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Schooling in habitats with aggregative sites: the case of tropical tuna and floating objects

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Abstract :

Many marine and terrestrial species live in groups, whose sizes and dynamics can vary depending on the type and strength of their social interactions. Typical examples of such groups in vertebrates are schools of fish or flocks of bird. Natural habitats can encompass a wide range of spatial heterogeneities, which can also shape the structure of animal groups, depending on the interplay between the attraction/repulsion of environmental cues and social interactions. A key issue in modern applied ecology and conservation is the need to understand the relationship between these ethological and ecological scales in order to account for the social behaviour of animals in their natural environments. Here, we introduce a modeling approach which studies animal groups within heterogeneous habitats constituted by a set of aggregative sites. The model properties are investigated considering the case study of tropical tuna schools and their associative behavior with floating objects, a question of global concern, given the thousands of floating objects deployed by industrial tropical tuna fisheries worldwide. The effects of increasing numbers of aggregative sites (floating objects) on tuna schools are studied. This study offers a general modeling framework to study social species in their habitats, accounting for both ethological and ecological drivers of animal group dynamics.

Highlights

- ▶ We develop a model to assess the impacts of human-induced habitat modifications on social animals.
- ▶ The model accounts for the interplay of increasing numbers of habitat heterogeneities on animal groups.
- ▶ The model properties are investigated considering the case study of tropical tuna schools.
- ▶ This study offers a general modeling framework to study social species in their habitats.
- ▶ This approach can accounts for both ethological and ecological drivers of animal groups dynamics.

Keywords : Animal groups, heterogeneous habitats, aggregations, associative behavior, schooling, tropical tuna.

28 **1. Introduction**

29 Animal groups can follow different levels of organization, from aggregations of insects to
30 schools of fish and flocks of birds (Costa, 2006; Krause, J., & Ruxton, 2002). Generally, living
31 in groups provides various advantages to animals, like higher reproductive rates (Allee,
32 1931), a reduction in predation due to both the dilution/confusion effect (Turner and
33 Pitcher, 1986) and the "many-eyes" effect (Pulliam, 1973; Roberts, 1996), increased foraging
34 success (Galef & Giraldeau, 2001), stress reduction in unfavorable situations (Allen et al.,

35 2009) or access to mutualistic endosymbiotic microbes (Lombardo, 2008). Conversely, the
36 presence of many individuals within the same group can also be deleterious, by facilitating
37 detection by predators (Ioannou, 2017), promoting disease or parasite transmissions
38 (Patterson & Ruckstuhl, 2013) and leading to increased competition for food (Rubenstein,
39 1978). Accordingly, the size of animal groups are often considered a result of trade-offs
40 between these factors (Ioannou, 2017; Krause, J., & Ruxton, 2002; Rubenstein, 1978).

41 At a larger scale, groups of animals share a given habitat with their congeners and the other
42 species (Goodale et al., 2017). Any natural habitat presents a certain degree of spatial
43 heterogeneity, e.g., an uneven spatial distribution of resources, variable environmental
44 conditions and/or spatial cues, which can affect their local structure and attractiveness
45 (Levin, 1992; Vinatier et al., 2011). This local habitat structure can have multiple impacts on
46 animal groups, by increasing their tendencies to disperse or gather together, depending on
47 the local properties of the habitats and their functional interest (Hart et al., 2020; Maeno &
48 Ebbe, 2018; Rahmani et al., 2020; Schmidt, 1982). However, while the effects of habitat
49 heterogeneities on the diversity of animal species have been widely studied (Tews et al.,
50 2004), little is known regarding their effects on the structure and dynamics of animal groups
51 (Rahmani et al., 2020).

52 An aggregation is defined as a gathering of individuals leading to a local density greater than
53 that of neighboring regions (Camazine et al., 2001). This phenomenon, referred to as
54 associative behavior, is present as much in bacteria or other unicellular organisms as in
55 arthropods or vertebrates (Parrish & Edelstein-Keshet, 1999). Aggregations can either be
56 explained exclusively through the local attractiveness of an environment or to social
57 interactions (Camazine et al., 2001). The former results from the sum of individual
58 responses to an external stimulus, whereas the latter is based on individual responses but
59 also on interactions between individuals. These two mechanisms leading to animal
60 aggregations are not mutually exclusive: very often, social interactions are influenced by
61 surrounding environmental cues. Aggregations of social animals can then be defined as a
62 gathering of individuals in the same place who interact with each other via the perception of
63 stimuli of varying nature from other individuals (e.g., sounds, vocalisms or visual cues)

64 and/or by local modifications of the environment (e.g., chemical marking, garbage, or trail
65 creation).

66

67 Several terrestrial and marine species simultaneously manifest such aggregative behavior
68 and collective group dynamics (Camazine et al., 2001; Parrish & Edelstein-Keshet, 1999). A
69 typical example of such behavior is shown by starlings, which can form large congregations
70 on trees and collective flocking behavior (Cavagna et al., 2009; Lyon & Caccamise, 1981).
71 The same behavior is also found in several fish species and more particularly in tropical
72 tunas, which can form large schools of several thousand individuals and also aggregate
73 around floating objects found at the sea surface (Fréon & Dagorn, 2000).

74

75 Tuna fisheries provide global yields of about 7 millions tonnes and feature among the
76 world's most important fisheries (FAO, 2020). Tropical tunas (yellowfin tuna - *Thunnus*
77 *albacares*, bigeye tuna - *Thunnus obesus* and skipjack tuna - *Katsuwonus pelamis*)
78 contribute to more than 90% of the major global tuna catches (ISSF, 2020). Skipjack tuna,
79 with a catch exceeding 3 millions tonnes in 2018, being the third highest marine species in
80 terms of total yield, following only Peruvian anchoveta (*Engraulis ringens*) and Alaska
81 pollock (*Gadus chalcogrammus*) (FAO, 2020). Tuna captured around floating objects account
82 for approximately half of the global tuna catch (Dagorn et al., 2013). The recent introduction
83 of thousands of artificial floating objects in the open ocean (termed Fish Aggregating
84 Devices or FADs) by industrial fisheries, has resulted in numerous questions on their impacts
85 on the size of tuna schools (Sempo et al., 2013), as well as their potential risk of forming an
86 ecological trap (Dagorn et al., 2013; Hallier & Gaertner, 2008; Marsac et al., 2000). These
87 ecological impacts brought on by the large-scale exploitation of FADs across all oceans
88 require the development of quantitative tools to study the effects of increasing FAD
89 numbers on tuna schools and, more globally, on the populations of pelagic fish species that
90 associate with them.

91

92 A wide variety of movement rules have been proposed to explain the formation and
93 dynamics of animal groups (Ballerini et al., 2008; Bialek et al., 2012; Herbert-Read, 2016;
94 Vicsek & Zafeiris, 2012). In particular, several models of fish schools have been developed in
95 the past (Lopez et al., 2012). Alternatively, ecologically-relevant parameters, such as the

96 amount of habitat heterogeneities, and the consequent associative behavior of animals
97 forming aggregations induced by these heterogeneities, have so far been neglected when
98 modeling animal group dynamics. Only a small number of recent studies have modeled
99 flocking behavior in complex environments considering repulsive environmental cues and
100 their consequences on the group-level coordination (Rahmani et al., 2020). Conversely,
101 ecological models tend to neglect the behavioral drivers which can affect species abundance
102 and distribution (Geary et al., 2020). The main reason for this theoretical partitioning
103 between ethological and ecological models can be related to the different spatial scales that
104 are considered, ranging between a few centimeters/meters in ethology to several hundreds,
105 or even thousands of kilometers in ecology.

106

107 Accounting for both ethological and ecological drivers is key to assess the effects of human-
108 induced habitat modifications on social species (Dirzo et al., 2014; Hoffmann et al., 2010).
109 Here, we introduce a new modeling framework to investigate the interplay between the
110 tendency of animals to live in groups (i.e., forming schools, flocks or other self-organized
111 forms of groups) and the presence of aggregative sites in their environment (i.e.,
112 attraction/retention sites). In so doing, we demonstrate the importance of such ecological
113 parameters on the behavior of social species in natural environments. Using tropical tuna
114 schools and their associative behavior around floating objects as a case study, we consider
115 the interplay between the formation of tuna aggregations induced by the local
116 environmental properties of their habitat and their schooling dynamics.

117

118 The principal novelty of this modeling approach relies on the fact that it borders between
119 ethology and ecology, accounting for both behavioral drivers (such as the tendency of tuna
120 to form schools) and ecological drivers (heterogeneous environments formed by attractive
121 sites).

122

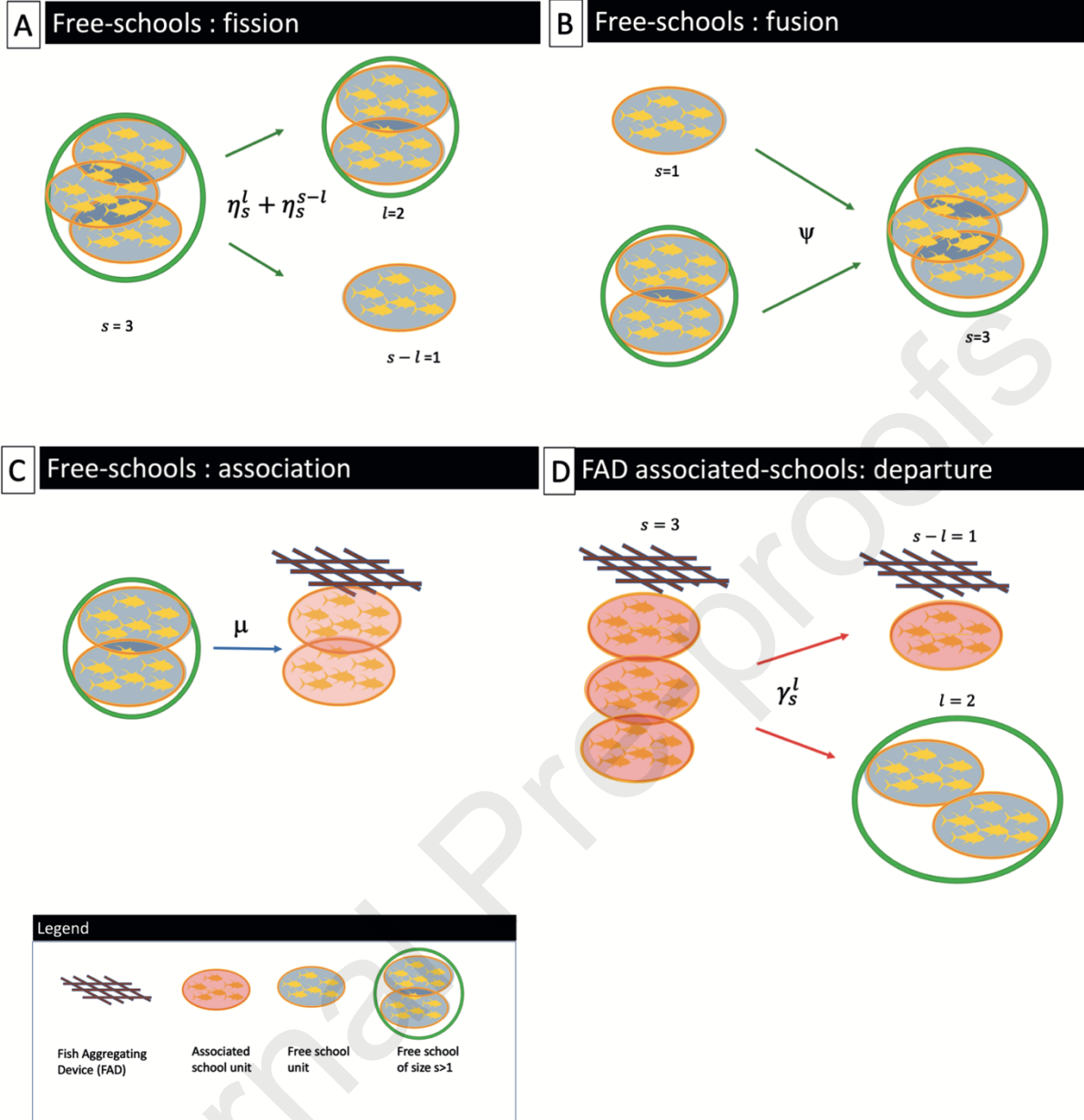
123 **2. Materials and methods**

124 **2.1 Model definition**

125 Due to tropical tunas being social species which live in schools (Fréon & Dagorn, 2000), the
126 model accounts for a set of N tuna *school units* within an array of P FADs. These school units
127 are considered to be constituted by individuals showing the same associative behavior with

