed annually,  
337 with estimations providing a range of 81,000 to 121,000 deployments worldwide, but these  
338 global estimates were made a decade ago (Baske et al., 2012; Gershman et al., 2015; Scott  
339 & Lopez, 2014). As a comparison, AFADs seem to be less numerous worldwide (13,000  
340 AFADs estimated in Scott & Lopez 2014), although there may be few areas with very high  
341 densities of AFADs, such as Indonesia (5,000-10,000, Proctor et al. 2019), the Philippines or  
342 Papua New Guinea.

343 In practice, despite efforts by tRFMOs to require the submission of DFAD data, accurately  
344 determining a simple indicator such as the total number of DFADs that are drifting in the  
345 world's oceans is a major challenge. The easiest way would be to monitor the number of  
346 deployments through logbooks or onboard observers or set up a FAD register (see Res  
347 23/02 of the IOTC). The number of operational buoys does not correspond to the number of  
348 DFADs in the water (and/or deployed) as some buoys can be attached to LOGs, can be  
349 deactivated, and some DFADs may lack positional trackers, but it can be used as a proxy to  
350 illustrate the trend in numbers. Therefore, as the number of operational buoys does not  
351 effectively limit DFAD deployments, the number of DFADs in the water and/or deployments  
352 could be larger than the limits adopted by the tRFMOs. Under the assumption that the  
353 number of natural floating objects remains relatively constant, the increasing number of  
354 electronic buoys used reflects an increase of the number of FOBs. In recent years, DFAD  
355 deployments were stable in the WCPO (2011-2019; Escalle et al. 2020), decreased in the IO  
356 (2016-2021; IOTC, 2022), increased in the Eastern Pacific Ocean (EPO, 2015-2020; Lopez  
357 et al. 2021) and buoy deployments increased in the AO (2007-2013; Maufroy et al. 2017).  
358 Hence, a characterisation of DFAD deployment trends at the global scale is needed.  
359 However, the clear trend in the number of DFAD sets or DFAD catches (Floch et al., 2019;

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

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

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

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

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

385 Hallier & Gaertner (2008) analysed conventional tagging data of SKJ and YFT in the Eastern  
386 Atlantic Ocean (EAO). Different migratory directional patterns and displacement rates were

387 observed between fish recaptures associated with DFADs and those in free-swimming  
388 schools. Displacement rates were significantly larger for both YFT and SKJ recaptured in  
389 association with DFADs (13 and 15 nm/day, respectively) than those recaptured in free-  
390 swimming schools (3 and 4.5 nm/day, respectively), which suggests that DFADs could  
391 relocate tunas to new areas. In the IO, Stehfest and Dagorn (2010) found similar results for  
392 SKJ, YFT and BET, but with lower displacement rates differences than in the AO. Hallier and  
393 Gaertner (2008) interpreted these results as indicating significant modifications of migratory  
394 patterns due to associations with DFADs, suggesting an influence of DFAD association  
395 strong-enough to disturb tropical tuna migratory patterns. However, Stehfest and Dagorn  
396 (2010) argue that it could only reflect an artefact of the non-uniform distribution of DFAD  
397 fishing. Also, authors of both studies agree that school type at recapture might not be  
398 representative of the associative history of individuals before their recapture. Using an  
399 advection-diffusion model, Kim (2015) also showed that including a DFAD attraction  
400 component to the model better fitted SKJ tagging data in the WCPO, suggesting an effect of  
401 DFADs on SKJ migratory patterns. Comparing DFAD induced movements in the 2000s with  
402 those in the 1990s, they showed that the rising DFAD density increased this modification of  
403 migration patterns. These studies were the only ones to assess differences of movement  
404 patterns induced by DFADs and, due to species and ocean differences, more studies would  
405 be needed to interpret these results at a global scale.

