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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.

1. Introduction

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

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

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

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

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

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

A wide variety of movement rules have been proposed to explain the formation and dynamics of animal groups (Ballerini et al., 2008; Bialek et al., 2012; Herbert-Read, 2016; Vicsek & Zafeiris, 2012). In particular, several models of fish schools have been developed in the past (Lopez et al., 2012). Alternatively, ecologically-relevant parameters, such as the amount of habitat heterogeneities, and the consequent associative behavior of animals forming aggregations induced by these heterogeneities, have so far been neglected when modeling animal group dynamics. Only a small number of recent studies have modeled flocking behavior in complex environments considering repulsive environmental cues and their consequences on the group-level coordination (Rahmani et al., 2020). Conversely, ecological models tend to neglect the behavioral drivers which can affect species abundance and distribution (Geary et al., 2020). The main reason for this theoretical partitioning between ethological and ecological models can be related to the different spatial scales that are considered, ranging between a few centimeters/meters in ethology to several hundreds, or even thousands of kilometers in ecology.

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

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

2. Materials and methods

2.1 Model definition

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

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

A. Fission of schools can occur in the free state. This fission dynamics is set by the probability $(\eta_s^l + \eta_s^{s-l})$ that a school of size s splits into two sub-schools of size l and $s-l$.

B. Fusion of two free schools can occur with probability ψ, independently of the school size.

C. Free schools have a probability μ to join a FAD, which is independent of their size. For each free school, the overall probability of associating with any of the P FADs is $P\mu$.

D. Multiple school units forming a FAD-aggregation can leave a FAD at the same time, leading to a free school of size $l > 1$. Namely, for a FAD aggregation of size s (i.e., composed of s school units), a school of size l can depart from the FAD with probability γ_s^l, leading to a FAD aggregation of size $s-l$ and a free school of size l.

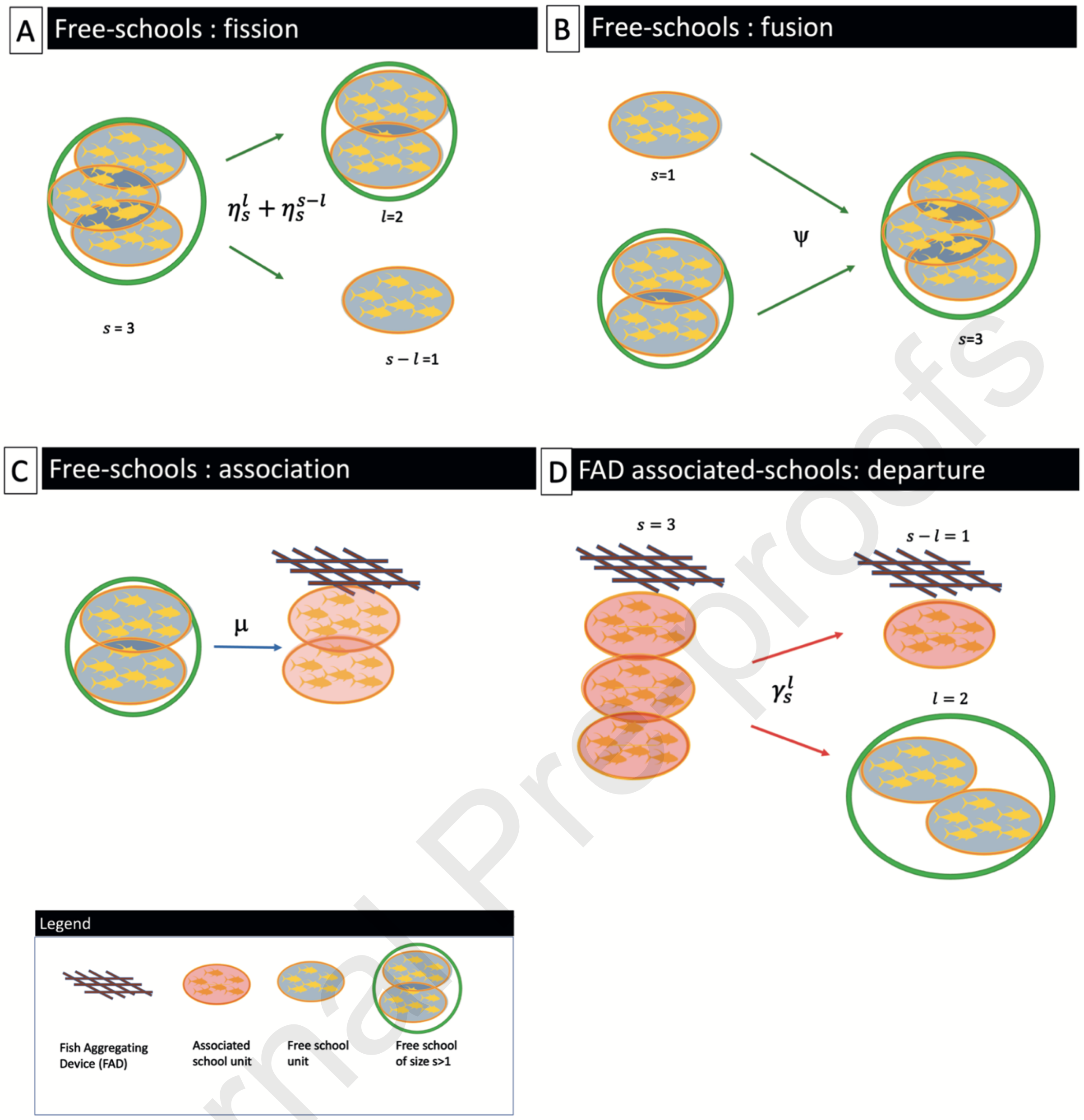

Figure 1: Schematic view of the model. (A-C) *Free-schools dynamics.* **(A)** Fission: a free school of size $s > 1$ can split into smaller schools of size l and $s - l$ with probability $(\eta_s^l + \eta_s^{s-l})$. **(B)** Fusion: two free schools can merge with probability ψ independent of their size.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

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

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

(Eq. 1)

$$\frac{dX_s}{dt} = \sum_{l=s}^{N} F_l \gamma_l^s - \mu X_s \sum_{l=0}^{\boldsymbol{N-s}} F_l + \sum_{l=s+1}^{N} \left(\eta_l^s + \eta_l^{l-s}\right) X_l - (1-\delta_{s,1})\, X_s \sum_{l=1}^{s-1} \eta_s^l +$$

$$-\psi X_s \sum_{l=1}^{N-s} (1+\delta_{s,l}) X_l + \psi \sum_{l=1}^{s-1} \frac{(1+\delta_{s-l,l})}{2} X_l X_{s-l}$$

(Eq.2)

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

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

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

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

$$\gamma_s^l = s\,\theta\,B(l-1;s-1,\beta_{agg}) \quad \text{(Eq.4)}$$

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

$$B(l-1;s-1,\beta_{agg}) = \binom{s-1}{l-1}\beta_{agg}{}^{l-1}(1-\beta_{agg})^{s-l} \quad \text{(Eq.5)}$$

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

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

$$\eta_s^l = s\,\phi\,B(l-1;s-1,\beta_{school}) \quad \text{(Eq.6)}$$

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

2.2 Model configuration

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

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

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

2.3 Numerical resolution of the model

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

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)

Table 1: Model parameters.