128 FADs, i.e., of the same species and size category (Rodriguez-Tress et al., 2017). The P FADs
 129 represent a set of aggregative sites present in the local tuna environment, that can
 130 attract/retain them in their vicinity, thus favoring the formation of aggregations of schools,
 131 corresponding to multiple schools localized near the FAD (Fréon & Dagorn, 2000). Each tuna
 132 school can be in one of two states, either free-swimming (not associated with any of the
 133 FADs, i.e., a free-swimming school, referred to as *free school* for simplicity in the remainder
 134 of the text) or associated to one of the P FADs. Both free schools and FAD aggregations can
 135 be constituted by one or more school units, due to the interplay between fission, fusion and
 136 association processes. The resulting association dynamics can be summarized according to
 137 the following rules (Figure 1):

- 138 **A.** Fission of schools can occur in the free state. This fission dynamics is set by the
 139 probability $(\eta_s^l + \eta_s^{s-l})$ that a school of size s splits into two sub-schools of size l and
 140 $s - l$.
- 141 **B.** Fusion of two free schools can occur with probability ψ , independently of the school
 142 size.
- 143 **C.** Free schools have a probability μ to join a FAD, which is independent of their size. For
 144 each free school, the overall probability of associating with any of the P FADs is $P\mu$.
- 145 **D.** Multiple school units forming a FAD-aggregation can leave a FAD at the same time,
 146 leading to a free school of size $l > 1$. Namely, for a FAD aggregation of size s (i.e.,
 147 composed of s school units), a school of size l can depart from the FAD with probability
 148 γ_s^l , leading to a FAD aggregation of size $s - l$ and a free school of size l .



149

150 **Figure 1: Schematic view of the model. (A-C) Free-schools dynamics. (A) Fission:** a free school of size
 151 $s > 1$ can split into smaller schools of size l and $s - l$ with probability $(\eta_s^l + \eta_s^{s-l})$. **(B) Fusion:** two
 152 free schools can merge with probability ψ independent of their size. **(C) Association:** any free school
 153 have probability μ to associate with a FAD, regardless of its size. **(D) Associated-schools dynamics:** for
 154 a FAD association of size s , a school of size l can depart (forming a free school) with probability γ_s^l .

155

156 Considering $F_s(t)$ as the number of FADs occupied by s school units at time t , and $X_s(t)$ the
 157 number of free schools of size s (i.e., composed of s school units) at time t , the temporal
 158 evolution of $F_s(t)$ and $X_s(t)$ follows Eq.(1) and Eq.(2) respectively:

159

$$\frac{dF_s}{dt} = -\mu F_s \sum_{l=1}^{N-s} X_l + \sum_{l=s+1}^N F_l \gamma_l^{l-s} + (1 - \delta_{s,0}) \left(\mu \sum_{l=1}^s F_{s-l} X_l - F_s \sum_{l=1}^s \gamma_s^l \right) \quad (\text{Eq. 1})$$

$$\begin{aligned} \frac{dX_s}{dt} = & \sum_{l=s}^N F_l \gamma_l^s - \mu X_s \sum_{l=0}^{N-s} F_l + \sum_{l=s+1}^N (\eta_l^s + \eta_l^{l-s}) X_l - (1 - \delta_{s,1}) X_s \sum_{l=1}^{s-1} \eta_s^l + \\ & - \psi X_s \sum_{l=1}^{N-s} (1 + \delta_{s,l}) X_l + \psi \sum_{l=1}^{s-1} \frac{(1 + \delta_{s-l,l})}{2} X_l X_{s-l} \end{aligned} \quad (\text{Eq.2})$$

with conservation of total number of FADs (P) and the total number of schools (N):

$$\sum_{s=0}^N F_s = P; \quad \sum_{s=1}^N s (F_s + X_s) = N. \quad (\text{Eq.3})$$

In the above equations, the δ symbol represents the Kronecker delta, namely $\delta_{i,j} = 1$ if $i = j$ and 0 otherwise. The terms in Eqs.(1-2) that depend on μ and γ_s^l are related to the FAD association dynamics, representing the association and departure of schools to/from FADs respectively. The probability per unit time for a free school (of any size) to associate with one FAD is represented by μ . Similarly, γ_s^l corresponds to the probability per unit time that a school of size l departs from a FAD aggregation of size s . In Eq.(2), the number of free schools of size s depends on the association and departure of free schools from FADs (terms in μ and γ_s^l , respectively, similar to Eq.(1)) and on the free school fusion and fission dynamics (terms in ψ and η_s^l , respectively). The two terms in $(\eta_l^s + \eta_l^{l-s})$ and η_s^l are related to the fission of free schools. Similarly to γ_s^l , the term η_s^l corresponds to the probability per unit time that a school of size l splits from a larger school of size s . The term in $(\eta_l^s + \eta_l^{l-s})$ corresponds to the overall fission probability per unit time for a free school of size l to split into two sub-schools, respectively of size s and $l - s$. The sum $(\eta_l^s + \eta_l^{l-s})$ is explained by the fact that two possible events can lead to a fission of school (of size l) into its

186 subcomponents s and $l - s$: either a school of size s splits from the larger school of size l
 187 with probability η_l^s , or a school of size $l - s$ splits with probability η_l^{l-s} . Finally, the free
 188 school fusion dynamics is set by the constant ψ , which corresponds to the probability per
 189 unit time that two schools (of any size) merge together forming a larger school.

190 In this study, the following definition of FAD-departure probabilities γ_s^l was considered:

$$191 \quad \gamma_s^l = s \theta B(l - 1; s - 1, \beta_{agg})$$

193 (Eq.4)

194 where θ represents the probability of departure, per unit time, for an individual school unit
 195 and $B(l - 1; s - 1, \beta_{agg})$ is the binomial probability mass function:

$$197 \quad B(l - 1; s - 1, \beta_{agg}) = \binom{s - 1}{l - 1} \beta_{agg}^{l-1} (1 - \beta_{agg})^{s-l}$$

198 (Eq.5)

199 where the term $\binom{s - 1}{l - 1}$ is the binomial coefficient. (Eq.5) represents the probability for
 200 $l - 1$ school units (with the $s - 1$ forming the remaining of the FAD aggregation) to join the
 201 departing school (leading to a free school of size l). The constant β_{agg} corresponds to the
 202 binomial probability of success, namely the probability for a FAD-associated school unit to
 203 follow the departing school. For a FAD aggregation of size s , Eq.(4) implies that each
 204 associated school unit has a probability of departure equal to $\theta (1 + (s - 1) \beta_{agg})$, namely,
 205 a school being part of large FAD aggregations has higher probabilities to leave the FAD. The
 206 average size of the school leaving the FAD is $1 + (s - 1) \beta_{agg}$. In the limit $\beta_{agg} \rightarrow 0$, for each
 207 time step, only individual school units ($s = 1$) can leave the FAD. Oppositely, for $\beta_{agg} \rightarrow 1$,
 208 the whole aggregation departs from the FAD, resulting in associated schools behaving as a
 209 single unit.

210 In the same way, the following probability η_s^l was considered for a school of size l to split
 211 from a larger school of size s :

$$212 \quad \eta_s^l = s \phi B(l - 1; s - 1, \beta_{school})$$

214 (Eq.6)

215

216 where ϕ represents the fission probability, per unit time, for an individual school unit (i.e.,
 217 the probability that a single school unit splits from the school) and $B(l-1; s-1, \beta_{school})$ is
 218 the binomial probability mass function that follows the same definition as in Eq.(5) above. In
 219 this case, the constant β_{school} corresponds to the binomial probability for another school
 220 unit to follow the school that split. In the limit $\beta_{school} \rightarrow 0$, only individual school units can
 221 split. Conversely, for $\beta_{school} \rightarrow 0.5$, free schools split, in average, into two sub-schools of the
 222 same size.

223

224 2.2 Model configuration

225 The sets of model parameters that were studied are summarized in Table 1. The
 226 probabilities of departure/arrival from/to a FAD (θ and μ) were fixed to 0.1 days^{-1} and 0.01
 227 days^{-1} respectively. The choice of the probabilities θ and μ respectively affect the residence
 228 times (the time schools spend associated with a FAD) and the absence times (the time spent
 229 between two FAD association, in the free state) which can be measured through electronic
 230 tagging (Capello et al., 2015). For a non-social model defined in an array of 10 FADs, these
 231 parameters imply average residence times and absence times of 10 days. Here, the choice
 232 of the model parameters θ and μ aimed at ensuring average residence and absence times of
 233 the same order of magnitude of those observed in past electronic tagging studies (Govinden
 234 et al., 2013, 2021; Robert et al., 2013; Rodriguez-Tress et al., 2017; Tolotti et al., 2020).
 235 These parameters were kept fixed, in order to study the model sensitivity to other
 236 parameters, whose ranges of values are unknown. For this purpose, a range of parameter
 237 values were tested for both the social interaction parameter at the FAD (β_{agg}) and the
 238 school fission and fusion probabilities (ϕ and ψ), resulting in five main model configurations
 239 (Table 2). The effects of social interactions at the FADs were studied considering three
 240 different values of β_{agg} :

- 241 - $\beta_{agg} = 0$, resulting in individual school units departing from FADs independently of
 242 each other (Non-social (NS)).
- 243 - $\beta_{agg} = 0.5$, resulting, in average, in half of the aggregation leaving the FADs
 244 simultaneously (Social (S)).
- 245 - $\beta_{agg} = 1$, resulting in the collective departure of the full aggregation from the FADs
 246 (Highly Social (HS)).