406 DFADs potential to modify large-scale movements of tunas can be investigated through  
407 archival tags by comparing tuna movements with the general drift patterns of DFADs. In the  
408 equatorial EPO, evaluation of archival tag data sets from 96 BET (54-159 cm in length, 1-5.5  
409 years of age) tagged between 2000 – 2005 (Schaefer et al., 2009; Schaefer & Fuller, 2010)  
410 did not support the hypothesis that the most probable BET tracks were related to the general  
411 drift patterns of DFADs. This suggests that the large-scale spatial dynamics of BET are not  
412 strongly influenced by DFADs at the densities and conditions found in the EPO. However, in  
413 the Central Pacific Ocean (CPO), a predominantly eastward extensive dispersion of BET  
414 tagged with conventional tags and archival tags was observed (Schaefer et al., 2015). The  
415 authors explain the strong regional fidelity of BET in the equatorial EPO by the high



416 concentration of food, leading to their residence and retention in that area. In the equatorial  
417 CPO, the strong eastward-flowing North equatorial countercurrent and BET searching for  
418 higher prey concentrations could explain the predominantly eastward dispersion of BET.

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

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

432 Acoustic tags and archival tags (only when a species exhibits a distinct vertical behaviour  
433 when associating with a floating object, as observed for BET or sometimes YFT) have been  
434 used by scientists to measure these parameters (Table 2). Passive acoustic tagging studies  
435 on DFADs revealed that the majority of residence times of tunas (i.e. continuous periods of  
436 time spent associated with a given DFAD) were of a few days. Mean values ranged from 0.2  
437 to 4.6 days for SKJ (Dagorn et al., 2007; Govinden et al., 2021; Matsumoto et al., 2014,  
438 2016), from 1.0 to 6.6 days for YFT and 1.4 to 10 days for BET (Dagorn et al., 2007;  
439 Govinden et al., 2021; Matsumoto et al., 2016, Phillips et al. 2019b). Long associations,  
440 however, have been observed on rare occasions – e.g. 27 days for YFT in the IO (Govinden  
441 et al., 2021) and up to 18, 50 and 30 days for SKJ, YFT and BET respectively, in the WCPO  
442 (Phillips et al. 2017, Phillips et al. 2019b). A recent study in the EAO (Tolotti et al., 2020)  
443 reported significantly larger mean residence times for the three tuna species, from 9 days

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

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

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

465 Because BET and sometimes YFT exhibit different vertical behaviour patterns when  
466 associated or non-associated with floating objects (Holland and Brill 1990, Abascal et al.  
467 2018), archival tags have been used to assess residence times at and between floating  
468 objects, and therefore percentage of days associated with floating objects, without the need  
469 to instrument all objects with acoustic receivers. Using satellite archival tagging data where  
470 individual BET tracks could be recorded over several months or even years, the percentage  
471 of time associated with floating objects was estimated to be between 4 % and 17 %

472 depending on the size of the fish and the oceanic region (Fuller et al., 2015; Phillips et al.,  
473 2017; Schaefer & Fuller, 2010, Leroy et al. 2013, Schaefer & Fuller 2002). Associative and  
474 non-associative behaviour with floating objects have also been described with archival tags  
475 for YFT (Phillips et al., 2017; Schaefer et al., 2009; Schaefer & Fuller, 2013, Leroy et al.  
476 2013), with estimates of the percentage of time spent associated with floating objects  
477 between 10% and 23%. These percentages are much lower than those estimated from  
478 acoustic telemetry data (e.g. 75 % for small BET based on the measurements in Phillips, et  
479 al. 2019b).

480 This inconsistency between studies using different tagging methods could result from the  
481 size of tagged individuals or the way the percentage of time spent by tuna associated and  
482 non-associated is calculated. Individuals monitored with archival tags were generally larger  
483 (fork length: 50-146 cm YFT and 46-102 cm BET in Phillips et al. 2017, 51-134 cm BET in  
484 Fuller et al. 2015, 88-134 cm BET in Schaefer & Fuller 2002, 54-159 cm BET in Schaefer &  
485 Fuller 2010) than those marked with passive acoustic tags (38-90 cm BET in Phillips et al.  
486 2019), even though size ranges largely overlap. This suggests that small BET spend a higher  
487 proportion of their time associated with FOBs than large individuals. This agrees with  
488 observed size distributions of DFAD catches, where smaller individuals are caught, and with  
489 the negative correlation between BET individual length and percentage of time associated  
490 found by Schaefer & Fuller (2002). However, Schaefer et al. (2009) found lower association  
491 percentages with archival tags on small tunas (10.4 and 15.9 % of the time associated for  
492 51-60 cm FL YFT and 65-99 cm FL BET respectively) than the work of Phillips et al. (2019)  
493 with acoustic tagging. This could suggest a potential bias in the different methodologies that  
494 need to be further investigated. A small percentage of time associated with floating objects  
495 would indicate no or little influence of DFADs, while a high percentage could indicate a  
496 potentially significant influence of DFADs which could result in impacts on large-scale  
497 movements.