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

		$\beta_{agg} = 0$	$\beta_{agg} = 0.5$	$\beta_{agg} = 1.0$
School fission-fusion dynamics (ϕ, ψ)	ϕ = *0* ψ = *0*	Non-social (NS)		
	$\phi = \mu$ ψ = *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)

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

2.4 Model properties

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

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

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

Similarly, two metrics were estimated to characterize FAD aggregations:

i. The mean size of a FAD aggregation (m), defined for the FADs occupied by at least one school, $m(t) = \frac{\sum_{s=1}^{N} s\, F_s(t)}{\sum_{s=1}^{N} F_s(t)}$.

ii. The fraction of FADs occupied by at least one school unit ($f1$), defined as $f1(t) = \frac{\sum_{s=1}^{N} F_s(t)}{P}$.

Finally, the relative number of associated schools over the full FAD array ($F_a(t)/N = \frac{1}{N} \sum_{s=1}^{N} s\, F_s(t)$) was estimated. For each combination of model parameters, each metric was calculated at equilibrium (stationary states: $\forall s \leq N$: $\frac{dF_s}{dt} = 0$; $\frac{dX_s}{dt} = 0$).

3. Results

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

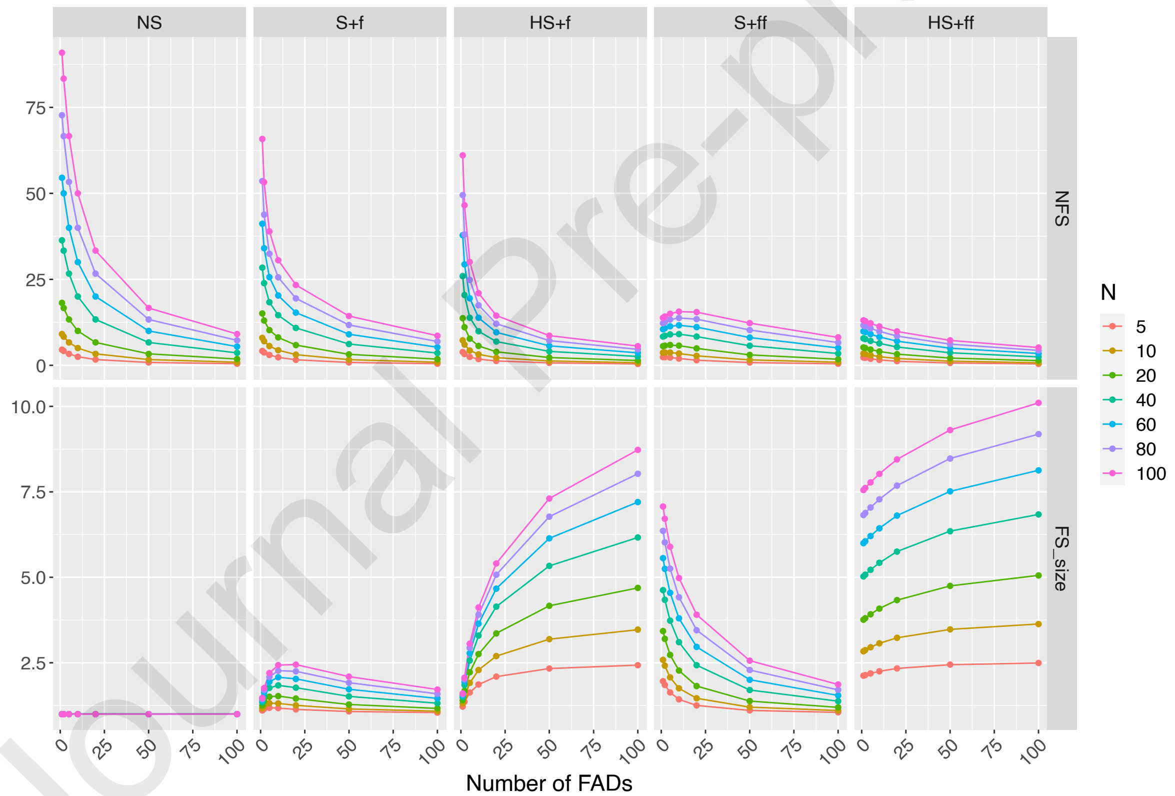

Figure 2. Free-swimming school metrics. Number of free-swimming schools (NFS) and average size of the free schools (FS_{size}) as a function of the number of FADs for different population sizes (colors). Each column represents a model configuration: Non-social (NS); Social with fission (S+f); Highly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