247 Because the NS model considers independent school units, the effects of the schooling
 248 dynamics were considered for the social models only. First, only the effect of school fission
 249 was studied, leading to models S+f and HS+f (Table 2). Secondly, both the fission and fusion
 250 parameters were considered, leading to models S+ff and HS+ff, see Table 2. In the school-
 251 fission process, the β_{school} parameter was kept fixed at 0.5, considering that the most likely
 252 fission process corresponded to a breakup of a school into two sub-schools of the same size.
 253 Finally, the model properties were studied for increasing numbers of tuna school units and
 254 FADs (Table 1).

255

256 2.3 Numerical resolution of the model

257 The mean-field equilibrium solutions of the model defined through Eqs.(1-2) and Table 2
 258 were numerically derived using the Euler method. Initial conditions were set considering all
 259 tuna schools in the free state ($F_s(0) = 0$, for any s) and all free schools corresponding to a
 260 school unit ($X_1(0) = N$). The Euler method was applied considering a time step $\Delta t = 0.01$
 261 days over a total of 50,000 time steps to ensure equilibrium (Supplementary Figures S1 and
 262 S2).

263

PARAMETER	DESCRIPTION	TESTED VALUES
N	Total number of tuna school units	5, 10, 20, 40, 60, 80, 100
P	Total number of FADs	1, 2, 5, 10, 20, 30, 40, 50
μ	Probability per unit time ($days^{-1}$) to associate with one FAD	0.01
θ	Probability per unit time ($days^{-1}$) of departure from FADs	0.1
β_{aggr}	Binomial probability of joint departure from FADs	0 (Non-social) 0.5 (Social) 1.0 (Highly social)
ϕ	Fission probability per unit time ($days^{-1}$)	0 (no fission), 0.01 (fission)
β_{school}	Binomial probability of joint fission	0.5
ψ	Fusion probability per unit time ($days^{-1}$)	0 (no fusion), 0.01 (fusion)

264 **Table 1: Model parameters.**

265

Binomial probability of joint departure from FADs (β_{aggr})

		$\beta_{agg} = 0$	$\beta_{agg} = 0.5$	$\beta_{agg} = 1.0$
School fission-fusion dynamics (ϕ, ψ)	$\phi = 0$ $\psi = 0$	Non-social (NS)		
	$\phi = \mu$ $\psi = 0$		Social + fission (S+f)	Highly Social + fission (HS+f)
	$\phi = \mu$ $\psi = \mu$		Social + fission + fusion (S+ff)	Highly Social + fission + fusion (HS+ff)

266 **Table 2. Summary of the five model configurations.** Non-social (NS, $\beta_{agg} = 0$, $\phi = 0$; $\psi = 0$); Social
 267 with fission (S+f, $\beta_{agg} = 0.5$, $\phi = 0.01$; $\psi = 0$); Highly Social with fission (HS+f, $\beta_{agg} = 1.0$, $\phi = 0.01$;
 268 $\psi = 0$). Social with fission and fusion (S+ff, $\beta_{agg} = 0.5$, $\phi = 0.01$; $\psi = 0.01$); Highly Social with fission
 269 and fusion (HS+ff, $\beta_{agg} = 1.0$, $\phi = 0.01$; $\psi = 0.01$). The other parameters are the same for all models,
 270 see Table 1.

271

272 2.4 Model properties

273 A set of metrics was defined to characterize tuna free schools and FAD aggregations. Two
 274 metrics were estimated to characterize free schools:

275 i. The total number of free schools (NFS), defined as $NFS(t) = \sum_s X_s(t)$.

276 ii. The mean size of free schools ($FS_{size}(t) = \frac{\sum_s s X_s(t)}{\sum_s X_s(t)}$)

277 Similarly, two metrics were estimated to characterize FAD aggregations:

278 i. The mean size of a FAD aggregation (m), defined for the FADs occupied by at least one

279 school, $m(t) = \frac{\sum_{s=1}^N s F_s(t)}{\sum_{s=1}^N F_s(t)}$.

280 ii. The fraction of FADs occupied by at least one school unit ($f1$), defined as $f1(t) =$

281 $\frac{\sum_{s=1}^N F_s(t)}{P}$.

282 Finally, the relative number of associated schools over the full FAD array ($F_a(t)/N = \frac{1}{N}$

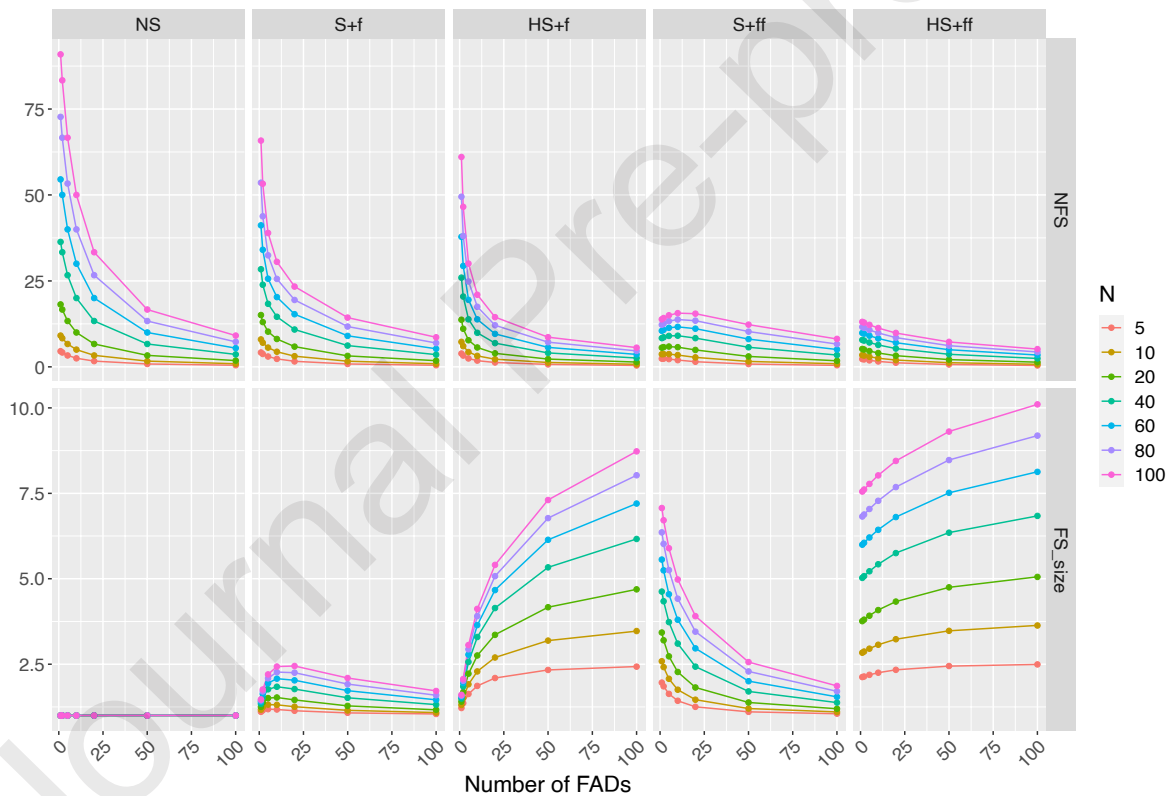
283 $\sum_{s=1}^N s F_s(t)$) was estimated. For each combination of model parameters, each metric was

284 calculated at equilibrium (stationary states: $\forall s \leq N: \frac{dF_s}{dt} = 0; \frac{dX_s}{dt} = 0$).

285

286 3. Results

287 Globally, the free-swimming school metrics (Figure 2) show larger school sizes and larger
 288 numbers of free schools for increasing population sizes, but very different trends relative to
 289 the number of FADs, depending on the model configuration. The average number of free
 290 schools follows a decreasing trend with the number of FADs for the non-social model (
 291 $NFS = \theta N / (P\mu + \theta)$). Similar trends are found for the social models with fission (S+f and
 292 HS+f). Conversely, in the case of model S+ff, the number of free schools shows a non-
 293 monotonic trend, first increasing with the number of FADs, then reaching a maximum and
 294 then decreasing. Finally, for model HS+ff; the number of free schools is higher for smaller
 295 FAD numbers, then decreases monotonically with the number of FADs and is globally
 296 smaller than the other models.

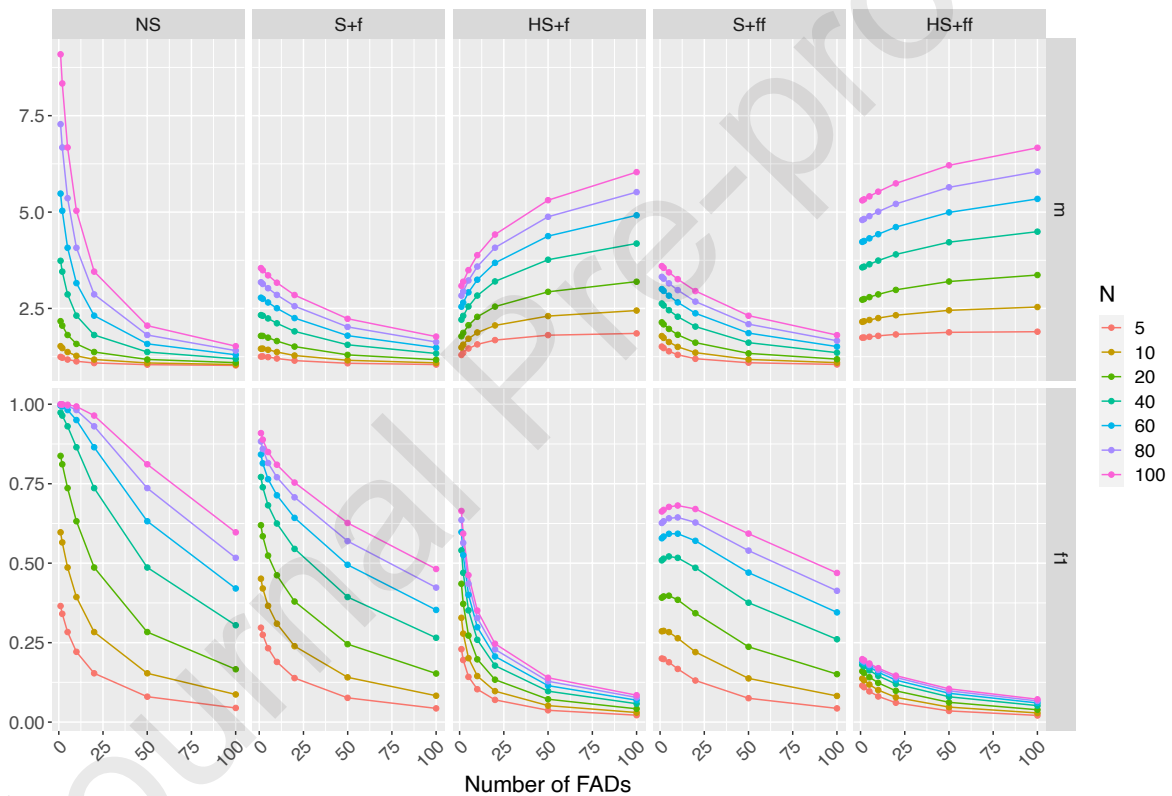


297

298 **Figure 2. Free-swimming school metrics.** Number of free-swimming schools (NFS) and average size
 299 of the free schools (FS_{size}) as a function of the number of FADs for different population sizes
 300 (colors). Each column represents a model configuration: Non-social (NS); Social with fission (S+f);
 301 Highly Social with fission (HS+f); Social with fission and fusion (S+ff); Highly Social with fission and
 302 fusion (HS+ff).