498 We are therefore far from understanding the effects of different densities of floating objects  
499 on tuna fine-scale movements nor the link between fine-scale and large-scale movements.  
500 Most electronic tagging efforts have been done on YFT and to a lesser extent BET, but more

501 behavioural data are clearly needed for all three tropical tuna species. One of the main  
502 difficulty is to disentangle the effects of DFADs from the impacts of other external signals  
503 (e.g. prey density) which can also influence tuna associative behaviour (Lopez et al. 2017,  
504 Nooteboom et al. 2023, Schaefer et al., 2009, Schaefer & Fuller, 2010).

#### 505 *Effects on schooling behaviour*

506 DFADs could also affect schooling behaviour, which can have a wide range of consequences  
507 on the life-history parameters and the movements of tunas. Dagorn & Fréon (1999) and  
508 Fréon & Dagorn (2000) suggested that tuna could associate with floating objects for social  
509 advantages such as facilitating the formation of larger schools. Tuna associative behaviour  
510 would have been selected because schooling behaviour provides several evolutionary  
511 advantages. It can be seen as an evolutionary trade-off between (i) increasing protection  
512 against predators, swimming and foraging efficiency, mating, and (ii) increasing detection by  
513 predators and intra- and inter-specific competition (Rubenstein 1978; Ioannou 2017; Maury  
514 2017). Hence, if tuna use FOBs for social behaviour, the number of FOBs could affect the  
515 size of schools and therefore reduce their evolutionary advantages, which could impact both  
516 tuna survival and reproduction, resulting in population-scale impacts. To date no result has  
517 been obtained on tropical tuna from DFADs regarding this question. If floating objects  
518 facilitate the schooling behaviour of tunas, then the deployment of large numbers of DFADs  
519 may have effects on school size, either by facilitating the formation of large (but less) schools  
520 or decreasing school size with DFADs offering too many aggregation sites (Figure 3, Dagorn  
521 et al., 2010). DFADs could also modify the size structure of tuna schools, allowing the  
522 formation of large aggregations composed of several unassociated schools of different size  
523 structures (Wang et al. 2012). Sempo et al. (2013) modelled the impact of the increasing  
524 deployment of DFADs on the distribution of social fish species such as tunas. They  
525 demonstrated that for social species, increasing the number of DFADs does not necessarily  
526 lead to an increase in the total amount of tuna associated with DFADs, a non-intuitive result.  
527 Capello et al. (2022) also showed that the number of DFADs with associated schools and the

528 size of associated schools were not linearly related to the total number of DFADs and that  
529 this relationship varied according to the considered social scenario.