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

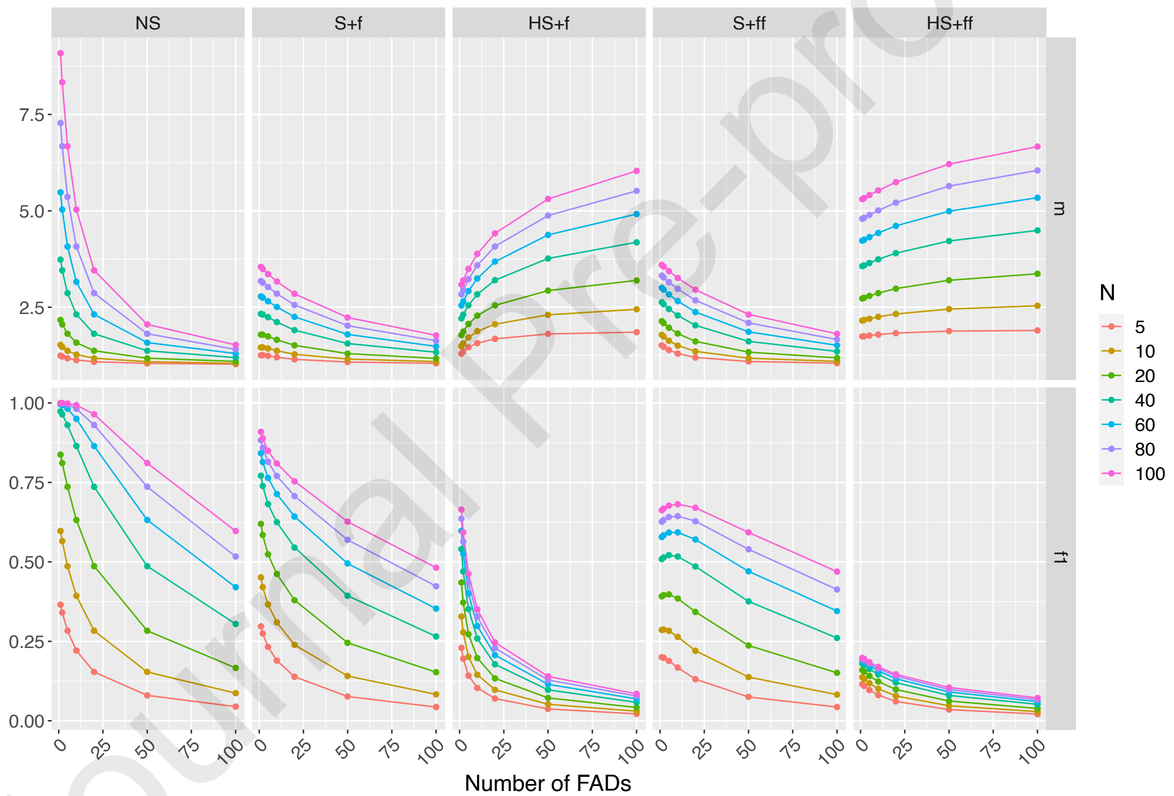

Figure 3. FAD aggregation metrics. Average number of school units associated with the FADs that are occupied by at least one school (m) and fraction of FADs occupied by at least one school ($f1$) as a function of the number of FADs (abscissa) for different population sizes (colors). Each column represents a model configuration : Non-social (NS); Social with fission (S+f); Highly Social with fission (HS+f); Social with fission and fusion (S+ff); Highly Social with fission and fusion (HS+ff).

The average size of FAD aggregations (m, Figure 3) show global increasing trends for larger population sizes. The social models, both with fission and fission+fusion (S+f and S+ff) show decreasing trends of FAD aggregation sizes for larger number of FADs, as found for the non-social model, but relatively smaller aggregation sizes for small number of FADs. Conversely, both highly-social models (HS+f and HS+ff) demonstrate an opposite trend, with average aggregation sizes increasing for increasing numbers of FADs.

The fraction of FADs occupied by at least one school unit ($f1$, Figure 3) shows a general decrease with the number of FADs and is larger for larger populations. However, model S+ff show a non-monotonic trend, with f1 having a clear maximum for larger population sizes. Moreover, the highly-social models with fission and fission+fusion (HS+f and HS+ff) demonstrate the highest and lowest sensitivity of f1 relative to the number of FADs respectively, while the size of the population appears less important.

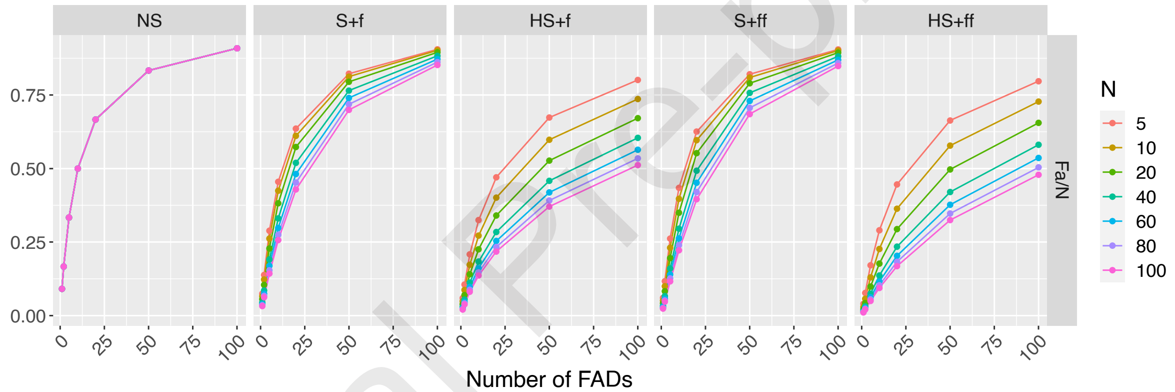

Figure 4. Relative number of associated schools. Ratio between the number of FAD-associated school units and the total number of school units, as a function of the number of FADs (abscissa) for different population sizes (colors). Each column represents a model configuration : Non-social (NS); Social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

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

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

4.Discussion

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

From the ethological to the ecological scale

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

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

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

<u>Model structure</u>

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

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

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

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

This study investigates the dynamics of tuna in an array of FADs considering a set of *school units* as the basic model components. These school units account for the innate schooling behavior of tuna: it is very unlikely to find an individual tuna alone in the open ocean and generally tuna reach and depart from FADs in schools. This behavior is particularly evident for small size categories (40-60 cm fork length), that show a strong associative behavior with FADs and constitute the major proportion of the tuna found in FAD aggregations (Fonteneau et al., 2013; Ménard et al., 2000). In the present model, all school units are equivalent and no intrinsic variability of their size is considered: the school units should be considered as the minimum size of a tuna school (e.g., 1 tonne, resulting in roughly 400 individuals with an average weight of 2.5 Kg), all other school sizes being composite schools built of these elementary units (Gerlotto & Paramo, 2003). It is plausible that a continuum spectrum of sizes of tuna schools exist. School size distributions of tuna school units could be added to the model, fitting the available data, i.e., from purse-seine catches of free tuna schools for a given species and size.

<u>Model parametrization for tropical tuna</u>

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

The values of the parameters μ and θ were fixed. Electronic tagging data, providing the time that tuna aggregations spent both at and away from FADs (termed residence and absence times), can be used to infer the model's probabilities of association and departure (Capello et al., 2015, 2016). Field studies also demonstrated that the associative behavior of tuna can be species and size-specific (Robert et al., 2012; Rodriguez-Tress et al., 2017). The choice of considering constant μ stems from previous electronic tagging studies, which demonstrated that the time that tagged individuals spent between two FAD associations follows exponential survival curves (Govinden et al., 2021; Robert et al., 2013; Rodriguez-Tress et al., 2017; Tolotti et al., 2020) and random walk types of movements (Girard, 2004; Pérez et al., 2020). Because the equilibrium solutions of the model depend on the ratio μ/θ and to reduce the number of free parameters, the values of μ and θ were considered constant and fixed to plausible values (average association/absence time of 10 days in an array of 10 FADs for the non-social model). For social models, the residence times also depend on the parameter β_{agg} (Eq.(4)). In addition, the number of FADs (P) indirectly affects the residence times for social models, since the aggregation's sizes depend on P and larger aggregation sizes imply higher probabilities of departure for $\beta_{agg} \neq 0$. Therefore, fitting the trends of residence times as a function of the number of FADs will be necessary to select the best model parameters. Further applications of the model would also require that the parameters were fitted to the field data for each tuna species and size category.