303

304 The average size of free schools (FS_{size}) is, by construction, equal to 1 for model NS. Larger
 305 average school sizes are found for all social models, with different trends relative to the
 306 number of FADs, depending on the model configuration. Remarkably, increasing free school
 307 sizes are found for increasing FAD numbers for both highly-social models HS+f and HS+ff,
 308 with the HS model with fusion and fission producing the larger school sizes. Alternatively,
 309 the social model with fission (S+f) shows a non-monotonic trend, with average school sizes
 310 first increasing with the number of FADs, then attaining a maximum and finally decreasing.
 311 Finally, when a fusion term is added to this model (S+ff) decreasing school sizes are found
 312 for increasing numbers of FADs.
 313



314
 315 **Figure 3. FAD aggregation metrics.** Average number of school units associated with the FADs that
 316 are occupied by at least one school (m) and fraction of FADs occupied by at least one school (f_1)
 317 as a function of the number of FADs (abscissa) for different population sizes (colors). Each column
 318 represents a model configuration : Non-social (NS); Social with fission (S+f); Highly Social with fission
 319 (HS+f); Social with fission and fusion (S+ff); Highly Social with fission and fusion (HS+ff).

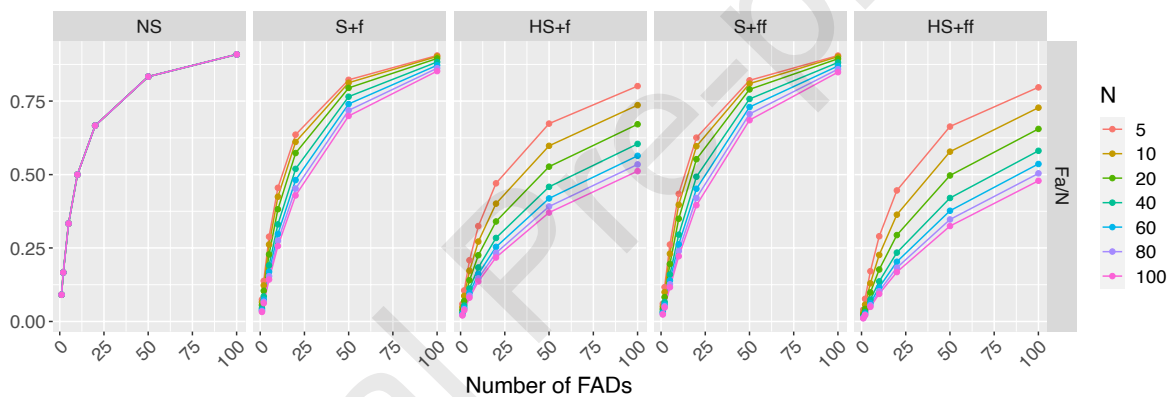
320
 321 The average size of FAD aggregations (m , Figure 3) show global increasing trends for larger
 322 population sizes. The social models, both with fission and fission+fusion (S+f and S+ff) show

323 decreasing trends of FAD aggregation sizes for larger number of FADs, as found for the non-
 324 social model, but relatively smaller aggregation sizes for small number of FADs. Conversely,
 325 both highly-social models (HS+f and HS+ff) demonstrate an opposite trend, with average
 326 aggregation sizes increasing for increasing numbers of FADs.

327

328 The fraction of FADs occupied by at least one school unit (f_1 , Figure 3) shows a general
 329 decrease with the number of FADs and is larger for larger populations. However, model S+ff
 330 show a non-monotonic trend, with f_1 having a clear maximum for larger population sizes.
 331 Moreover, the highly-social models with fission and fission+fusion (HS+f and HS+ff)
 332 demonstrate the highest and lowest sensitivity of f_1 relative to the number of FADs
 333 respectively, while the size of the population appears less important.

334



335

336 **Figure 4. Relative number of associated schools.** Ratio between the number of FAD-associated
 337 school units and the total number of school units, as a function of the number of FADs (abscissa) for
 338 different population sizes (colors). Each column represents a model configuration : Non-social (NS);
 339 Social with fission (S+f); Highly Social with fission (HS+f); Social with fission and fusion (S+ff); Highly
 340 Social with fission and fusion (HS+ff).

341

342 Finally, the fraction of associated schools (F_a/N , Figure 4) increases with the number of
 343 FADs for all models. However, differences between social models and the non-social model
 344 exist. Increasing trends of F_a/N , independent of the population size, are found for the non-
 345 social model (NS), whereas, for all social models, larger populations imply smaller fractions
 346 F_a/N . This effect is amplified in the highly social models (HS+f and HS+ff).

347

348 Figures S3 and S5 show the equilibrium distribution of F_s and X_s , respectively. The
349 distribution of F_s appears to be zero-inflated for the social models, particularly for the
350 highly social configurations (Figure S3-4). The trends of X_s in semi-logarithmic and
351 logarithmic scale (Figures S6 and S7, respectively) demonstrate that the distribution of
352 school sizes follows an exponential decay. The mean-to-variance relations of F_s (Figure S8)
353 are equidispersed for the NS model and for social models with small population sizes or
354 large numbers of FADs. Reversely, for social models with large population sizes/small
355 numbers of FADs the distributions of F_s show an overdispersion, with different trends
356 relative to the number of FADs, depending on the model (Figure S8). Similarly,
357 overdispersed free-school size distributions (X_s) characterize social models with large
358 population sizes (Figure S9). Finally, Figures S10 and S11 provide, for all model parameters,
359 the free-school and FAD aggregation metrics divided by the total population size (N).

360

361 **4. Discussion**

362 This paper introduces a modeling approach to study the effects of habitat heterogeneities
363 (here consisting of aggregative sites termed FADs) on groups of animals that display a
364 schooling/shoaling behavior (tropical tunas in this case).

365

366 From the ethological to the ecological scale

367 The field of collective animal behavior has flourished in recent decades, deciphering the
368 effects of local interactions between animals on their movements and behavior through
369 self-organization (Camazine et al., 2001; Krause, J., & Ruxton, 2002; Parrish & Edelstein-
370 Keshet, 1999; Sumpter, 2006). From a theoretical point of view, a variety of models were
371 developed to explain the structure of the fish schools (Lopez et al., 2012) and more
372 generally, groups of animals (Cavagna et al., 2009; Sumpter, 2006; Vicsek & Zafeiris, 2012).
373 Very often, ecological applications of these models remain absent (Gordon, 2014). One of
374 the reasons that can explain the disciplinary compartmentalization of such models could be
375 attributed to the relatively small spatial scales that are considered. If interactions of few
376 body-lengths can account for the formation of animal groups, accounting for the group
377 responses to their habitats requires a shift to larger scales.

378

379 The present model accounts for the group dynamics of social animals (fission and fusion of
380 tropical tunas in this case) at scales comparable to the spatial extent of their local habitat,
381 which include numbers of spatial heterogeneities and other schools. For tropical tuna that
382 display an associative behavior with floating objects in the open ocean, these scales can
383 extend up to several tens (or even hundreds) of kilometers. In this respect, while this study
384 still accounts for ethological processes related to social interactions such as collective
385 departure from FADs, school fission and fusion, it also allows for the consideration of a
386 series of ecological drivers, i.e., variable numbers of aggregative sites, that can also affect
387 the groups' dynamics.

388

389 Previous studies conducted in the field of social ecology also considered the behavior of
390 gregarious animals located into heterogeneous environments (Ame et al., 2004; Camazine
391 et al., 2001; Halloy et al., 2007). Because these studies focused essentially on social insects
392 or arthropods, that do not form groups beyond of the aggregative locations, they cannot be
393 directly transposed to social animals such as tunas, that display grouping behaviour both at
394 and away from of the aggregation sites (forming aggregations and schools respectively). This
395 study builds upon these modeling approaches and those developed for tropical tuna
396 (Capello et al., 2016; Robert et al., 2014; Sempo et al., 2013), explicitly adding a schooling
397 component.

398

399 Model structure

400 Three main model parameters set the associative dynamics of tuna schools around spatial
401 heterogeneities (FADs in this case): (i) the probability for a school to associate with a FAD (μ
402), (ii) the probability that a school initiates a departure from a FAD (θ) and (iii) the
403 proportion of the aggregation leaving (β_{agg}). Moreover, three parameters determine the
404 free school fission/fusion dynamics: (i) the probability that a school unit splits from a larger
405 school (ϕ) (ii) the proportion of school units that split (β_{school}) and (iii) the probability that
406 two schools merge together (ψ).

407

408 The collective departure of multiple schools from a FAD (or from a school, for the fission
409 events), follow a "starter" and "follower" rule. As such, the probability of initiating a
410 departure is considered constant for every school unit (parameters θ and ϕ , respectively).

411 The proportion of followers is simply expressed through a binomial law (that depends on
412 the parameters β_{agg} and β_{school} , respectively). This dynamics implies that, every time the
413 collective departure parameters (β_{agg} and β_{school}) are non-zero, the individual probability of
414 leaving the FAD (or the school) increases with the aggregation (school) size. Conversely, the
415 probabilities of associating with a FAD and to merge with another school (μ and ψ ,
416 respectively) are considered constant and are thus independent of the school size.
417 Alternative rules of association and school fusion could be studied, depending on the
418 biological models of interest, with probabilities μ and ψ that depend on the school or the
419 aggregation sizes. Similarly, more complex collective departure rules than the binomial laws,
420 like sigmoidal functions presenting a characteristic threshold, could be studied, but would
421 imply a larger number of parameters. The model studied herein aimed at considering a
422 relatively simple dynamics, yet accounting for possible social interactions.

423

424 In the model, all FADs are considered equivalent to each other. The equivalence between a
425 spatialized model and the current approach holds when the tuna diffusion coefficient is
426 large relative to the scale of the FAD array and the spatial distribution of the free schools is
427 homogeneous. For large and dense FAD arrays, where these conditions do not hold
428 anymore, the model still accounts for the behavior of tuna schools at a local scale (i.e., the
429 FAD of association and its neighboring FADs), where tuna have an equal probability of
430 reaching all FADs of a given array through a random walk. This local scale can range from
431 some few tens to a few hundred kilometers, depending on the FAD density and type of FAD
432 array (Capello et al., 2016; Govinden et al., 2013; Robert et al., 2013; Rodriguez-Tress et al.,
433 2017). Recent studies demonstrated that the time between two associations can be
434 explained in terms of random walk movements between FADs (Pérez et al., 2020), indicating
435 that this hypothesis is the most parsimonious and plausible for tuna. Further modeling
436 studies fitting the movement dynamics of tuna in a FAD array from field data using more
437 realistic types of random walks (e.g. correlated random walks), should quantify the spatial
438 scale of validity of the model for variable FAD densities.