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

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

#### 534 *Effects on feeding*

535 In his review on DFAD impacts on tropical tunas, Taquet (2013) recommended comparative  
536 analyses of stomach contents on tropical tunas. Such analyses have shown that small-sized  
537 tunas may not feed while associated with DFADs in the Atlantic (Hallier & Gaertner, 2008;  
538 Ménard et al., 2000), Indian (Grande et al., 2013; Jaquemet et al., 2011; Zudaire et al., 2015,  
539 Malone et al. 2011, Hallier & Gaertner, 2008) and Western and Central Pacific (Machful et  
540 al., 2021) oceans. Small YFT and SKJ captured in DFAD-associated schools had a higher  
541 fraction of empty stomachs, lower stomach fullness or daily food rates (in the EAO; Hallier &  
542 Gaertner 2008, Ménard et al. 2000; and in the IO, Hallier & Gaertner 2008), and lower prey  
543 weight (in the IO; Grande et al. 2013, Zudaire et al. 2015) than those captured in free-  
544 swimming schools. These results support the hypothesis that the quantity of prey present in  
545 DFAD assemblages is not sufficient to sustain the dietary requirements of large aggregations  
546 of small-sized tuna commonly found at DFADs (several tens of tons) (Fréon & Dagorn,  
547 2000). Hence, if tuna were to spend more time associated with FOBs, due to the increase in  
548 the number of FOBs induced by the deployment of DFADs, it could impact their feeding  
549 behaviour, potentially resulting in an increase in their natural mortality. However, evidence is  
550 still too scarce to allow the determination and quantification of this potential increase of  
551 natural mortality. Also, except in Hallier & Gaertner (2008), the influence of the sampling time  
552 of tunas on the stomach content was not taken into account. Purse seine vessels mainly fish  
553 on DFADs at dawn (Forget et al., 2015) and on free-swimming schools during daytime. First,  
554 feeding activities are believed to often take place in the early evening on organisms

555 performing diel vertical migration between the deep scattering layer and the surface  
556 (Schaefer & Fuller, 2002), resulting in prey being fully digested by the time the fish are  
557 caught and sampled, at dawn. Second, free-swimming schools of tunas are almost  
558 exclusively caught when actively feeding at the sea surface, hence higher levels of stomach  
559 fullness are to be expected. Nevertheless, the association of tunas with DFADs could also  
560 affect the composition and quality of their diet, as shown for YFT in the Western IO (WIO)  
561 and WCPO and for SKJ in the WCPO (Zudaire et al. 2015, Allain et al. 2010). Differences of  
562 diet composition were observed for these species, that may be due to their associative  
563 behaviour despite the above-mentioned sampling bias, with associated tuna in the WCPO  
564 feeding on shallower prey than free-swimming tunas (Allain et al. 2010), which is in  
565 agreement with YFT staying closer to the surface when associated (Holland and Brill, 1990,  
566 Schaefer et al. 2009).

567 Independently of the trophic role of DFADs, the deployment and the drift trajectories of  
568 DFADs could create new zones of high floating object densities, which may be unfavourable  
569 for the foraging success of tunas, resulting in an increase of natural mortality (Marsac et al.  
570 2000). In the Western Indian Ocean, Jaquemet et al. (2011) found that in “rich” forage areas,  
571 DFADs have no impact on the feeding pattern of tunas, whereas in “poor” forage areas,  
572 tunas associated with DFADs had lower stomach fullness compared to tunas in free-  
573 swimming schools. The authors suggested that the impact of DFADs on feeding success  
574 could be location-dependent, leading them to emphasize the possible detrimental effect on  
575 the condition of tuna associated with DFADs if associated tunas drift towards areas with poor  
576 forage resources. However, such an effect relies on the assumption that a tuna’s probability  
577 to depart from a DFAD is independent of their local environment which seems in  
578 disagreement with behavioural studies (Fuller et al. 2015, Nooteboom et al. 2023).

579 In the Pacific Ocean, Hunsicker et al. (2012) observed that predation on SKJ and YFT by  
580 large pelagic fishes sampled from DFAD sets was greater than for those captured via other  
581 fishing methods (e.g. free-swimming schools). These authors concluded that by aggregating  
582 small-sized SKJ, YFT, and BET, DFADs enhance their vulnerability to predators such as  
583 sharks and billfishes, and thus increase natural mortality of small sized tunas. The foraging

584 arena theory (Ahrens et al. 2012), considers that individuals alternate between vulnerable  
585 and invulnerable states, being only part of their time available to their predators. If the risk of  
586 being predated increases when associated with a FOB, by increasing the time they spend  
587 associated, DFADs could increase the time tropical tuna spend in a “vulnerable” state which  
588 would increase their mortality by predation. To date, the study by Hunsicker et al. (2012) is  
589 the only study assessing the impact of DFADs on tuna vulnerability to predators, hence  
590 additional data from other regions would be needed for further testing these assumptions.