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

<u>Model properties and implications for tropical tuna</u>

The free school metrics show a variety of trends that depend on the model configuration. Interestingly, three social model configurations (S+f, HS+f and HS+ff) indicate that the presence of FADs leads to the formation of larger free schools. These trends are in agreement with the meeting point hypothesis (Fréon & Dagorn, 2000), which explains the natural associative behavior of tuna as means of meeting their congeners and forming larger schools. For model S+f, there is an optimal number of FADs that maximizes the school size. For the highly-social models HS+f and HS+ff, the school size is an increasing monotonic function of the number of FADs, with no maximum. Conversely, the social model S+ff shows an inverse trend, with decreasing school sizes for increasing numbers of FADs. One of the potential negative impacts of increasing numbers of FADs is school fragmentation (Dagorn et al., 2013; Sempo et al., 2013). This study suggests that this scenario strongly depends on the type of schooling and association dynamics in play. Interestingly, all these scenarios come from the same model structure. This continuous set of model solutions could mimic the behavioral plasticity of animals, that can adapt their dynamics to respond to a variable environment. These model's variants could also be considered as multi-species variants of the same associative behavior.

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

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

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

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

Conclusion and Perspectives

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

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

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Author contributions

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

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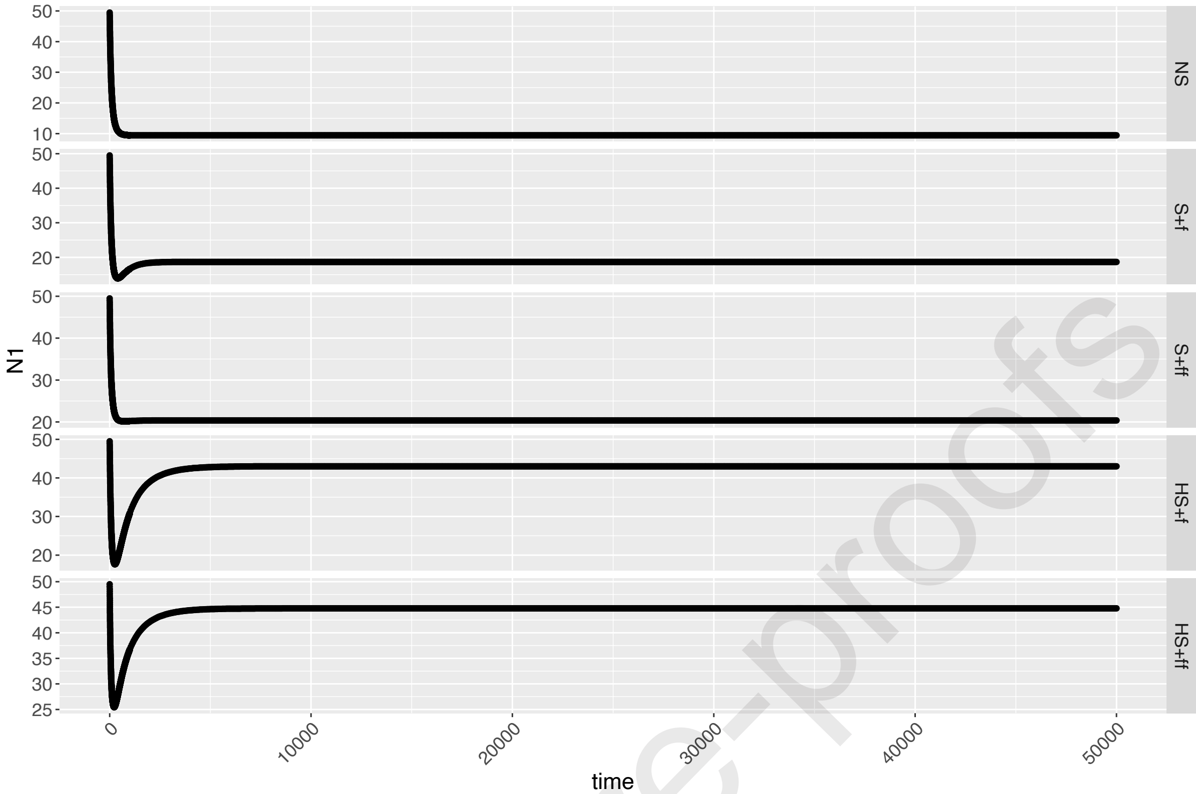
811 **Supplementary Figures**



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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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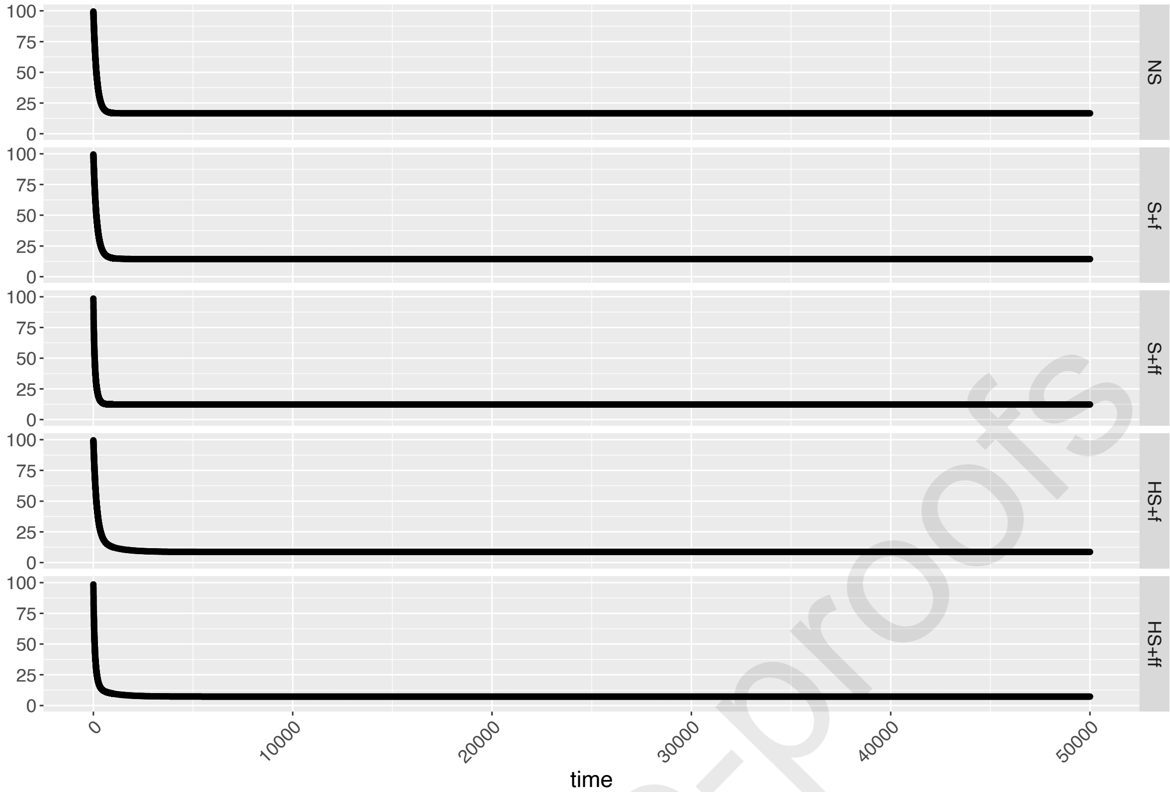