439

440 This study investigates the dynamics of tuna in an array of FADs considering a set of *school*
441 *units* as the basic model components. These school units account for the innate schooling
442 behavior of tuna: it is very unlikely to find an individual tuna alone in the open ocean and

443 generally tuna reach and depart from FADs in schools. This behavior is particularly evident
444 for small size categories (40-60 cm fork length), that show a strong associative behavior with
445 FADs and constitute the major proportion of the tuna found in FAD aggregations (Fonteneau
446 et al., 2013; Ménard et al., 2000). In the present model, all school units are equivalent and
447 no intrinsic variability of their size is considered: the school units should be considered as
448 the minimum size of a tuna school (e.g., 1 tonne, resulting in roughly 400 individuals with an
449 average weight of 2.5 Kg), all other school sizes being composite schools built of these
450 elementary units (Gerlotto & Paramo, 2003). It is plausible that a continuum spectrum of
451 sizes of tuna schools exist. School size distributions of tuna school units could be added to
452 the model, fitting the available data, i.e., from purse-seine catches of free tuna schools for a
453 given species and size.

454

455 Model parametrization for tropical tuna

456 The model introduced in this study presents a continuum set of solutions, from the least
457 social to the most aggregative, with very different properties depending on the choice of
458 parameters. Five main sets of model parameters were studied for tropical tuna, that aimed
459 at investigating the sensitivity of the model's properties to variable degrees of collective
460 tuna departures from the FADs (β_{agg}), as well as variable tuna school fission/fusion
461 dynamics (ϕ and ψ).

462

463 The values of the parameters μ and θ were fixed. Electronic tagging data, providing the time
464 that tuna aggregations spent both at and away from FADs (termed residence and absence
465 times), can be used to infer the model's probabilities of association and departure (Capello
466 et al., 2015, 2016). Field studies also demonstrated that the associative behavior of tuna can
467 be species and size-specific (Robert et al., 2012; Rodriguez-Tress et al., 2017). The choice of
468 considering constant μ stems from previous electronic tagging studies, which demonstrated
469 that the time that tagged individuals spent between two FAD associations follows
470 exponential survival curves (Govinden et al., 2021; Robert et al., 2013; Rodriguez-Tress et
471 al., 2017; Tolotti et al., 2020) and random walk types of movements (Girard, 2004; Pérez et
472 al., 2020). Because the equilibrium solutions of the model depend on the ratio μ/θ and to
473 reduce the number of free parameters, the values of μ and θ were considered constant and
474 fixed to plausible values (average association/absence time of 10 days in an array of 10 FADs

475 for the non-social model). For social models, the residence times also depend on the
476 parameter β_{agg} (Eq.(4)). In addition, the number of FADs (P) indirectly affects the residence
477 times for social models, since the aggregation's sizes depend on P and larger aggregation
478 sizes imply higher probabilities of departure for $\beta_{agg} \neq 0$. Therefore, fitting the trends of
479 residence times as a function of the number of FADs will be necessary to select the best
480 model parameters. Further applications of the model would also require that the
481 parameters were fitted to the field data for each tuna species and size category.

482
483 For the parameter choices of the social models, two main scenarios were studied, where on
484 average, half ($\beta_{agg} = 0.5$) and the entire ($\beta_{agg} = 1$) tuna aggregation collectively leave the
485 FAD during a departure event, resulting in the social (S) and highly-social (HS) model
486 respectively. Obviously, intermediate cases could occur in nature. Unfortunately, the
487 current state of knowledge and the current field data available from echosounder buoys
488 (Baidai et al., 2020) do not allow for the assessment of this parameter for tropical tuna and
489 more generally, for all marine species that display the same associative behavior. New field
490 data, using sonars for instance (Brehmer et al., 2019), which provide accurate information
491 on the temporal evolution of the associated biomass beneath the FAD, could allow for the
492 assessment of this parameter. Furthermore, as knowledge on the fission and fusion
493 dynamics of tuna schools is limited, the ψ and ϕ parameters were set equal to the
494 probability of association μ . Faster fission dynamics ($\phi \gg \mu$) would result in the non-social
495 model. Similarly, the limit $\psi \ll \mu$, would make the fusion of schools negligible with respect
496 to the FAD association dynamics.

497 498 Model properties and implications for tropical tuna

499 The free school metrics show a variety of trends that depend on the model configuration.
500 Interestingly, three social model configurations (S+f, HS+f and HS+ff) indicate that the
501 presence of FADs leads to the formation of larger free schools. These trends are in
502 agreement with the meeting point hypothesis (Fréon & Dagorn, 2000), which explains the
503 natural associative behavior of tuna as means of meeting their congeners and forming larger
504 schools. For model S+f, there is an optimal number of FADs that maximizes the school size.
505 For the highly-social models HS+f and HS+ff, the school size is an increasing monotonic

506 function of the number of FADs, with no maximum. Conversely, the social model S+ff shows
507 an inverse trend, with decreasing school sizes for increasing numbers of FADs. One of the
508 potential negative impacts of increasing numbers of FADs is school fragmentation (Dagorn
509 et al., 2013; Sempo et al., 2013). This study suggests that this scenario strongly depends on
510 the type of schooling and association dynamics in play. Interestingly, all these scenarios
511 come from the same model structure. This continuous set of model solutions could mimic
512 the behavioral plasticity of animals, that can adapt their dynamics to respond to a variable
513 environment. These model's variants could also be considered as multi-species variants of
514 the same associative behavior.

515

516 More globally, the analysis of the model's properties leads to a series of metrics with non-
517 monotonic trends that are not completely intuitive. In the case of the size of free schools
518 mentioned above, for the S+f model, the non-monotonic trend of FS_size (Figure 2) can be
519 explained by the propensity of FADs to aggregate multiple schools for small FAD numbers
520 (and thus promote the departure of larger schools for $\beta_{agg} \neq 0$) and their tendency to
521 disperse schools over different FADs (with one or few schools each), in the limit of large FAD
522 numbers. This dispersive effect, which explains a reduction of the size of free schools
523 (school fragmentation) for increasing number of FADs, is not apparent for the HS+f model.
524 In this model, the higher aggregative capacity of FADs for $\beta_{agg} = 1$ counterbalances the
525 fragmentation of schools due to increasing numbers of FADs for the range of model
526 parameters tested. On the other hand, in the presence of a fusion term, increasing FAD
527 numbers also contribute to the reduction the number of free schools and thus their fusion
528 rates. This effect can explain the monotonic decreasing trend of the size of free schools for
529 increasing numbers of FADs for model S+ff. Reversely, for model HS+ff, the higher
530 aggregative capacity of FADs for $\beta_{agg} = 1$ counterbalances this effect, similar to model HS+f.

531

532 Another example of non-monotonic trend is found for the number of free schools recorded
533 for the S+ff model, which first increases with the number of FADs, then reaches a maximum
534 and finally decreases. Generally, the number of free schools depends on the total associated
535 population (which decrease with the number of FADs for all models, Figure 5) and the
536 competition between the fission and fusion terms. For $\beta_{agg} = 0.5$, if a single school of size

537 $s > 1$ associates to a FAD, it has a non-null probability to depart into multiple schools, thus
538 increasing the number of free schools. Therefore, the presence of FADs can first increase
539 the number of free schools for this model configuration. On the other hand, in the limit of
540 large FAD numbers, the decreasing free population and the presence of smaller FAD
541 aggregations/school sizes prevail and thus cause a decreasing number of free schools.

542

543 The fraction of FADs occupied by tuna in a FAD array can be derived using both fisheries-
544 dependent (Sempo et al., 2013) and independent data (Baidai et al., 2020). This is facilitated
545 through the large-scale collection of data derived from echosounder buoys attached to FADs
546 (Moreno et al., 2016) as well as of catch data. Similarly, purse-seine catch data can provide
547 insight into the size of FAD aggregations and free schools. Assessing their trends for
548 increasing numbers of FADs will be essential to parametrize the model. However, to date,
549 the information on the total number of floating objects at fine spatial and temporal scales is
550 still considered sensitive data and is only partially available to scientists though specific
551 agreements with their national fleets. Moving towards the complete availability of data on
552 all FADs present in the ocean at a local scale is key to parametrize the model and thus
553 provide science-based advices on the impacts of increasing numbers of FADs. This study
554 outlines an increasing trend in the fraction of associated schools with increasing FAD
555 numbers, across all model configurations. Assessing which model best fits tuna behavior will
556 be key to quantitatively evaluating the increase in vulnerability of tuna populations to the
557 purse seine fishery induced by increasing numbers of FADs. Finally, the model
558 parametrization could benefit future technological improvements in the acoustic
559 discrimination of tuna species (Moreno et al., 2019) and in the biomass estimates obtained
560 from echosounder buoys (Baidai et al., 2020), which could allow for the evaluation of the
561 dynamics of a FAD aggregation independently of catch data.

562

563 Conclusion and Perspectives

564 The availability of new technologies to study wild animals in their natural environment at
565 multiple spatial scales continues to increase (Hughey et al., 2018). In the case of tropical
566 tuna and FADs, a variety of technologies can be used to characterize the associative
567 behavior of tuna and the aggregation dynamics (Brehmer et al., 2019; Moreno et al., 2016).

568 These multiple data sources could be used to parametrize the models developed here. For
569 tropical tuna, combining different data sources from electronic tagging, acoustic data and
570 fisheries-dependent data could allow for estimations of the model parameters. This field-
571 based model could be used as a FAD-operating model to predict trends in several fisheries-
572 related metrics for variable tuna populations/FAD numbers, as well as to predict the impacts
573 of increasing numbers of FADs on the ecology of these species. It could also be used to test
574 the reliability and robustness of novel indicators of abundance developed for tuna (Capello
575 et al., 2016; Santiago et al., 2016). More generally, this modeling approach could be applied
576 to the study of social species living in groups in their natural environment, and allow for the
577 evaluation of the impacts of habitat modifications due to anthropogenic activities and global
578 change. In environments which are highly modified by humans, models such as the one
579 summarized in this article, based on understanding the processes involved in the dynamics
580 of animal groups in their habitats, will be increasingly necessary as management and
581 prediction tools (Evans, 2012).

582

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585

586 **Author contributions**

587 MC: Conceptualization; MC and JR: Formal analysis; MC, JR and JLD: Methodology; JLD and
588 LD: Supervision; MC: original draft writing; All authors discussed the results, contributed to
589 the writing and gave final approval to the manuscript.