### 591 *Effects on body condition*

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

612 reflect normal variations and does not necessarily imply detrimental physiological  
613 consequences, or (2) some specific areas where NLOGs have always been in high numbers  
614 could also have negatively impacted the condition of tunas that passed through and stayed in  
615 these areas.

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

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



640 *Effects on reproduction and growth*

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

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

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

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

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

680 DFADs have been representing one of the key management priorities and challenges of  
681 tRFMOs over the last decade. Since fishers started using them, DFADs numbers  
682 continuously increased until first management measures limiting the number of operational  
683 buoys were adopted in the mid-2010s (Song & Shen 2022). The massive use of DFADs in all  
684 oceans has been generating major concerns on the sustainability of this fishing mode.  
685 DFADs increase the catchability of tropical tunas leading to large catches of small BET and  
686 YFT (Dagorn et al., 2013b; Fonteneau et al., 2013), generate more bycatch, including  
687 vulnerable species such as some shark species, silky (*Carcharhinus falciformis*) and oceanic  
688 whitetip (*Carcharhinus longimanus*) sharks (Dagorn et al., 2013b; Fonteneau et al., 2013;  
689 Leroy et al., 2013), and can strand on coastal areas causing damage to marine habitats  
690 (Imzilen et al., 2021; Maufroy et al., 2015, Escalle et al. 2019). Although there is increasing  
691 knowledge and literature on DFADs, the issue of their impacts on tuna natural mortality and  
692 reproductive potential remains an open scientific question. Several pieces of evidence  
693 demonstrate that DFADs increase tuna catchability, increasing their fishing mortality (Davies  
694 et al. 2014; Wain et al. 2021). However, if impacts on tuna natural mortality and reproductive  
695 potential were to be demonstrated at the population level, DFAD impacts could be even  
696 greater. Furthermore, these impacts, added to the increase of fishing mortality, could have

697 cumulative effects on tuna populations. All knowledge collected and reviewed on the  
698 behaviour and life-history parameters of tunas at DFADs clearly reveals a lack of converging  
699 scientific results on the long term consequences on tuna (at the individual and/or population  
700 levels) of increased numbers of floating objects. Therefore, if DFADs seem to affect the  
701 short-term condition of tropical tunas, we are not currently able to conclude whether DFADs  
702 affect the movements and/or other life-history parameters of tunas in a way that could  
703 significantly affect the fitness of individuals and the demography of their populations. As  
704 such, there is a need to improve our observation and understanding of this associative  
705 phenomenon to determine with certainty the impacts of DFADs on the life-history parameters  
706 and behaviour of tropical tuna, quantify the magnitude of these impacts and provide  
707 evidence-based advice.

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

723 Another research priority is to develop experimental studies to identify the biological and  
724 behavioural processes involved in tuna associative behaviour. The only scientific consensus  
725 is the fact that in a given area, conditions of tunas associated with floating objects often

726 seem to be lower than those of fish in free-swimming schools. However, the different  
727 indicators used to assess tuna condition are not always well correlated (Sardenne et al.  
728 2016), and experimental studies are needed to validate them against proper benchmarks,  
729 allowing to determine how representative they are of individuals' health. Then, understanding  
730 how fast these indicators change with the fish's associative behaviour appears essential.  
731 This could also be achieved through studies on captive tropical tunas (e.g., Estess et al.  
732 2017), but non-lethal observations should be promoted (e.g. BIA) in order to track changes  
733 throughout the fish lifespan. No evidence exists suggesting whether the lower condition at  
734 DFADs is the consequence or the cause of their association with DFADs. Often the  
735 robustness of the findings of investigation on the life-history parameters of tunas is hampered  
736 by the lack of knowledge of the time spent associated with a DFAD or in an array of DFADs  
737 by each specimen analysed. The history of each individual tuna is a hidden variable that  
738 must be taken into account in statistical analyses, which is a challenge. Studies combining  
739 behavioural observations (tagging) and condition of the individuals (e.g. BIA or biochemical  
740 analyses of biopsies made at the time of tagging) should then be encouraged. Ideally, tags  
741 equipped with physiological sensors would clearly help understanding the interplay between  
742 associative behaviour and tuna physiology. Such tags, however, are only starting to be  
743 developed.