Figure S2: Total number of free schools versus time (initial condition: $F_s(0) = 0 \; \forall \; s$; $X_1(0) = N$; $X_{s>1}(0) = 0$), for the five model configurations (see Table 2), with $N = 100$ and $P = 50$.

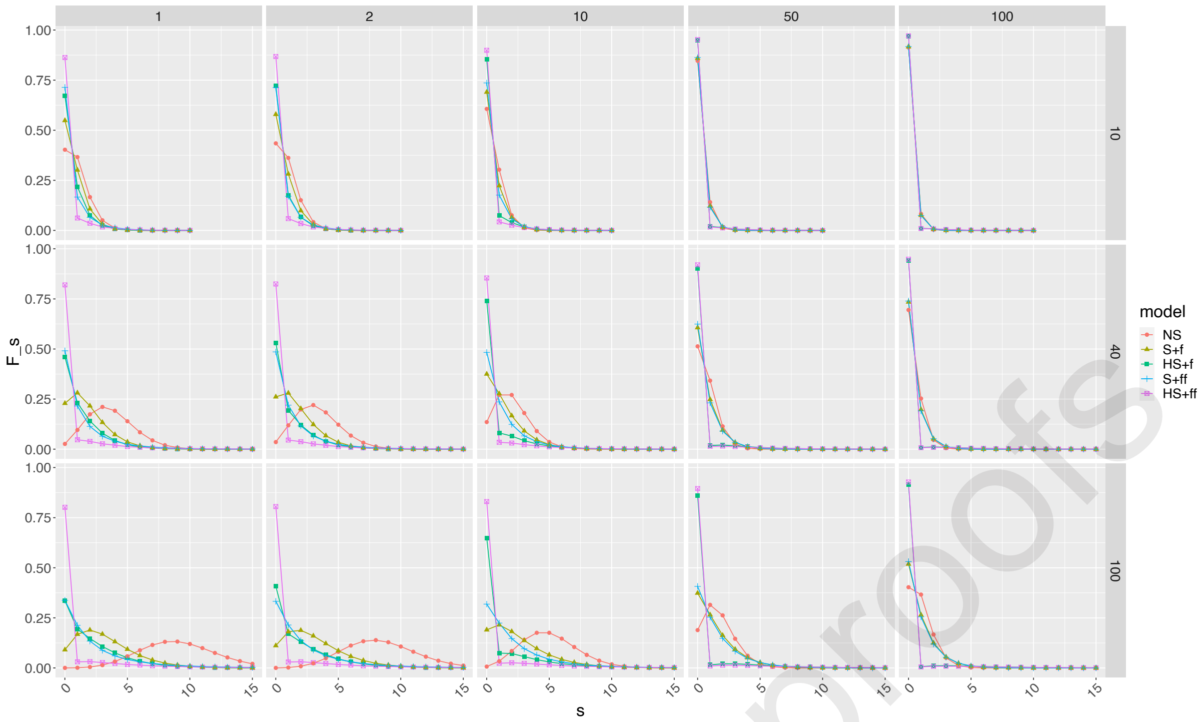

Figure S3 : Equilibrium distribution of the number of FAD aggregations of size s (F_s). Rows correspond to different population sizes (from top to bottom: N=10, 40, 100) and columns correspond to different numbers of FADs (from left to right: P=1, 2, 10, 50, 100). Each color indicates one of the five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

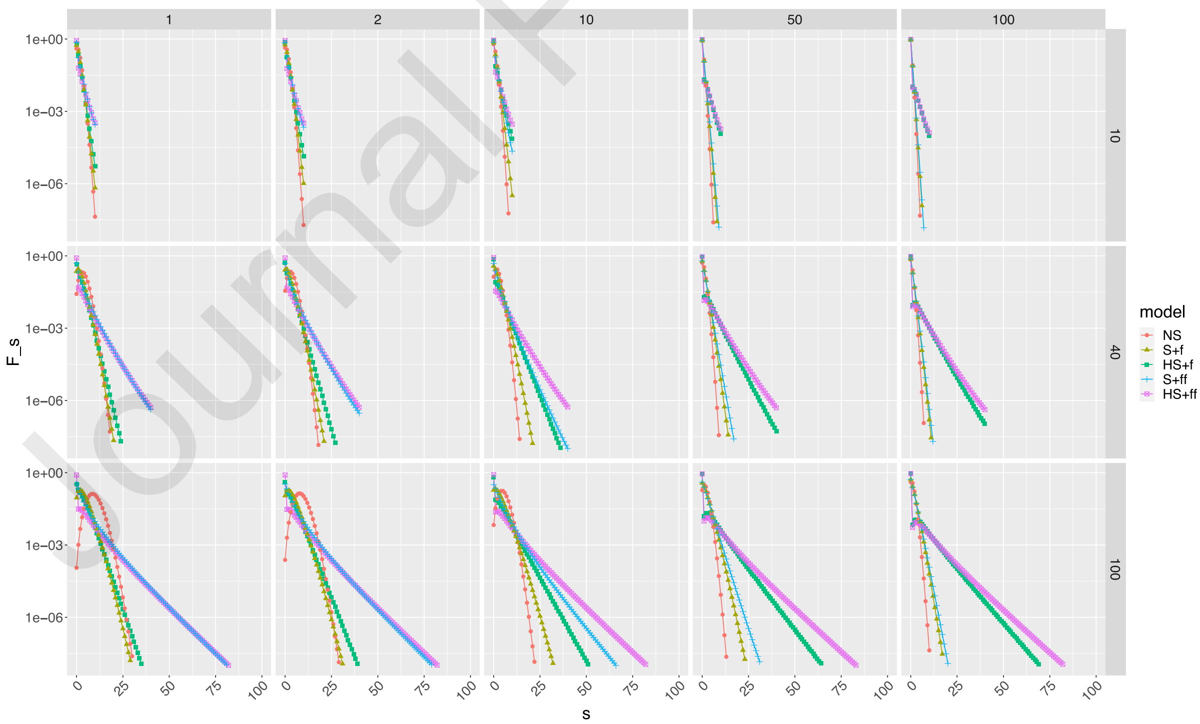

Figure S4 : The same as Figure S3 in semi-logarithmic scale.