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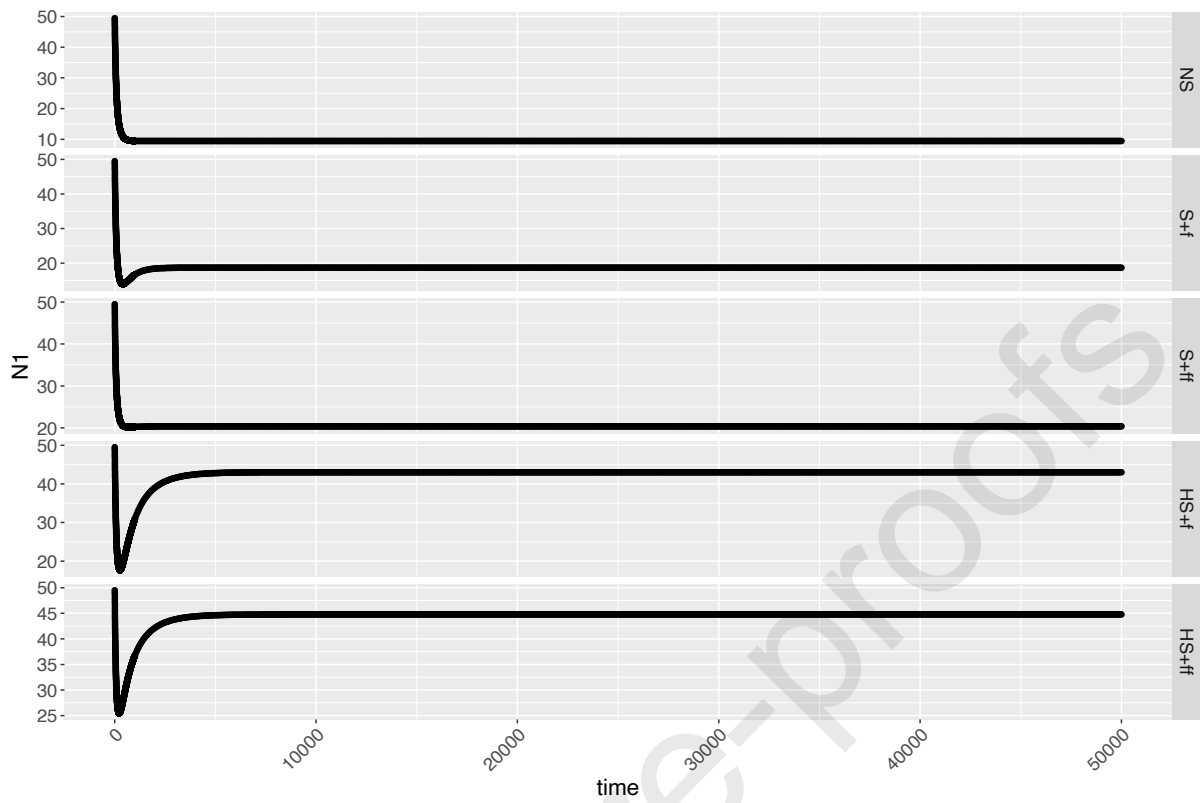
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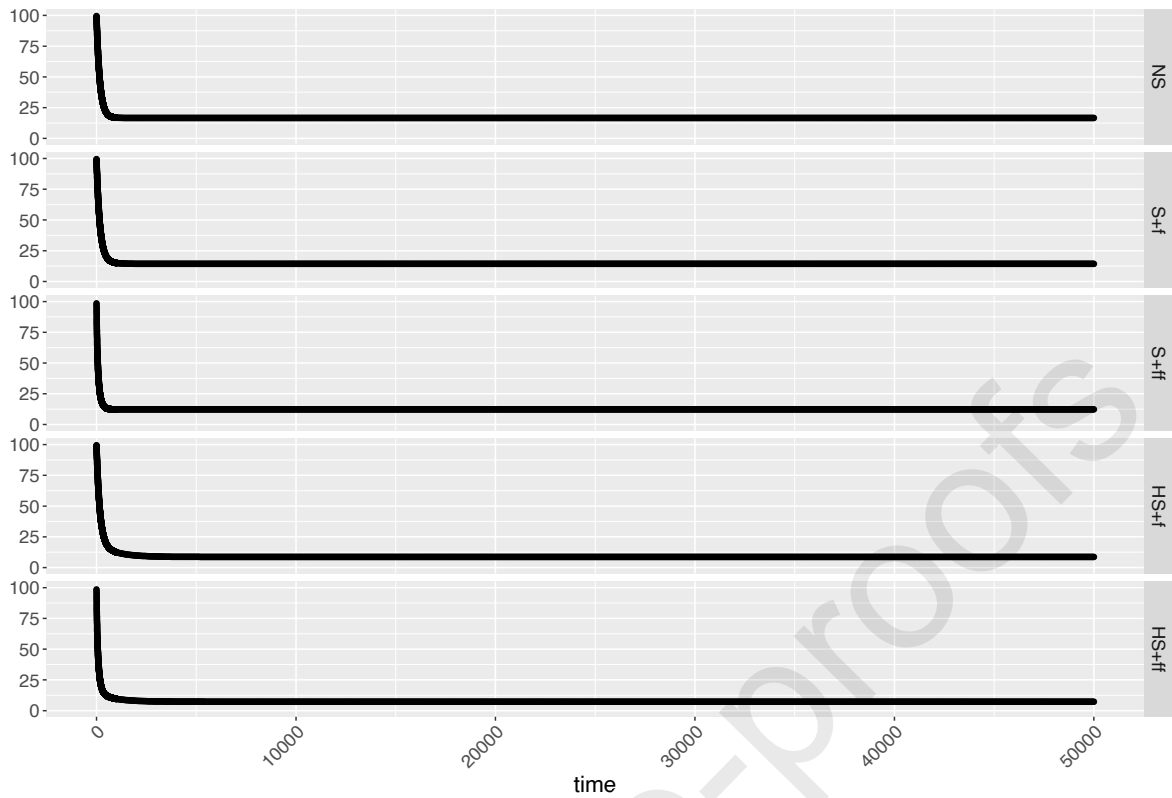
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811 **Supplementary Figures**

812

813 **Figure S1: Number of unoccupied FADs ($F_0(t)$) versus time** (initial condition: $F_s(0)$
 814 $= 0 \forall s$; $X_1(0) = N$; $X_{s>1}(0) = 0$), for the five model configurations (see Table 2), with
 815 $N = 100$ and $P = 50$.

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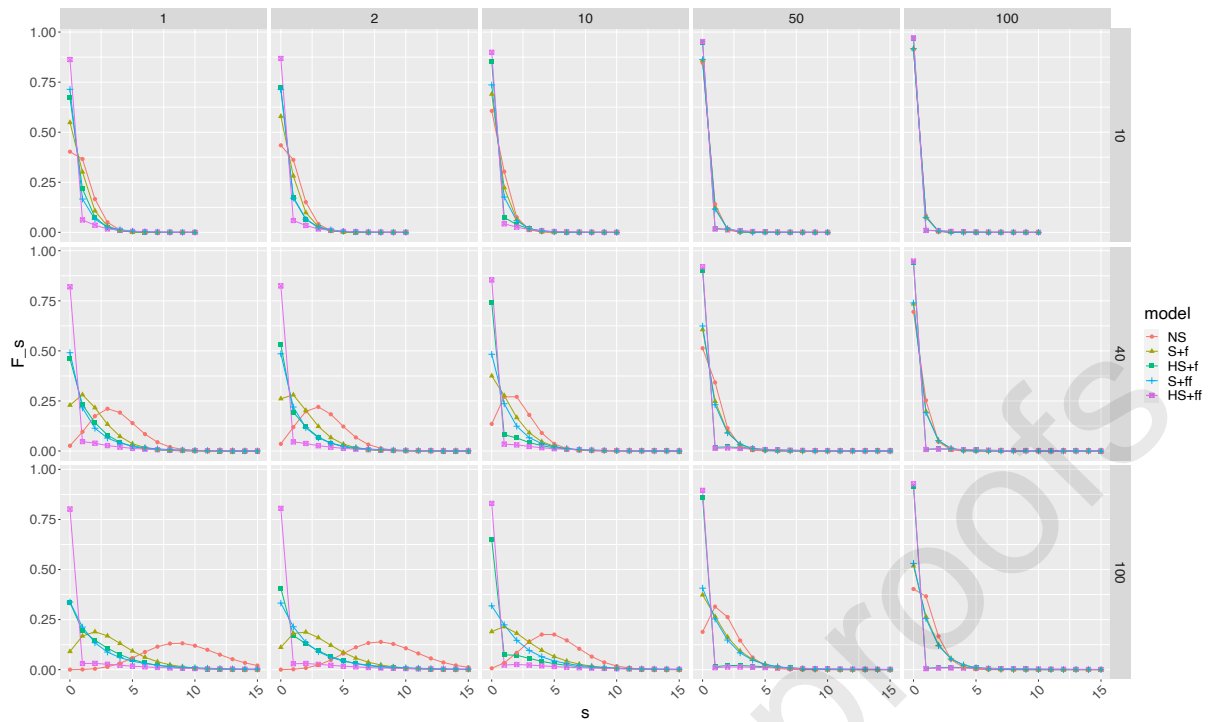


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818 **Figure S2: Total number of free schools versus time** (initial condition: $F_s(0) = 0 \forall s$; $X_1(0)$ 819 $= N$; $X_{s>1}(0) = 0$), for the five model configurations (see Table 2), with $N = 100$ and820 $P = 50$.