744 Studies on AFADs could provide insights to the questions addressed in this manuscript: as  
745 argued by Dagorn et al. (2010), AFADs also alter the natural environment (by adding floating  
746 objects to the ocean). However, it remains questionable if they are comparable due to the  
747 fact that AFADs are generally located nearshore, with corresponding particular  
748 oceanographic conditions, and they do not move with water masses. Papua New Guinea, the  
749 Philippines and Indonesia are examples of areas with very high numbers of AFADs (Proctor  
750 et al. 2019) and as such, these dense arrays of AFADs could generate the same concerns  
751 on tuna life-history parameters and behaviour that those described for DFADs.  
752 Understanding the behaviour of tunas around AFADs can also improve our general  
753 understanding of tunas around all types of floating objects and help design new, well focused  
754 studies for DFADs. For practical reasons, more studies have been performed on the

755 behaviour of tuna at AFADs than at DFADs (e.g. Dagorn et al., 2007; Govinden et al., 2013;  
756 Holland et al., 1990; Ohta & Kakuma, 2005; Rodriguez-Tress et al., 2017). They provided  
757 estimates of residence times between two AFAD associations and therefore of the  
758 percentage of time spent associated to AFADs (e.g. Pérez et al., 2020; Robert et al., 2013b;  
759 Rodriguez-Tress et al., 2017), which still needs to be further explored at DFADs. For  
760 example, Pérez et al. (2020) used acoustic tagging data on AFAD arrays to demonstrate that  
761 when inter-AFAD distance decreases, tuna visit more AFADs, spend less time travelling  
762 between AFADs and more time associated with them. Concerning DFADs, as actual  
763 densities of drifting floating objects are difficult to obtain, studies using a modelling approach  
764 based on experimental data should be promoted (Pérez et al. 2022, Capello et al. 2023).  
765 These studies should investigate the consequences of changes in floating object density on  
766 tuna school sizes and associative behaviour. These modelling studies could be  
767 complemented and/or calibrated by studies which use data from echosounder buoys  
768 deployed by fishers on floating objects. Recent methodological advances allowed the  
769 prediction of tuna presence or absence under FOBs (Baidai et al., 2020; Orue et al., 2020).  
770 Using an extensive dataset from echosounder buoys in the WCPO (more than 3.8 million  
771 transmissions), Escalle et al. (2021c) determined different profiles of acoustic signals related  
772 to different types of aggregations. Other studies also show that multi-frequency echosounder  
773 buoys could allow the discrimination of tropical tuna species under DFADs (Moreno et al.  
774 2019, Sobradillo et al. 2023). These new methodological developments, in combination with  
775 tagging data, both conventional and electronic, and modelling approaches offer promising  
776 perspectives for the study of tuna aggregation behaviour under FOBs and the potential  
777 impact of DFAD density on tuna schooling behaviour.

778 Tuna RFMOs set limits on the number of operational buoys (IATTC: up to 340 depending on  
779 the vessel size, Res C-21-04; ICCAT: 300 in Rec 22-01; IOTC: 300 in Res 19/02; WCPFC:  
780 350 in CMM 2021-01). These limits are essentially set to control the fishing effort and the  
781 catches of tunas and non-target species, hence to control fishing mortality. How such limits  
782 also act on the number of deployed DFADs and the potential impacts of DFADs on tuna's  
783 natural mortality, is unknown. In theory, all purse seine vessels could use at least the same

784 amount of DFADs than the maximum number of operational buoys authorized in each of the  
785 regions. Multiplying this maximum number of operational buoys authorized per vessel by the  
786 number of large-scale purse seine vessels in each ocean provides a global authorized limit of  
787 about 238,000 operational buoys (details of the calculation in Supplementary Materials 1).  
788 This number is about twice higher than the estimate of the global number of DFADs  
789 deployments made by Gershman et al. (2015), based on data from 2013. Hence, it would  
790 mean that the global purse seine fishery could have increased the number of DFADs in the  
791 ocean while still respecting the current limits on the number of active buoys. Most tRFMOs  
792 now require that DFAD identification, characteristics, deployment date and deployment  
793 location are reported (e.g. ICCAT Rec 22-01; IOTC Res. 19/02; IATTC C-21-04). Some  
794 studies evidenced different regional trends of DFAD deployments (IOTC, 2022, Escalle et al.  
795 2020, Lopez et al. 2021, Floch et al., 2019; Maufroy et al., 2017), but no study assessed this  
796 trend on a global scale after 2013 (Gershman et al., 2015). Tuna RFMOs should continue to  
797 collect and make fine-scale DFAD data available to scientists to allow regular estimations of  
798 the extent of the habitat modifications generated by DFADs, which should be addressed at a  
799 global scale.