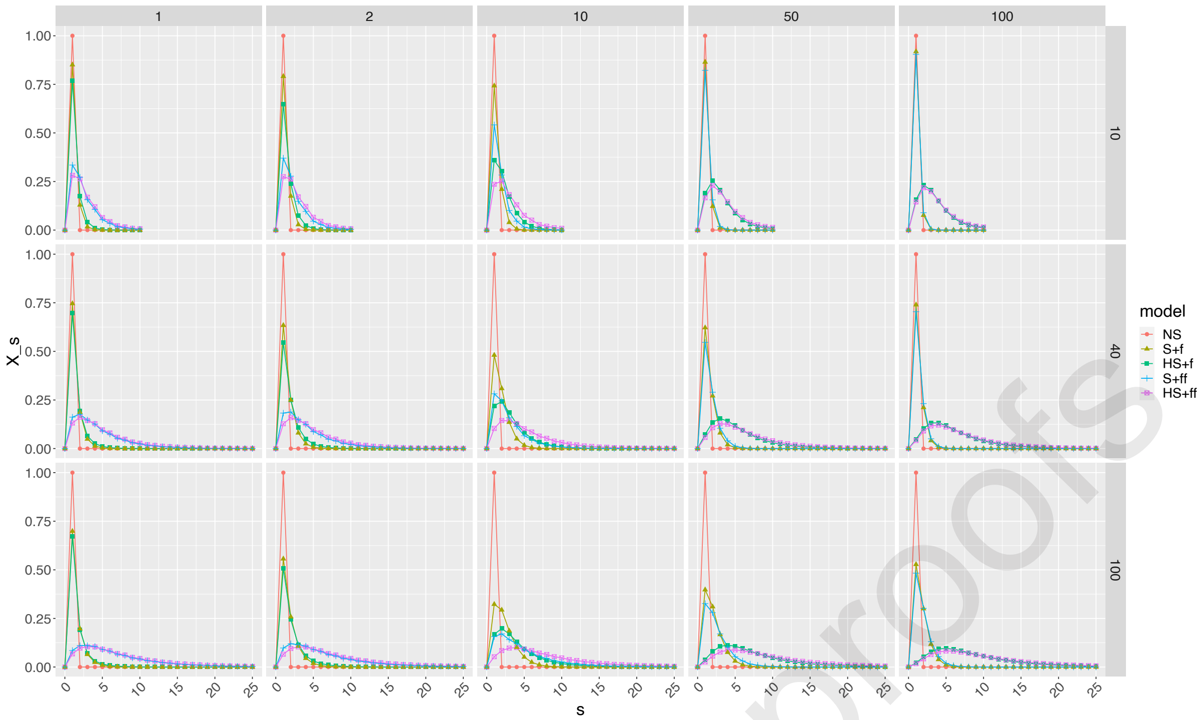

Figure S5 : Equilibrium distribution of the number of free schools of size s (X_s). Rows correspond to different population sizes (from top to bottom: N=10, 40, 100) and columns correspond to different numbers of FADs (from left to right: P=1, 2, 10, 50, 100). Each color indicates one of the five model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

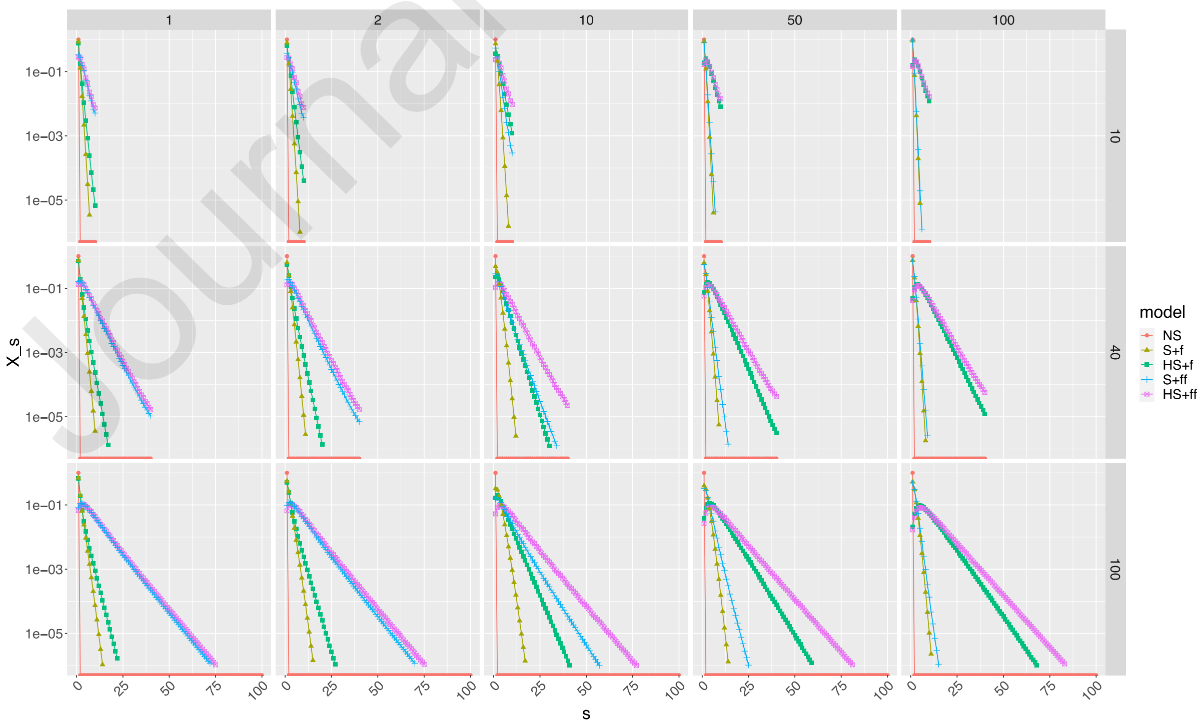

Figure S6 : The same as Figure S5 in semi-logarithmic scale.