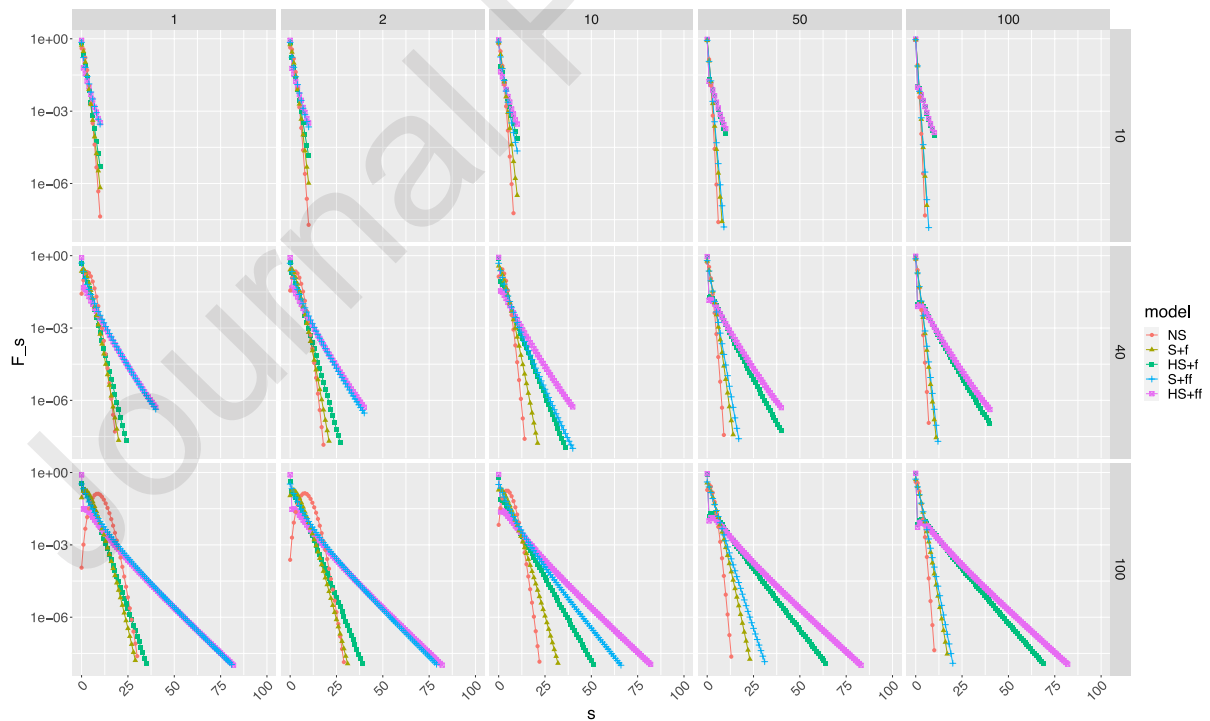
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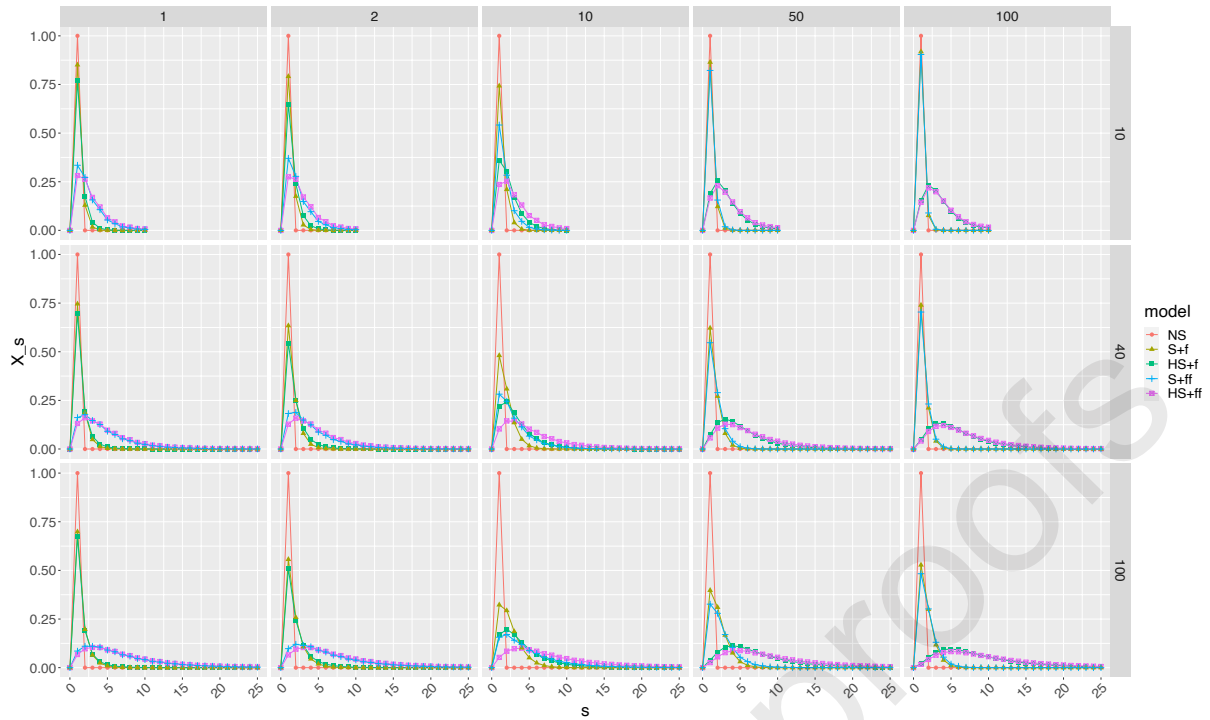
824 **Figure S3** : Equilibrium distribution of the number of FAD aggregations of size s (F_s). Rows
 825 correspond to different population sizes (from top to bottom: $N=10, 40, 100$) and columns
 826 correspond to different numbers of FADs (from left to right: $P=1, 2, 10, 50, 100$). Each color
 827 indicates one of the five model configurations considered (see Table 2).



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829 **Figure S4** : The same as Figure S3 in semi-logarithmic scale.

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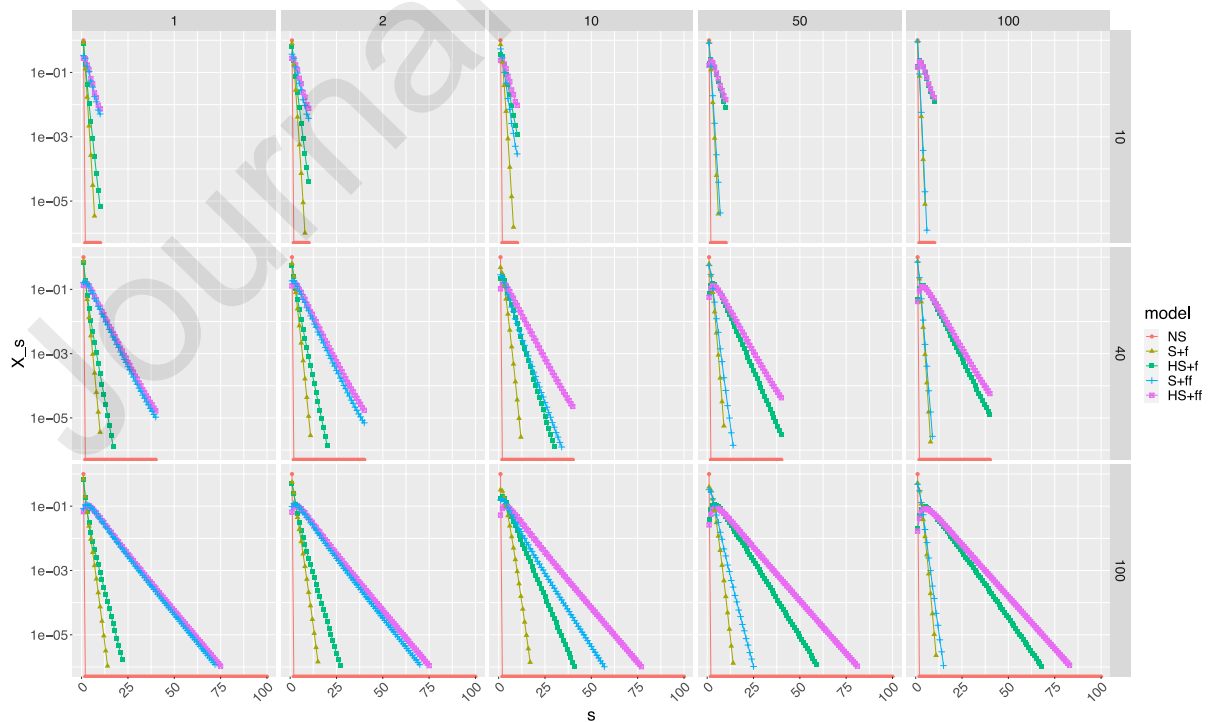


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832 **Figure S5 : Equilibrium distribution of the number of free schools of size s (X_s).** Rows
 833 correspond to different population sizes (from top to bottom: $N=10, 40, 100$) and columns
 834 correspond to different numbers of FADs (from left to right: $P=1, 2, 10, 50, 100$). Each color
 835 indicates one of the five model configurations considered (see Table 2).

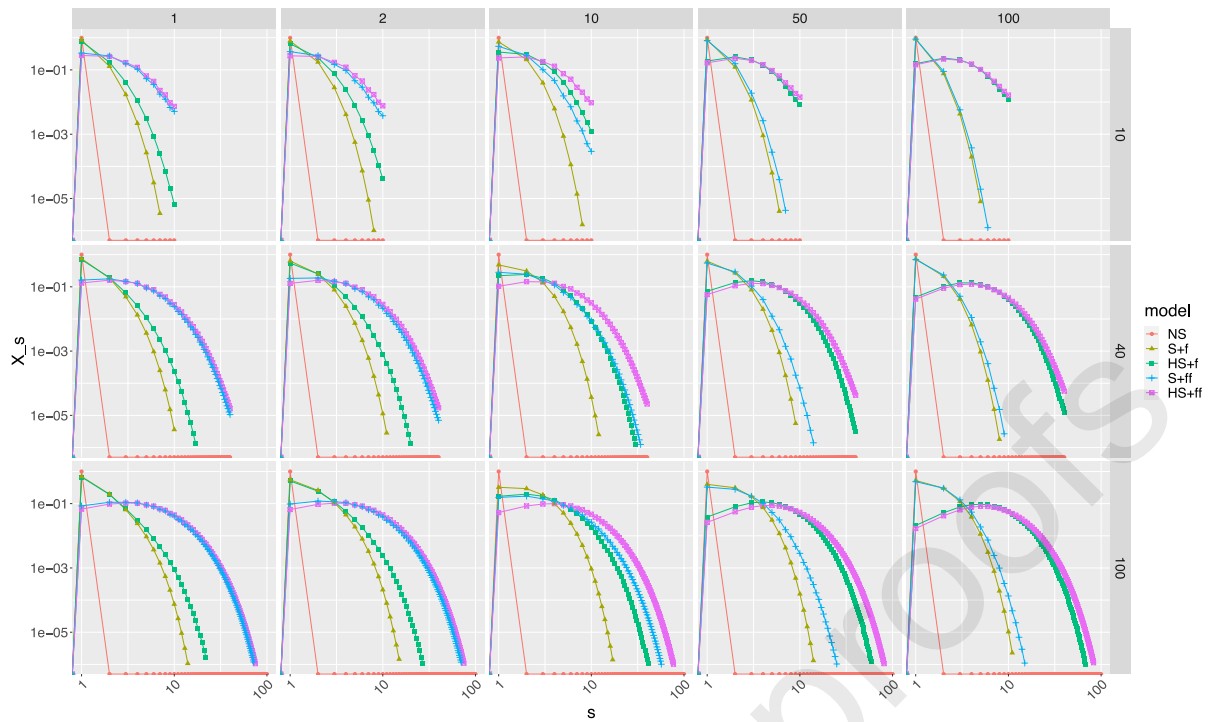
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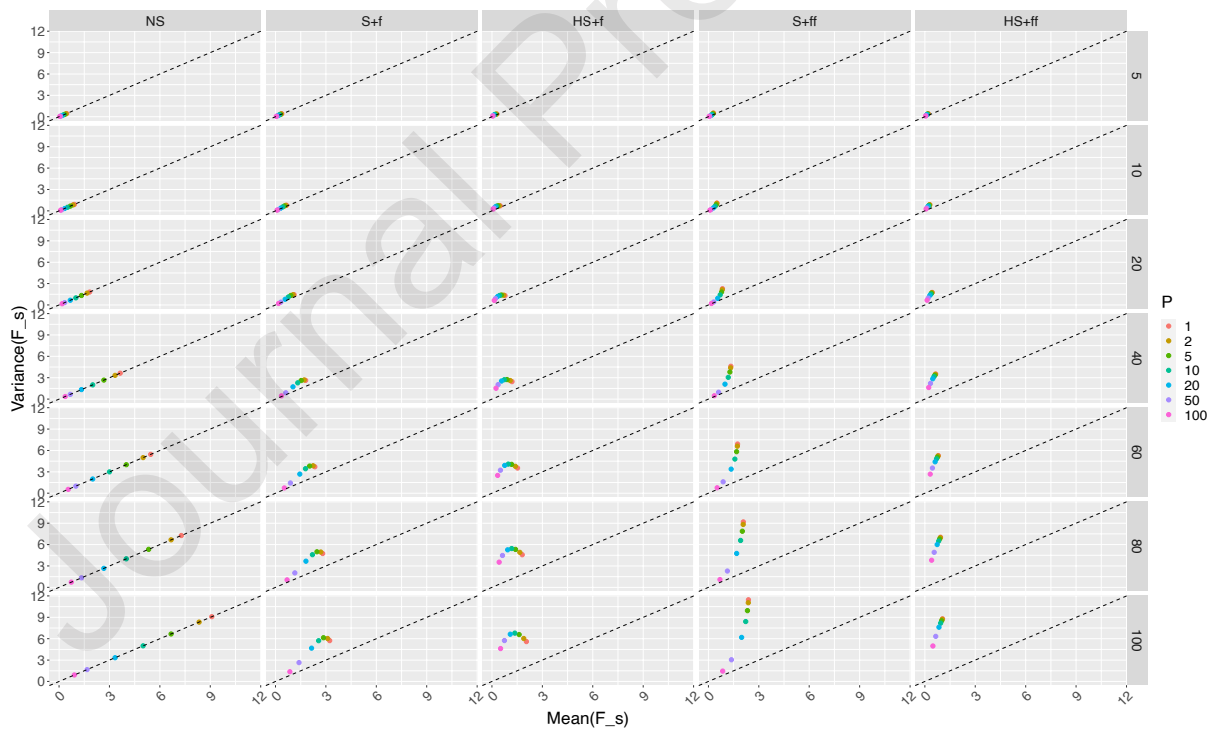
839 **Figure S6 : The same as Figure S5 in semi-logarithmic scale.**