## 800 **Conclusion**

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

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

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

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

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

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

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833 Access, a CC-BY public copyright licence has been applied by the authors to the present  
834 document and will be applied to all subsequent versions up to the Author Accepted  
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836 **Data availability statement**

837 Data used in the supplementary material were obtained from Justel-Rubio et al. (2023) and  
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1381 **Tables**

1382 **Table 1: Summary of main findings from previous studies on the numbers of**  
 1383 **monitored floating objects or the number of DFADs used in large-scale tropical tuna**  
 1384 **purse seine fisheries.**

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

Indian Ocean	2003-2005	Daily active buoys	45 vessels	2,100	Moreno et al. (2007)
	2007-2013	Monthly 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)

1385 **Table 2: Summary of main findings from previous studies on tuna individual CRT and CAT assessed under anchored and drifting FADs.**  
 1386 CRT: Continuous Residence Time – continuous bouts of time spent at the same FAD without any absence longer than 24h. CAT: Continuous Absence  
 1387 Time – the time between two associations with a FAD. FL: fork length, YFT: *Thunnus albacares*, SKJ: *Katsuwonus pelamis*, BET: *Thunnus obesus*).

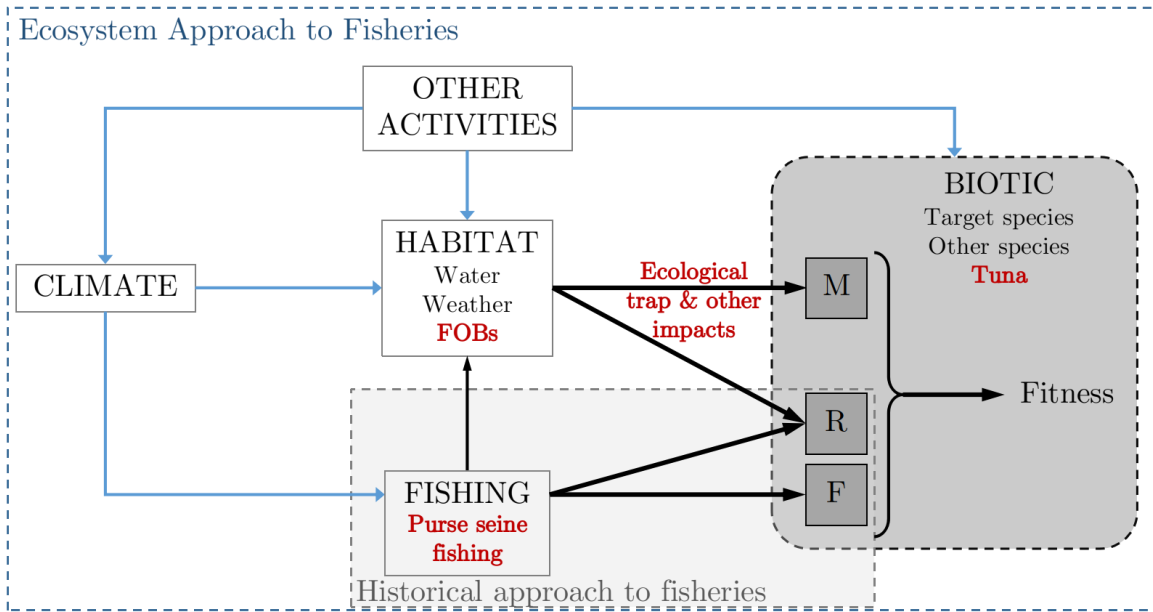
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FAD type	Study location	Metric	Findings	Reference
Drifting	Eastern Atlantic Ocean	CRT	YFT (34-82 cm FL): average of 19.15 days (maximum value of 55 days) SKJ (39-61 cm FL): average of 9.19 days (maximum value of 15 days) BET (45-61 cm FL): average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