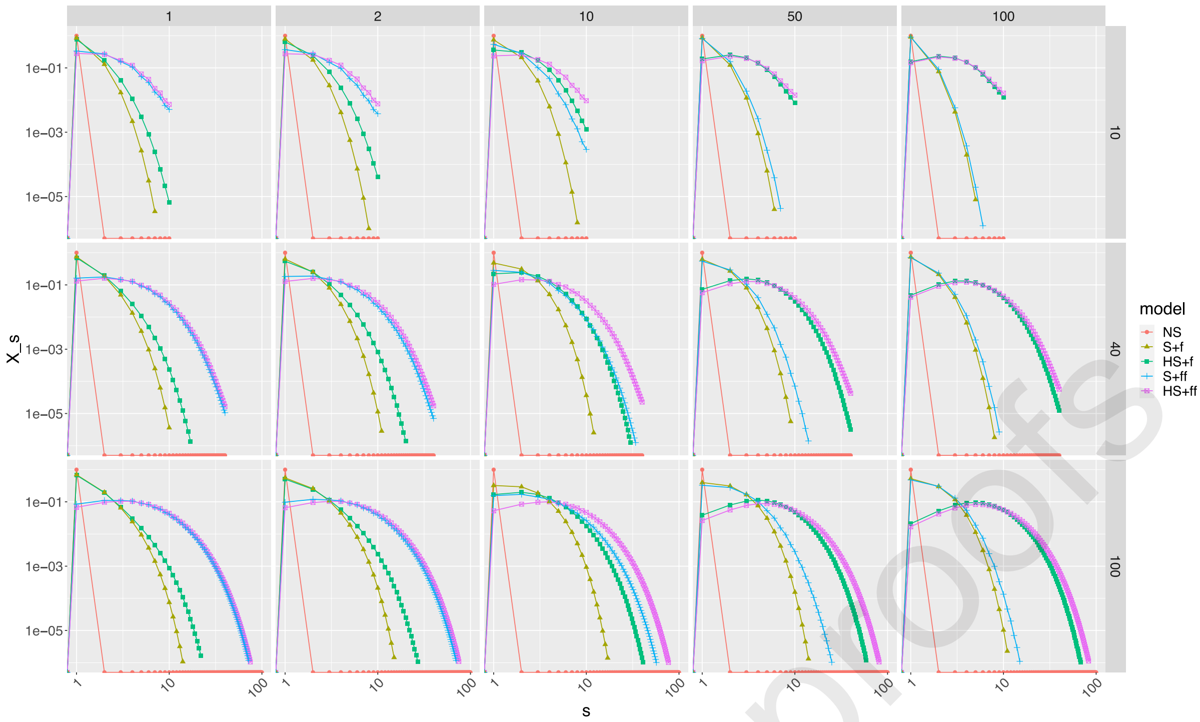

Figure S7 : The same as Figure S5 in log-log scale.

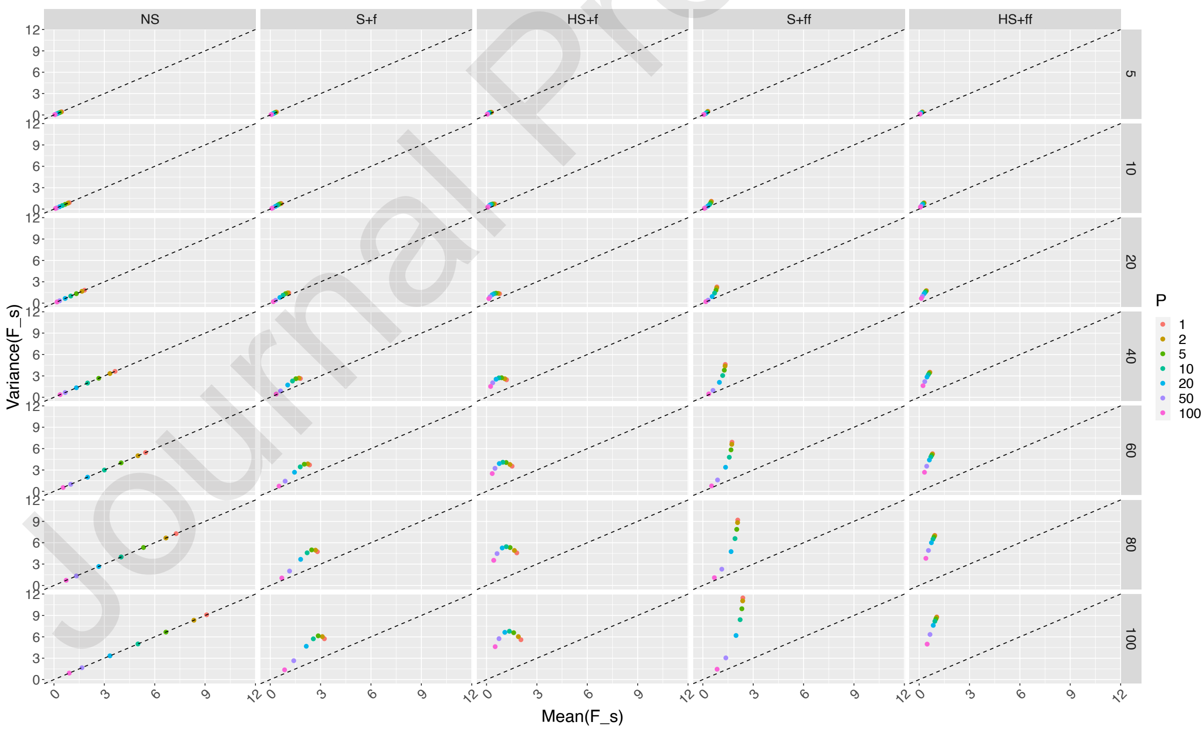

Figure S8 : Mean (x-axis) to variance (y-axis) relation for the size of FAD aggregations (F_S). Each column corresponds to a model configuration (Table 2). Rows denote the population sizes and colors the number of FADs. The dashed line corresponds to y=x (equidispersion).