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841 **Figure S7** : The same as Figure S5 in log-log scale.

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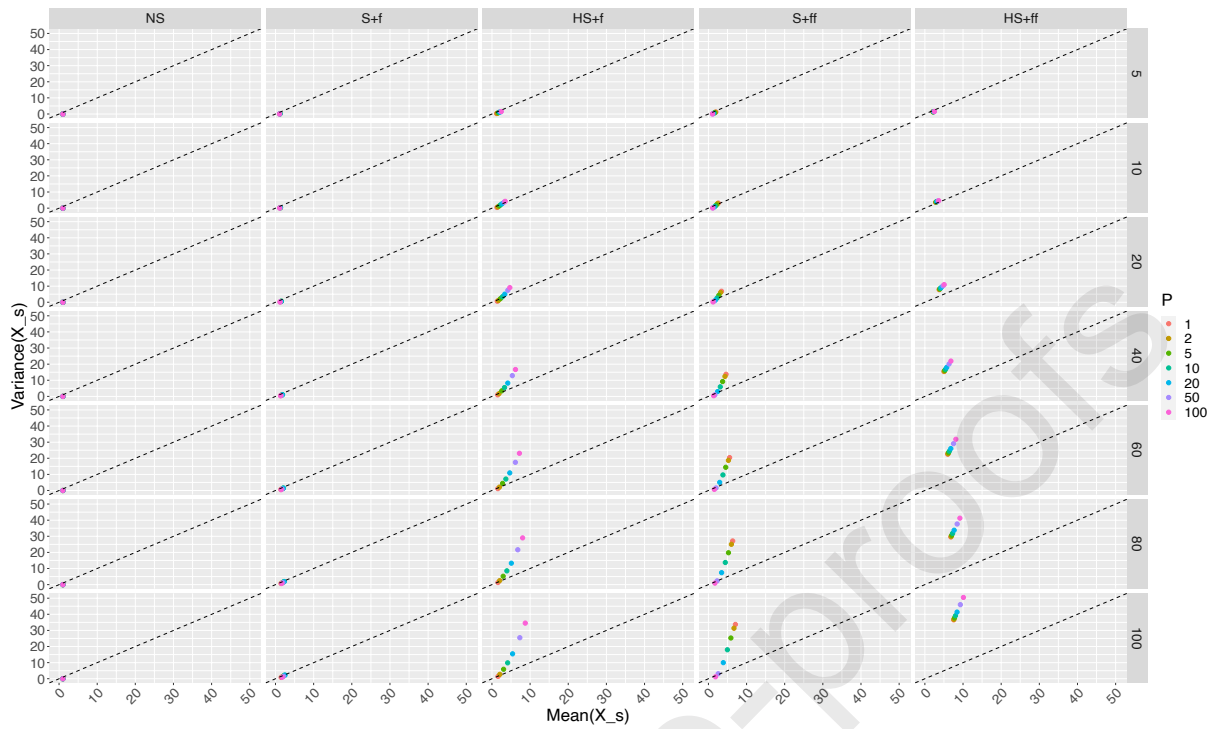
844 **Figure S8** : Mean (x-axis) to variance (y-axis) relation for the size of FAD aggregations (F_s).

845 Each column corresponds to a model configuration (Table 2). Rows denote the population

846 sizes and colors the number of FADs. The dashed line corresponds to $y=x$ (equidispersion).

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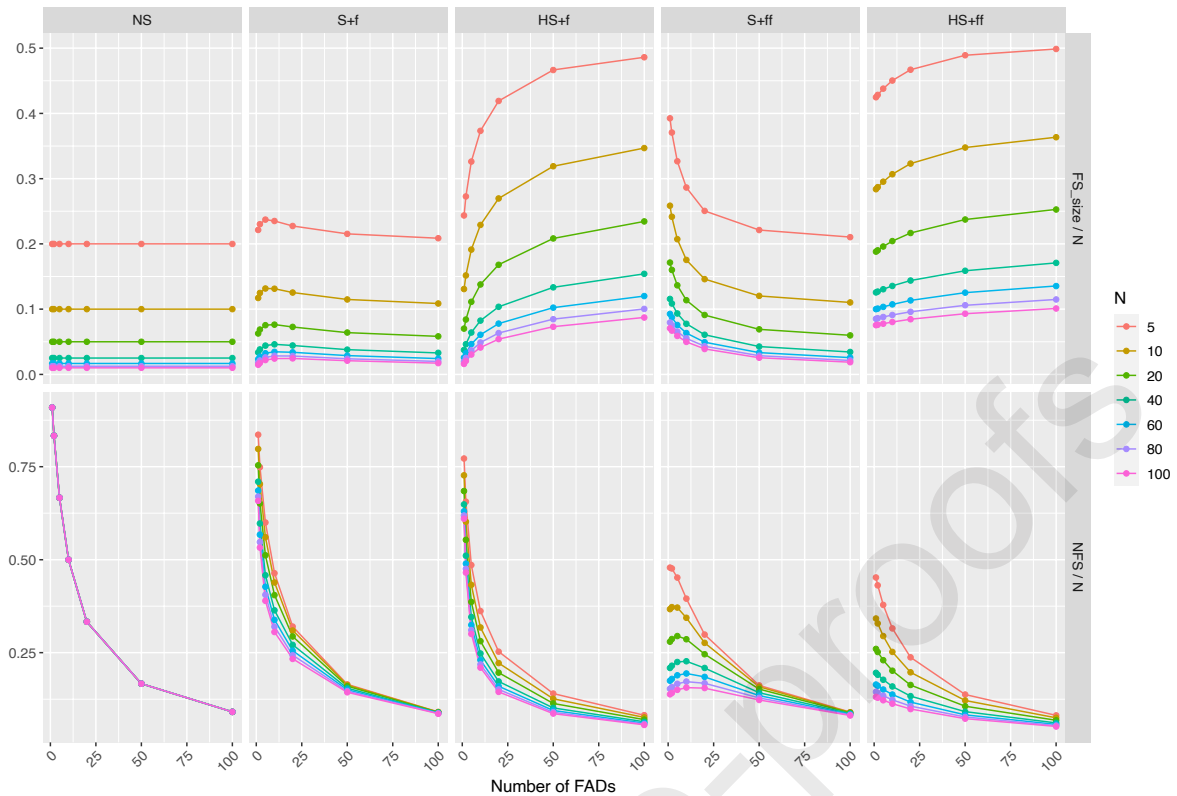
Figure S9 : Mean (x-axis) to variance (y-axis) relation for the size of free schools (X_s). Each column corresponds to a model configuration (Table 2). Rows denote the population sizes and colors the number of FADs. The dashed line corresponds to $y=x$ (equidispersion).

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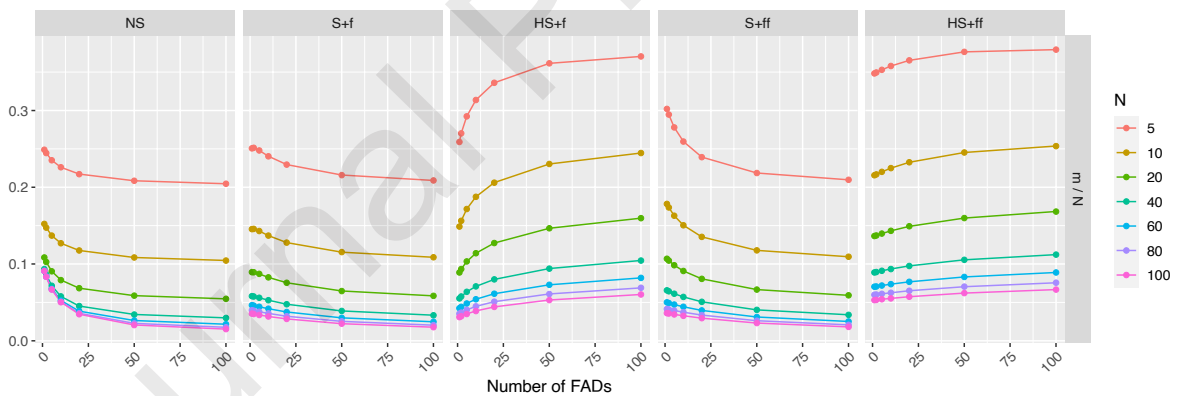
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858 **Figure S10: Free school aggregation metrics (same as Figure 3) divided by N.**

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861 **Figure S11: FAD aggregation metrics (m) divided by N.**

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- 864• We develop a model to assess the impacts of human-induced habitat modifications on social animals.
- 865• The model accounts for the interplay of increasing numbers of habitat heterogeneities on animal groups.
- 866
- 867• The model properties are investigated considering the case study of tropical tuna schools.
- 868• This study offers a general modeling framework to study social species in their habitats.
- 869• This approach can accounts for both ethological and ecological drivers of animal groups dynamics.

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871

872 **Author contributions**

873 MC: Conceptualization; MC and JR: Formal analysis; MC, JR and JLD: Methodology; JLD and
874 LD: Supervision; MC: original draft writing ; All authors discussed the results, contributed to
875 the writing and gave final approval to the manuscript.

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Journal Pre-proofs