(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)

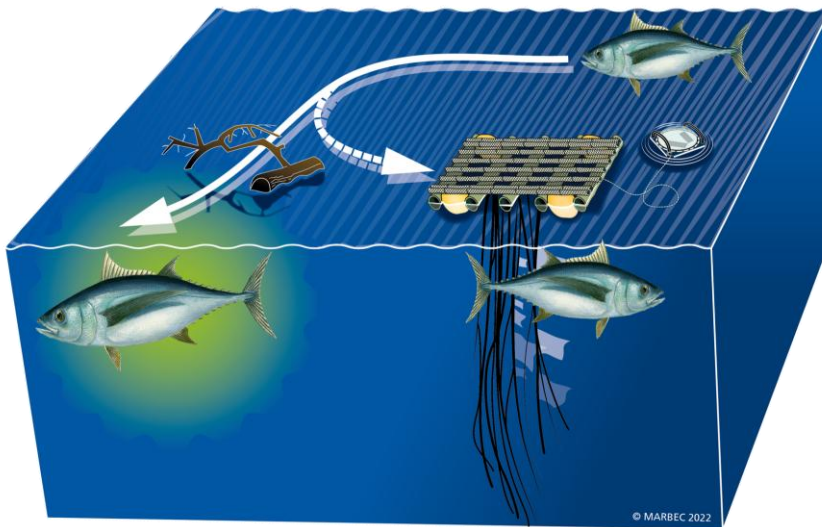
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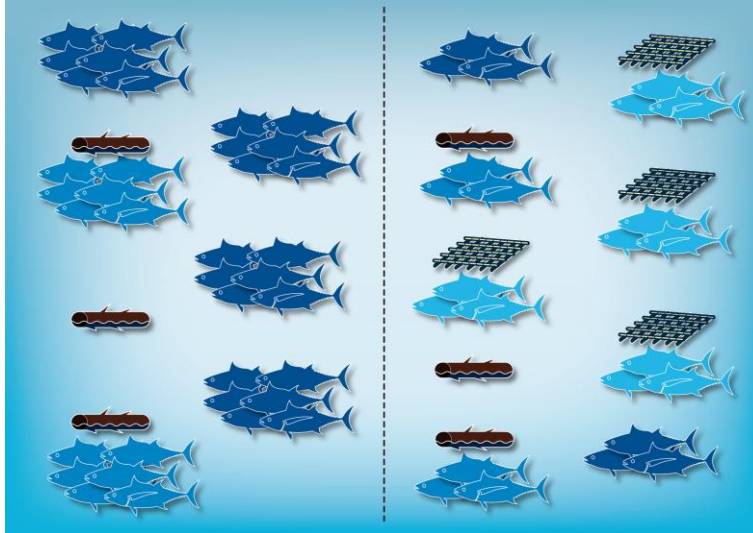
1395 **Figure 1: Drifting Fish Aggregating Devices impacts on tropical tuna natural mortality**  
 1396 **and reproductive potential in the framework of the Ecosystem Approach to Fisheries.**  
 1397 Words in red refer to the specific case study developed in this paper. FOB: floating object;  
 1398 M: Natural mortality; R: Reproductive potential; F: Fishing mortality.

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1400 **Figure 2: Schematic representation of the ecological trap hypothesis applied to**



1401 **Drifting Fish Aggregating Devices (DFADs), as originally formulated.** Under this  
1402 hypothesis, before DFADs introduction, when only natural floating objects (NLOGs) were  
1403 present, floating objects were indicators of productive areas. Hence, by associating with  
1404 floating objects, tuna selected high quality habitats. DFAD massive deployment modified  
1405 the distribution of floating objects (FOBs), which are not representative of rich areas  
1406 anymore. By associating with FOBs, tunas can be attracted to or retained in habitats of  
1407 lesser quality.



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