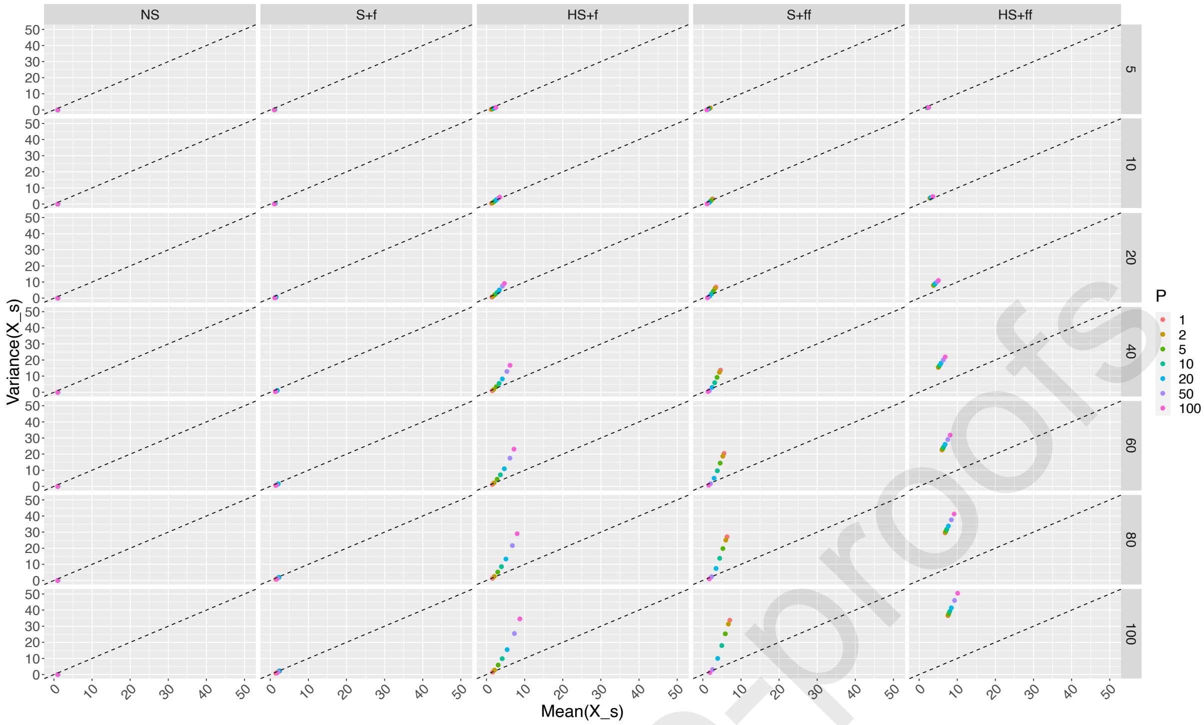

Figure S9 : Mean (x-axis) to variance (y-axis) relation for the size of free schools (X_S). Each column corresponds to a model configuration (Table 2). Rows denote the population sizes and colors the number of FADs. The dashed line corresponds to y=x (equidispersion).

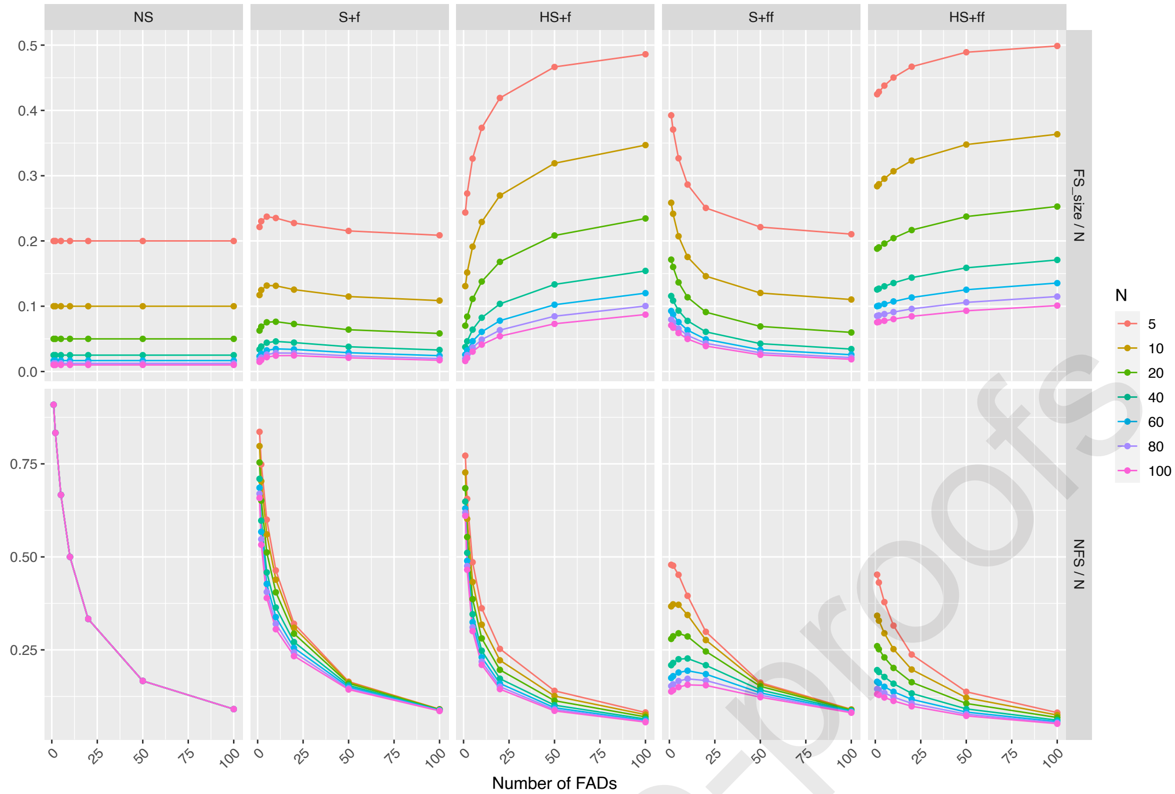

Figure S10: Free school aggregation metrics (same as Figure 3) divided by N.

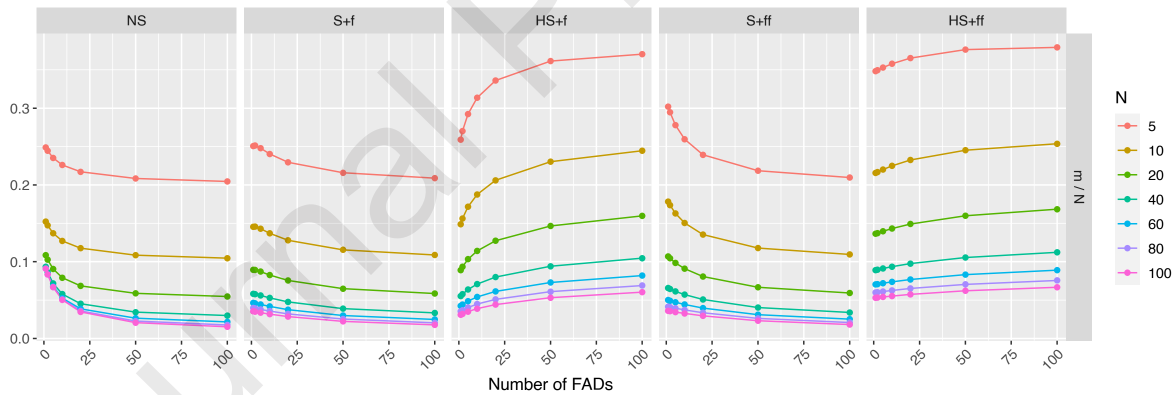

Figure S11: FAD aggregation metrics (m) divided by N.

- 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.

Author contributions

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